Molecular phylogenetics and morphology of *Beaucarnea* (Ruscaceae) as distinct from *Nolina*, and the submersion of *Calibanus* into *Beaucarnea*

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Abstract Despite the economic importance and longstanding worldwide commercialization of representatives of the *Beaucarnea* lineage, it remains poorly known systematically. One of the main systematic problems is lack of certainty regarding the validity of the genus itself. Some authors consider *Beaucarnea* a synonym of its close relative *Nolina*, whereas others consider *Beaucarnea* a distinct genus. In addition to the *Beaucarnea* vs. *Nolina* controversy, the boundary between *Beaucarnea* and *Calibanus* is an issue that has not yet been addressed. Here we show that *Beaucarnea* is a well-supported entity, distinct from *Nolina* on molecular and morphological grounds. Additionally, we demonstrate the absence of reciprocal monophyly between *Beaucarnea* and *Calibanus* and formally include *Calibanus* within *Beaucarnea*. These decisions were based on maximum parsimony, Bayesian, and maximum likelihood analyses of datasets including ten species of *Beaucarnea*, two species of *Calibanus*, six species of *Nolina*, and five species of *Dasylirion*, with sequences from the nuclear ITS and plastid *trnL-F* and *ycf1* regions. Our taxonomic decisions were also based on morphological observations of herbarium specimens and on the literature. We illustrate the diagnostic features of the genera with phylogenetic character mapping. Finally, we offer a redescription of *Beaucarnea* to accommodate the former *Calibanus* species and give a key to the taxonomically valid *Beaucarnea* species.

Keywords *Beaucarnea*; *Calibanus;* Central America; *Nolina*; Mexico; molecular phylogeny; taxonomic controversy

Supplementary Material The Electronic Supplement (Tables S1–S3; Figs. S1–S6) is available in the Supplementary Data section of the online version of this article at http://ingentaconnect.com/content/iapt/tax

■ INTRODUCTION

Beaucarnea Lem. species, commonly known as ponytail or elephant foot palms, are among the most charismatic of houseplants. They are well known because of their massive trunks, greatly swollen at the base, and their ponytail-like sprays of leaves (Fig. 1). At least seven species are endemic to Mexico, where they occur in very restricted semiarid and dry tropical areas. The other three species reach Central America (Rose, 1906; Hernández, 1993a; Lott & García-Mendoza, 1994; Rivera-Lugo & Solano, 2012). Some species were introduced to cultivation in Europe in the mid-nineteenth century (Lemaire, 1861; Baker, 1872; Gillot, 2009), and are now commercialized worldwide. Surprisingly, despite the long history of horticulture of these economically important plants, little work has been carried out regarding their systematics. As a result, many taxonomic problems persist in the genus, including the validity of the genus *Beaucarnea* itself.

Clarifying the relationships and diagnostic features of genera, especially of economically important ones such as *Beaucarnea*, is one of the central aims of plant systematics. That *Beaucarnea* is not considered a valid genus has potentially important consequences. Most species are in danger of extinction because of the nursery trade (e.g., Cardel & al., 1997), and any attempt to conserve and manage them is hindered without a clear knowledge of their taxonomic circumscription. That the species are simply a few of many species of *Nolina* Michx., which is widespread in North America, versus a unique and geographically restricted lineage with few highly threatened species, is an important distinction under Mexican conservation law (SEMARNAT, 2010). Whatever its source, the confusion regarding the distinctness of the genera and their diagnostic features is real, and has manifestations in both the scientific and commercial treatment of the genera.

To help disentangle this confusion, we address three taxonomic issues. We first test the validity of the genus *Beaucarnea*, given that many recent broad phylogenetic studies of monocotyledons have considered *Beaucarnea* a synonym of *Nolina* (Chase & al., 1993, 2000, 2009; Duvall & al., 1993; Rudall & al., 2000; Yamashita & Tamura, 2000; APG II, 2003;

Kim & al., 2010; Seberg & al., 2012). Here we clarify the boundaries between *Beaucarnea* and *Nolina*. Second, we compare *Beaucarnea* and *Calibanus* Rose, because recent discoveries of new species (Hernández & Zamudio, 2003) have highlighted a continuum of morphological variation between the genera, blurring the traditional boundaries between them. Finally,

we explore species circumscriptions within the *Beaucarnea-Calibanus* clade in the first phylogenetic hypothesis proposed to date based on molecular data.

To test the monophyly of *Beaucarnea*, *Calibanus*, and *Nolina*, we carried out maximum parsimony, Bayesian, and maximum likelihood phylogenetic analyses based on the
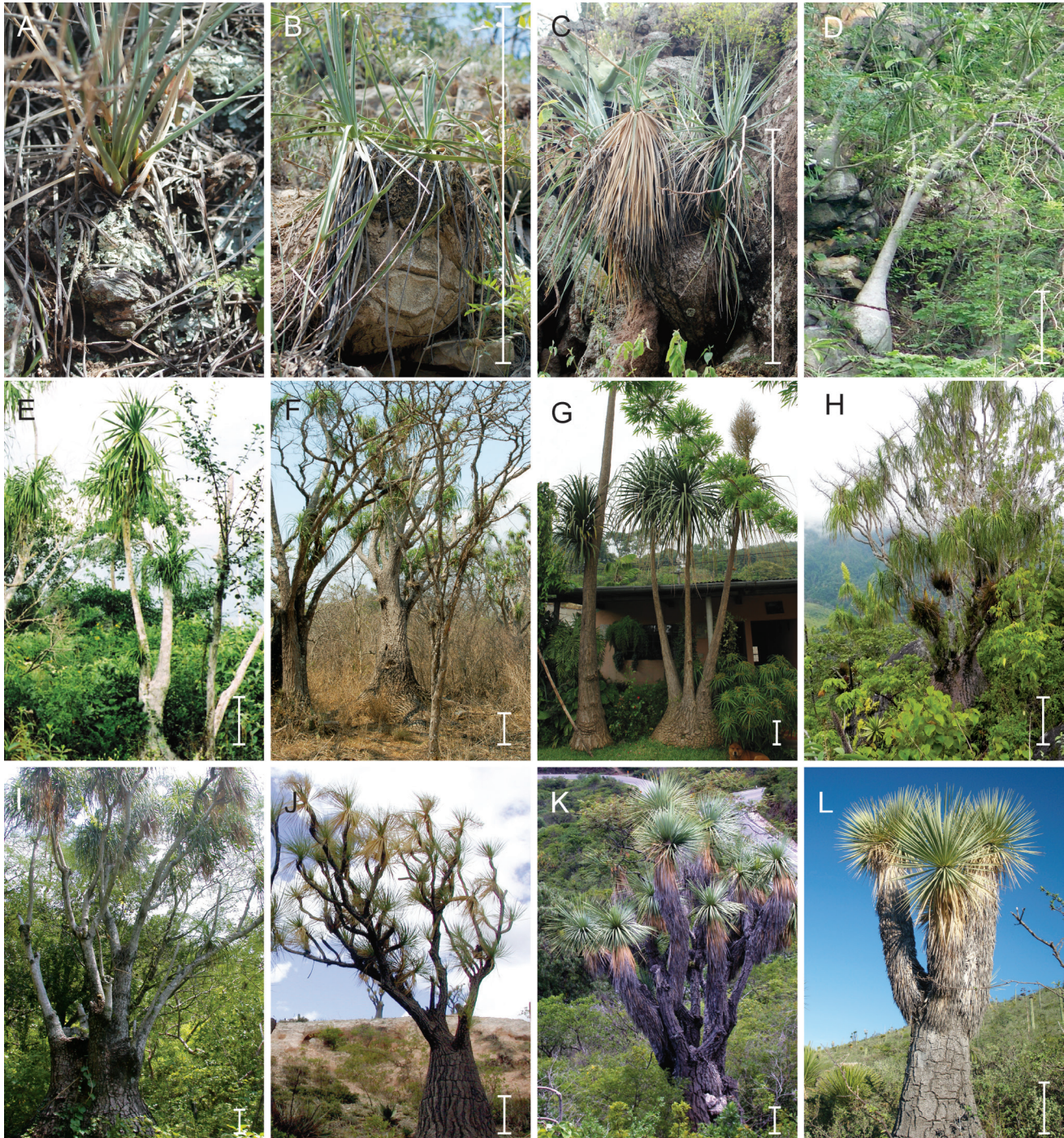

Fig. 1. *Beaucarnea* Lem. and *Calibanus* Rose habit diversity. All images from the wild except for *B. guatemalensis* Rose. The images show the greatly swollen bases and ponytail-like sprays of leaves characteristic of these genera. **A,** *Calibanus hookeri* (Lem.) Trel.; **B,** *Calibanus glassianus* L.Hern. & Zamudio; **C,** *Beaucarnea compacta* L.Hern. & Zamudio; **D,** *Beaucarnea hiriartiae* L.Hern.; **E,** *Beaucarnea pliabilis* (Baker) Rose; **F,** *Beaucarnea goldmanii* Rose; **G,** *Beaucarnea guatemalensis* Rose; **H,** *Beaucarnea sanctomariana* L.Hern.; **I,** *Beaucarnea recurvata* Lem.; **J,** *Beaucarnea gracilis* Lem.; **K,** *Beaucarnea stricta* Lem.; **L,** *Beaucarnea purpusii* Rose. — Scale bars approximately 60 cm.

nuclear ITS region and two plastid markers, *trnL-F* and *ycf1*. We included ten species and two putative species of *Beaucarnea*, two species of *Calibanus*, five species of *Dasylirion* Zucc., and six species of *Nolina*. We included samples of *Dasylirion* because it is closely related to the other three genera (Hernández, 1993a; Eguiarte & al., 1994; Bogler & Simpson, 1995, 1996; Bogler & al., 1995; Eguiarte, 1995; Rudall & al., 2000). We show that *Beaucarnea* is a well-supported entity, and confirm its distinctness from *Nolina*. Also, we demonstrate the absence of reciprocal monophyly between *Beaucarnea* and *Calibanus*. We formally include *Calibanus* in *Beaucarnea*, update the description of *Beaucarnea*, and present a taxonomic key to the species. Finally, we discuss issues of species circumscription within the *Beaucarnea-Calibanus* clade and comment on possible nomenclatural changes.

■ MATERIALS AND METHODS

Taxon sampling. — We sampled 1–3 individuals from 1–4 populations per species of all known *Beaucarnea* species (10 species according to Hernández-Sandoval & al., 2012), except for *B. inermis* (S.Watson) Rose. This species is usually regarded as synonymous with *B. recurvata* Lem., and we do not distinguish between them here. We included one sample of a specimen collected in the Isthmus of Tehuantepec, Oaxaca, here labeled as *Beaucarnea* sp1, to determine whether it is more closely related to *B. recurvata* or *B. stricta* Lem., because specimens collected in this area have been labeled with both of these names; these plants have also been labeled with the unpublished name "*B. congesta*". We included two samples collected in southwestern Puebla, here labeled as *Beaucarnea* sp2, to see whether they might belong to an undescribed species. The total number of *Beaucarnea* samples was 24 and were all wild-collected. We also included three samples from three populations of *Calibanus hookeri* (Lem.) Trel., and three samples from the only known population of *C. glassianus* L.Hern. & Zamudio. These samples were collected in the wild except for two samples of *C. hookeri*, which came from live plants cultivated in the botanical garden at the Instituto de Biología, UNAM. We also included six species of *Nolina* and five species of *Dasylirion*. These samples came from live plants cultivated in the botanical garden and from dried specimens in MEXU. The ingroup was thus made up of 41 samples. To root the tree we used a sample of *Ophiopogon planiscapus* Nakai (Ruscaceae s.l., Ophiopogoneae s.str.), obtained from a dried MEXU specimen. The selection of the outgroup was based on Rudall & al. (2000), Yamashita & Tamura (2000), Hilu & al. (2003), and Kim & al. (2010). Taxa and vouchers are listed in Appendix 1.

DNA extraction, amplification, sequencing, and alignment. — We obtained DNA from nitrogen frozen leaf tissue using DNeasy Plant Mini Kits (Qiagen, Valencia, California, U.S.A.), following the manufacturer's protocol. We performed polymerase chain reactions (PCR) using a thermal cycler (DNA Engine, Peltier Thermal Cyclers, Bio Rad, Hercules, California, U.S.A.).

We amplified the nuclear region ITS1-5.8S-ITS2 using the primers AB101 and AB102 (Douzery & al., 1999). For *trnL-F* we used the primers B49317 and A50272, and for sequencing we added the internal primers A49855 and B49873 (Taberlet & al., 1991). These primers include the intron *trnL*(UAA), and the intergenic spacer between the *trnL*(UAA) 3′ exon and the *trnF*(GAA) intron. For the chloroplast open reading frame (ORF) *ycf1* we used the primers 1F and 1200R (Neubig & al., 2009). This ORF is the second-longest in the plastid genome with 5500 bp (Raubeson & Jansen, 2005). Because of its length, we only amplified approximately 1000 bp of the 3′ end.

PCR reactions used the following quantities: 10–100 ng of template DNA, 3–5 µl 10× PCR buffer, 6–10 µl 5× Q-solution, 0.6–1 µl of 25 mM $MgCl_2$, 1.2–1.5 µl of 10 mM dNTP mix in an equimolar ratio, 0.6–1 µl each of 10 µM primers, and 0.25–0.3 µl units of *Taq* polymerase. All reagents were Qiagen except for the dNTP-mix from Invitrogen (Foster City, California, U.S.A.). We used the following PCR cycling conditions for ITS1-5.8S-ITS2: 94°C, 2 min; 35× (94°C, 40 s; 48°C–60°C, 1 min; 72°C, 1 min); 72°C, 3 min. PCR cycling conditions for the plastid region *trnL-F* were as follows: 94°C, 2 min; 35× (94°C, 1 min; 55°C, 1 min; 72°C, 2 min); 72°C, 5 min. Finally, for the plastid *ycf1* we used a "touchdown" protocol as follows: 94°C, 3 min; 8× (94°C, 30 s; 60°C–51°C reducing 1°C per cycle, 1 min; 72°C, 3 min); 30× (94°C, 30 s; 50°C, 1 min; 72°C, 3 min); 72°C, 3 min.

We visualized PCR products on 1% agarose gels using a UV transilluminator (Kodak EDAS 290). We purified and sequenced products at the University of Washington High-Throughput Genomics Unit (http://www.htseq.org). We edited and assembled sequences using Sequencher v.4.8 (Gene Codes, Ann Arbor, Michigan, U.S.A.). We aligned the sequences using Se-Al v.2.0a11 (Rambaut, 2002), aligning sites based first on their similarity, understood as base identity, and then based on their topological connectivity to invariant adjacent sequences (Patterson, 1982). Varying sites and indels were aligned only with reference to topological connectivity, minimizing the number of evolutionary events implied. GenBank accession numbers are given in Appendix 1.

Molecular data analyses. — We performed maximum parsimony (MP), Bayesian posterior probability, and maximum likelihood (ML) analyses of the regions individually and in combination. For our Bayesian and ML analyses, we first determined the model of evolution that best fit each dataset using jModelTest v.0.1.1 (Posada, 2008).

We performed MP analyses using PAUP* v.4.10 (Swofford, 2002) for each region separately and for all regions combined. We carried out heuristic searches with TBR branch swapping and 1000 replicates of random stepwise additions, saving 10 trees per replicate. All characters were unordered and had equal weight. We measured support for reconstructed clades using 1000 bootstrap (BP) replicates (Felsenstein, 1985), with the starting tree generated by simple addition and tree bisection-reconnection branch swapping. We performed Bayesian analyses using MrBayes v.3.1.2 (Ronquist & Huelsenbeck, 2003) on XSEDE (Extreme Science and Engineering Discovery Environment) through the CIPRES Science Gateway v.3.1. (http://www.phylo.org/sub_sections/portal/; Miller & al., 2010) under

the optimal model of evolution for each dataset. For the combined datasets, we analyzed each partition individually under their best-fitting model. We ran two simultaneous analyses for 2×10^7 generations, saving one tree every 200 generations. Each analysis included 4 simultaneous Markov chains, and started from random trees. Aside from the model, generation time, and heating parameter, which was set to 0.001 for the cold chain to fluctuate randomly within a more or less stable range, all other settings were default. We visually determined that the two runs converged on a stationary distribution when the average standard deviation of split frequencies was >0.001, and determined that we had a good sampling of the posterior probability distribution when we saw no trend in the log likelihood values plot, and when the potential scale reduction factor reached ≈1.0. We visually evaluated that analyses had reached stasis after the 25% burn-in with Tracer v.1.5 (Rambaut & Drummond, 2009). We discarded 25% of the trees obtained during the first 20 million generations, and with the remaining trees we calculated the posterior probabilities (PP), and obtained a consensus tree. We performed ML analyses using RAxML-HPC2 on XSEDE (v.7.4.2) through the CIPRES Science Gateway v.3.3 (Miller & al., 2010). The analysis of each dataset was performed under the GTR+G model. The analysis with the concatenated datasets was also performed under the GTR+G model, but considering each partition as independent. We estimated bootstrap support (MLBP) values from 1000 random replicates.

Morphological observations. — To identify characters diagnostic of each genus, and to determine the similarity or lack thereof between *Beaucarnea* and *Nolina*, and between *Beaucarnea* and *Calibanus*, we analyzed variation in vegetative and reproductive characters among 165 specimens of *Beaucarnea*, *Calibanus*, *Dasylirion*, and *Nolina* from the following herbaria: CAS, F, GH, LL, MEXU, MICH, MO, NY, TEX and US (Appendix 2). Type material was analyzed from herbaria when possible, or from JSTOR Global Plants (http://plants.jstor.org).

We analyzed the habit, leaves, inflorescences, flowers, fruits, and habitat for diagnostic differences between the genera. A detailed description of each character and variation among genera is given in the Results section. We complemented our data with morphological and ecological information from the literature (Lemaire, 1861; Rose, 1906; Trelease, 1911; Hernández, 1992, 1993a, b, 2001; Bogler, 1998a, b; Hernández & Zamudio, 2003). We selected the most important diagnostic characters to trace them on the phylogenetic hypothesis that best represents the relationships between genera. We individually mapped the diagnostic characters using Mesquite v.2.75 (Maddison & Maddison, 2011) on the strict consensus tree of the concatenated datasets derived from the maximum parsimony analysis.

■ RESULTS

Sequences

The length of the ITS multiple alignment was 805 bp. There were 172 variable sites and 128 parsimony-informative characters. The parsimony analysis found 9450 most parsimonious trees of 233 steps (consistency index, CI = 0.7940; retention index, RI = 0.9354). The length of the *trnL-F* multiple alignment was 1008 bp. There were 26 variable sites and 11 parsimony-informative characters. The analysis found 1532 most parsimonious trees of 28 steps (CI = 0.9286; RI = 0.9649). The length of the *ycf1* multiple alignment was 921 bp. There were 17 variable sites and 12 parsimony-informative characters. The parsimony analysis found 36 most parsimonious trees of 20 steps (CI = 0.8500; RI = 0.9667). Finally, the length of the ITS+*trnL-F*+*ycf1* multiple alignment was 2736 bp. The total number of variable sites was 216 and there were 150 parsimony-informative characters. The parsimony analysis found 12 most parsimonious trees of 294 steps (CI = 0.7823; RI = 0.9279).

The nucleotide divergence between pairs of sequences of the concatenated datasets was distributed as follows. Ingroup+outgroup ranged from 2.6% to 3.9%, with the highest value being between *Beaucarnea hiriartiae* L.Hern. and *Ophiopogon planiscapus*. Ingroup pairs of sequences ranged from 0% to 2.8%, with the highest value being between *Nolina duranguensis* Trel. and *Beaucarnea guatemalensis* Rose. *Beaucarnea+Calibanus* sequence pairs ranged from 0% to 1.8%, with the highest value being between *Beaucarnea guatemalensis* and *Calibanus hookeri*. *Beaucarnea+Dasylirion* ranged from 2.1% to 2.6%, with the highest value being between *Beaucarnea guatemalensis* and *Dasylirion berlandieri* S.Watson. Ranges of nucleotide divergence between pairs of sequences per partition and in combination are given in Table S1 (Electr. Suppl.).

Molecular analyses

Nuclear and plastid datasets. — The MP, ML, and Bayesian analyses of the nuclear dataset recovered *Beaucarnea* as paraphyletic (BP = 98%; MLBP = 96%; PP = 0.99), with *Calibanus* completely nested within *Beaucarnea* (BP = 96%; MLBP = 83%; PP = 0.95), and *Dasylirion* and *Nolina* as monophyletic (*Dasylirion*: BP = 100%; MLBP = 100%; PP = 1.0; *Nolina*: BP = 88%; MLBP = 67%; PP = 0.97) (Fig. 2; see also Electr. Suppl.: Fig. S1 for the MP topology). These analyses recovered *Dasylirion* as sister to the *Beaucarnea-Calibanus* complex (the "B-C complex") (BP = 99%; MLBP = 96%; PP = 0.99). The position of *Nolina* was unresolved with the MP and Bayesian analyses, but the ML analysis recovered it as sister to the other three genera.

Within the B-C complex, we recovered a well-supported clade made up of *B. recurvata*, *B. sanctomariana* L.Hern., and *B.* sp1 (BP = 87%; MLBP = 97%; PP = 1.0), here referred as the "recurvata" clade. We also recovered a clade made up of different population samples of *B. gracilis* Lem., the "gracilis" clade (BP = 63%; MLBP = 87%; PP = 0.87); a group made up of *B. compacta* L.Hern. & Zamudio, *C. glassianus*, and *C. hookeri*, the "calibanus" clade (BP = 96%; MLBP = 99%; PP = 1.0); a clade comprising *B. stricta* and *B.* sp2 (BP = 84%; MLBP = 87%; PP = 1.0); a well-supported clade made up of *B. hiriartiae* and *B. purpusii* Rose (BP = 98%; MLBP = 100%; PP = 1.0); and a clade made up of *B. goldmanii* Rose, *B. guatemalensis* Rose, and *B. pliabilis* (Baker) Rose, the "southern" clade (BP = 100%; MLBP = 100%; PP = 1.0). The three analyses recovered the "southern" clade as sister to the rest of the B-C complex (BP = 99%; BPML = 96%;

PP = 0.99). The other five clades were recovered as a group, but its internal relationships were unresolved in the MP analysis (Electr. Suppl.: Fig. S1). However, the ML and Bayesian analyses recovered the "gracilis" and "recurvata" clades as sister (MLBP = 72%; PP < 0.90), with the "calibanus" clade as sister to both (MLBP = 83%; PP = 0.95) (Fig. 2).

The plastid analyses (not shown) recovered some well- to medium supported clades, which were also recovered with the nuclear data. These clades are highlighted with solid gray lines for *trnL-F*, and dashed lines for *ycf1* in Fig. 2. For example, we recovered the "recurvata" clade (BP = 65%; MLBP = 73%; PP = 0.99), and the "gracilis" clade (MLBP = 50%) with the *trnL-F* analyses, although with low support values. We also recovered *B. compacta* and *C. glassianus* as a group with both plastid partitions (*trnL-F*: BP = 65%; MLBP = 62%; PP = 0.99; *ycf1*: BP = 63%; MLBP = 69%; PP = 0.99). We recovered *B. purpusii*

and *B. hiriartiae* as sister with the *trnL-F* analyses (BP = 62%; MLBP = 76%; PP = 1.0), and the "southern" clade with both plastid partitions (*trnL-F*: MLBP = 68%; PP = 0.72; *ycf1*: BP = 64%; MLBP = 100%; PP = 0.99). Finally, with the plastid *trnL-F* we recovered *Dasylirion* as monophyletic (BP = 56%; MLBP = 71%; PP = 1.0), and with the *ycf1* Bayesian analysis we recovered *Nolina* as monophyletic (PP = 0.75). Bootstrap and PP values supporting each clade derived from nuclear and plastid datasets of MP, ML, and Bayesian analyses are shown in Table S2 (Electr. Suppl.).

Concatenated datasets. — The MP, ML, and Bayesian topologies derived from the combined nuclear and plastid datasets were congruent with one another (Fig. 3; Electr. Suppl.: Fig. S2). The main difference between the three topologies was the ambiguous position of *B. stricta*. The MP and ML topologies recovered *B. stricta* as sister to *Beaucarnea* minus
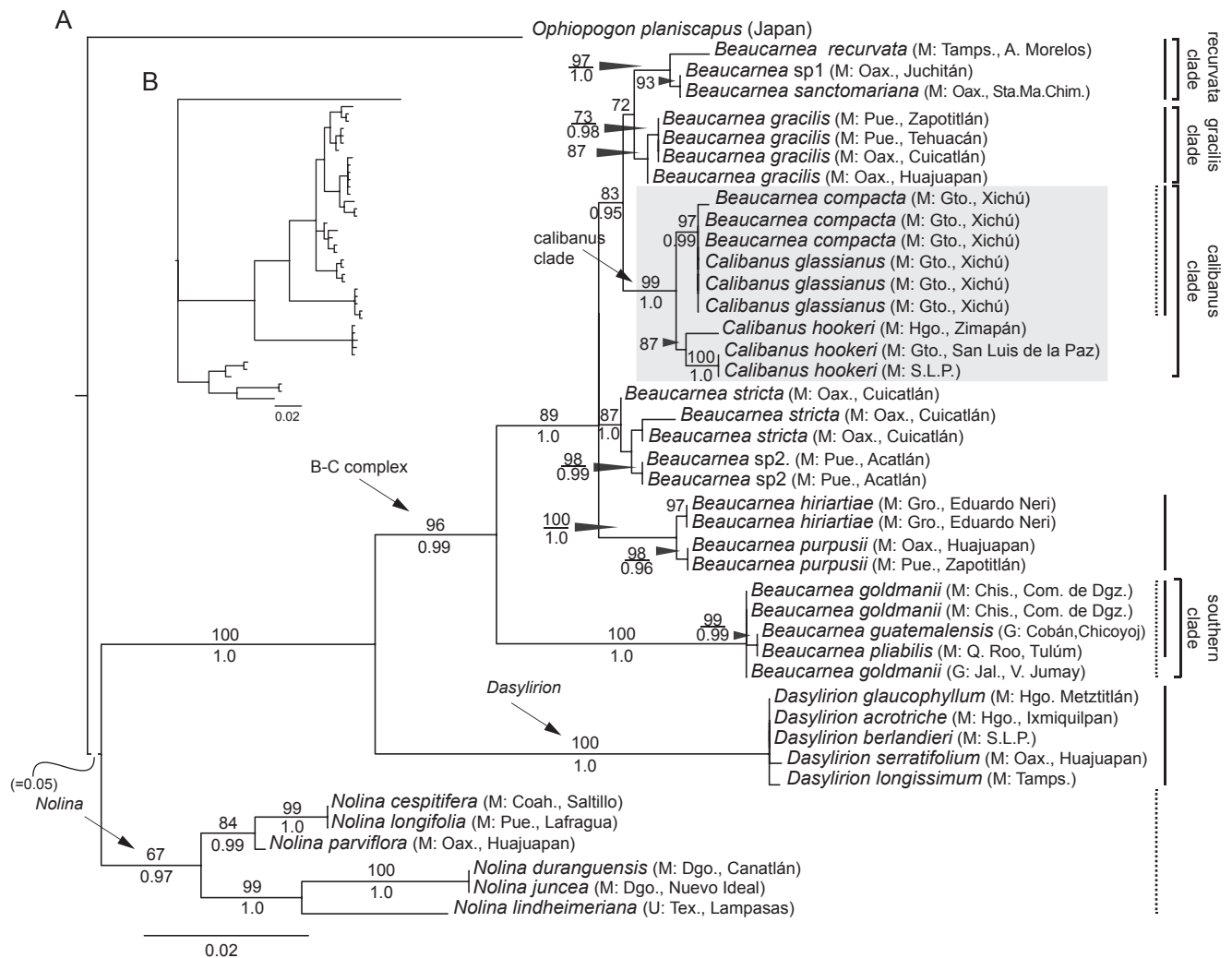

Fig. 2. Maximum likelihood (ML) and Bayesian trees derived from the nuclear ITS gene analyses. **A,** maximum likelihood phylogram showing high support values for the paraphyly (highlighted by gray rectangle) of *Beaucarnea* and *Calibanus* (B-C complex), and the monophyly of *Dasylirion* and *Nolina*. Country is given in parentheses (G, Guatemala; M, Mexico; U, United States of America), followed by state and locality of each sample. ML bootstrap values ≥60% are shown above branches and posterior probability values ≥0.90% of 20 million generations are shown below branches. Dotted lines highlight species associations recovered with the plastid *ycf1* analyses and solid lines highlight species associations recovered with the plastid *trnL-F* analyses. **B,** Bayesian strict consensus tree.

the "southern" clade, whereas the Bayesian topology recovered *B. stricta* as sister to the "southern" clade (Fig. 3, highlighted with gray arrows). Additional differences were the unresolved positions of the "calibanus", "gracilis", and "recurvata" clades in the MP topology (Electr. Suppl.: Fig. S2), which were resolved in the ML and Bayesian topologies (Fig. 3).

The three analyses recovered *Beaucarnea* as paraphyletic (BP = 99%; MLBP = 99%; PP = 1.0), with *Calibanus* nested within *Beaucarnea* (BP = 95%; MLBP = 90%; PP = 0.99), and *Dasylirion* (BP = 100%; MLBP = 100%; PP = 1.0) and *Nolina* (BP = 94%; MLBP = 86%; PP = 1.0) as monophyletic (Fig. 3), as in the nuclear analyses. Within the B-C complex, we recovered six main clades. The "recurvata" clade was well supported (BP = 95%; MLBP = 99%; PP = 1.0), and within it we recovered the putative species *B. sp1* as sister to *B. sanctomariana* (BP = 62%; MLBP = 97%; PP < 0.90), with these two Isthmian entities forming a clade sister to *B. recurvata* in the ML and Bayesian

analyses. The "gracilis" clade was well supported (BP = 64%; MLBP = 88%; PP = 0.92), and was sister to the "recurvata" clade, although this association was weakly supported (BP < 60%; MLBP < 60%; PP < 0.90). Within the "calibanus" clade we recovered *B. compacta* and *C. glassianus* as a group (BP = 86%; MLBP = 98%; PP = 0.98), with *C. hookeri* from Hidalgo as its sister taxon (BP < 60%; MLBP = 89%; PP = 1.0), and *C. hookeri* from San Luis Potosí and Guanajuato as sister to the rest (BP = 95%; MLBP = 98%; PP = 1.0). This species group was well supported and was completely nested within *Beaucarnea* (BP = 74%; MLBP = 90%; PP = 0.99). *Beaucarnea purpusii*, *B. hiriartiae*, and *B. sp2* were recovered as a well-supported clade (BP = 78%; MLBP = 85%; PP = 1.0), here referred as the "purpusii" clade. These results were different from the nuclear analyses, in which *B. sp2* was recovered as sister to *B. stricta*. Within the "purpusii" clade we recovered *B. purpusii* (BP = 64%; MLBP = 98%; PP = 0.90) and *B. hiriartiae* (BP = 87%;
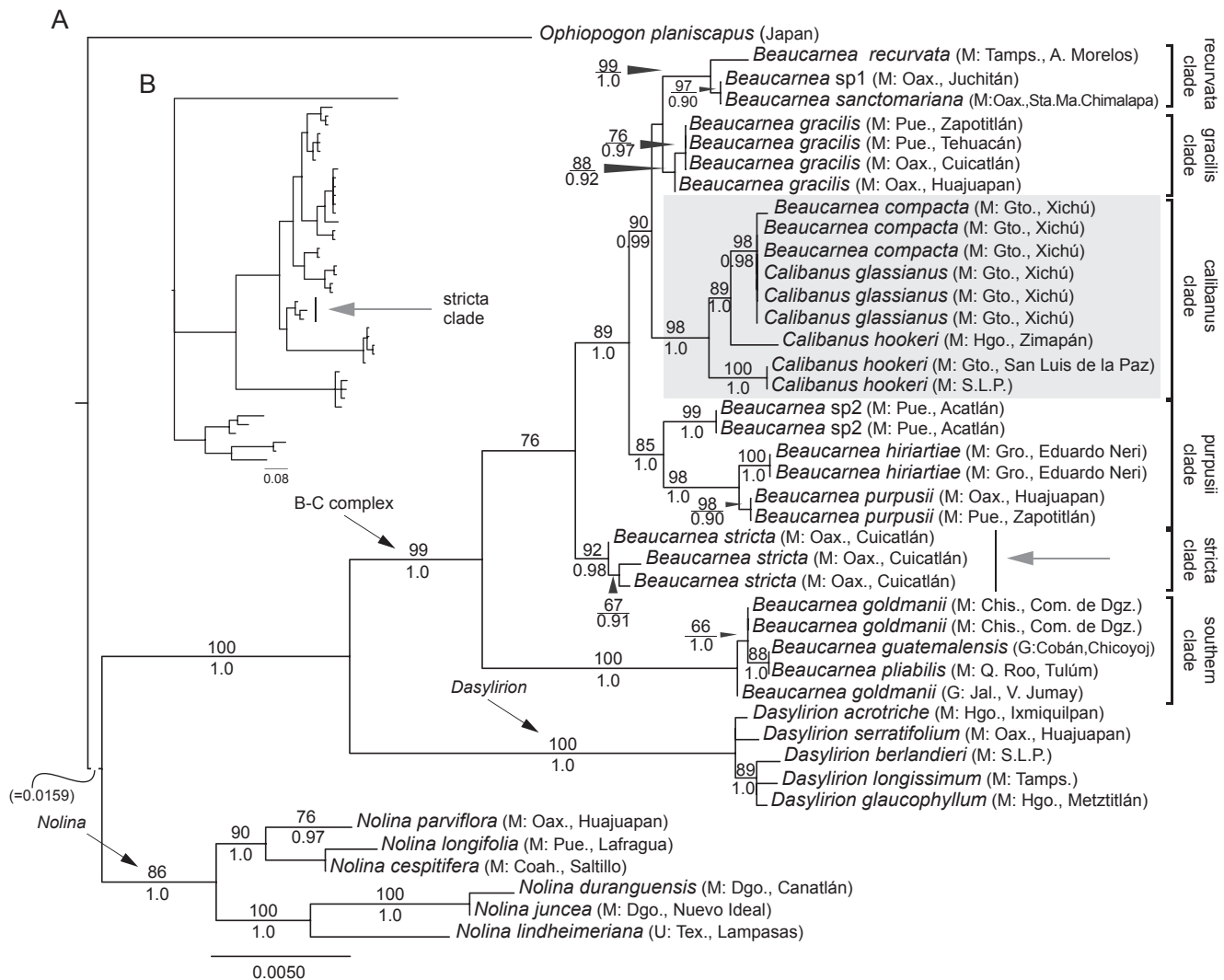

Fig. 3. Maximum likelihood (ML) and Bayesian trees derived from analysis of the concatenated datasets (ITS-*trnLF-ycf1*). **A,** maximum likelihood phylogram showing high support values for the paraphyly (highlighted by gray rectangle) of *Beaucarnea* and *Calibanus* (B-C complex), and the monophyly of *Dasylirion* and *Nolina*. Abbreviations as in Fig. 2. **B,** Bayesian strict consensus tree. A and B have almost the same topology except for the ambiguous position of *B. stricta*, highlighted with gray arrows.

MLBP = 100%; PP = 1.0) as sister species (BP = 97%; MLBP = 98%; PP = 1.0), and *B.* sp2 from SW Puebla (BP = 96%; MLBP = 99%; PP = 1.0) as sister to these two species (BP = 78%; MLBP = 85%; PP = 1.0). The "stricta" clade was made up of different samples of *B. stricta*. It was well supported (BP = 80%; MLBP = 92%; PP = 0.98), but of ambiguous position. The MP and ML analyses recovered it as sister to the rest of *Beaucarnea* minus the southern clade (BP = 97%; MLBP = 76%), and the Bayesian analyses recovered it as sister to the southern clade (PP = 0.86). Finally, the "southern" clade was well supported (BP = 100%; MLBP = 100%; PP = 1.0), and within it we recovered *B. guatemalensis* and *B. pliabilis* as sister species (BP = 88%; MLBP = 88%; PP = 1.0), with *B. goldmanii* from Chiapas as sister to these two species (BP = 64%; MLBP = 66%; PP = 1.0), and *B. goldmanii* from Guatemala as sister to the rest (BP = 100%; MLBP = 100%; PP = 1.0). Bootstrap and PP values supporting each clade derived from the concatenated datasets of the MP, ML and PP analyses are shown in Table S2 (Electr. Suppl.).

Morphological observations

The valid genera can be clearly distinguished based on reproductive and vegetative morphological characters (Figs. 1, 4–7). The morphological matrix used to trace the diagnostic characters onto the MP tree is given in the Electr. Suppl.: Table S3. We detail the distinctive features of the valid genera here (summarized in Fig. 8), as well as the non-distinctiveness of *Calibanus* from *Beaucarnea*.

Habit. — The four genera have similar habits, but all have readily recognizable attributes useful in their identification. *Beaucarnea* species are mostly arborescent, and they are easily distinguished from the other genera because of their massively swollen bases (Figs. 1C–L, 4A), and because most species reach greater heights (5–8(–18) m). *Beaucarnea compacta* is the exception regarding height, because it is less than 1 m tall (Fig. 1C). *Calibanus glassianus*, one of the two species of

Calibanus, resembles *Beaucarnea compacta* in its aboveground globular to conical stem (Fig. 1B). The other species of *Calibanus*, *C. hookeri*, has an underground or semiunderground globular stem (Figs. 1A, 4B). *Nolina* has a wide range of habits. *Nolina* species can be acaulescent, shortly caulescent, or arborescent. Arborescent species of *Nolina*, such as *N. parviflora* (Kunth) Hemsl. (Fig. 4C), resemble *Beaucarnea*, except for the greatly swollen bases characteristic of *Beaucarnea*. One of the diagnostic characters of the *Beaucarnea* + *Calibanus* complex are thus their massively swollen stem bases (Fig. 8). Regarding *Dasylirion*, most species have shortly caulescent habits, but at least one species, *D. simplex* Trel., is acaulescent. Caulescent species of *Dasylirion* are easily identified because of their cylindrical and sparingly branched caudex (Fig. 4D). This feature can be considered diagnostic of *Dasylirion* (Fig. 8).

Bark. — The outer bark or phellem is useful in the identification of the genera. In *Beaucarnea* it is smooth or tessellated, sometimes forming irregular grooves along the length of the stem (Figs. 1C–L, 4A). *Calibanus* also has tessellated bark (Figs. 1A–B, 4B), and in *Nolina*, the bark is conspicuously tougher than in *Beaucarnea*, and tends to form irregular longitudinal grooves in arborescent species, rather than geometric patterns (Fig. 4C). In *Dasylirion*, the cylindrical caudex of caulescent species is completely covered by a layer of abundant persistent leaf bases (Fig. 4D). This characteristic is very useful in distinguishing *Dasylirion* from the other three genera (Fig. 8).

Leaves. — Features of the leaf margin, leaf apex, leaf grooves, and leaf surface are useful characters in the identification of specimens at the generic level. The four genera have leaves in dense terminal rosettes. Blades are long linear, acicular to ensiform, or quadrangular as in *Dasylirion longissimum* Lem. *Beaucarnea* and *Calibanus* have leaves with microserrulate margins and entire leaf apices (Electr. Suppl.: Fig. S3A, a–b). In *Nolina*, the leaf margin is entire, filiferous, or serrulate, and the leaf apex is entire or lacerate (Electr. Suppl.: Fig. S3A, c). *Dasylirion* is easily identified because most species
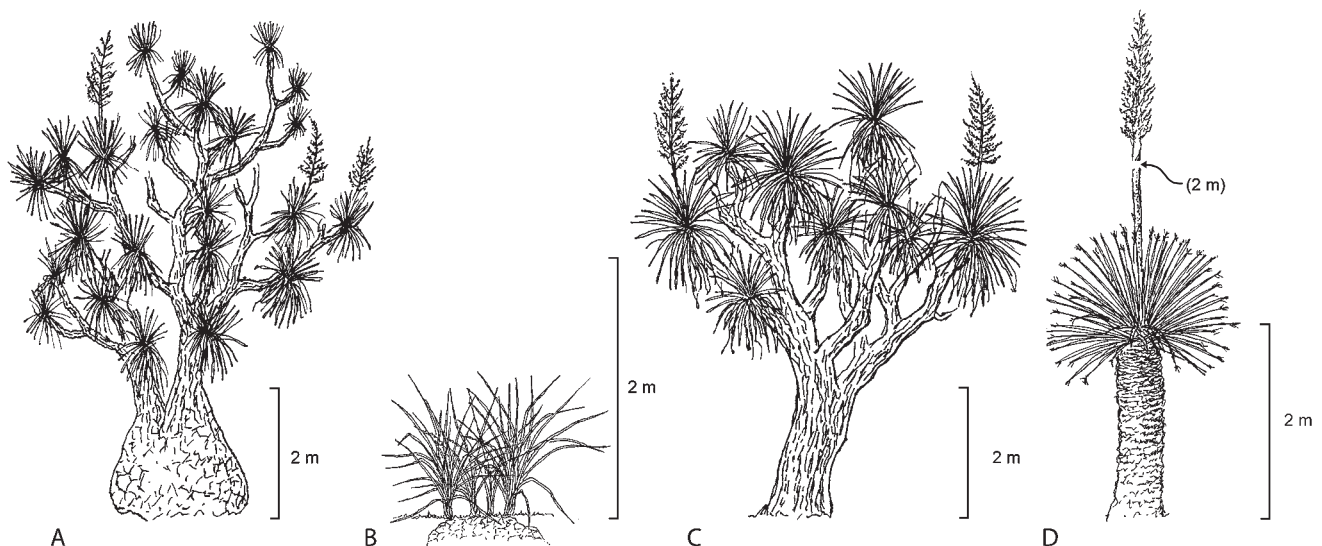

Fig. 4. Representative habits of **A,** *Beaucarnea*, **B,** *Calibanus*, **C,** *Nolina*, and **D,** *Dasylirion*.

have leaf margins with prominent sharp prickles, easily seen with the naked eye, and the apices are often brush-like (Electr. Suppl.: Fig. S3A, d). The leaf margin and apex in these genera thus provide useful diagnostic features, indicated in Fig. 8. Leaf grooves in some species of *Beaucarnea* and in the two species of *Calibanus* are deep and armed with long epidermal papillae (Electr. Suppl.: Fig. S3B, a–b, e–f), whereas some species of *Beaucarnea* have shallow grooves and lack papillae (Electr. Suppl.: Fig. S3B, c–d). The leaf grooves in *Nolina* are deep and armed with tiny epidermal papillae, and in *Dasylirion* the leaf grooves are shallow and lack papillae or they are mostly absent.

Inflorescence. — The general morphology of the inflorescence is useful particularly for the identification of *Dasylirion*. The four genera have thyrses with primary, secondary, and sometimes tertiary orders (Fig. 5A). The last unit of the thyrse is a reduced rhipidium (Fig. 5B). In *Beaucarnea*, *Calibanus*, and *Nolina* (Fig. 5, i–iii), the branches of the thyrse are considerably longer than in *Dasylirion*. In *Dasylirion* the internode between rhipidia is very short, resulting in a readily recognizable spike-like form (Fig. 5, iv), making this condensed thyrse in *Dasylirion* a readily diagnostic character (Fig. 8).

Flowers. — The attributes that best reflect the distinctness between the four genera are reproductive ones, especially those from the pistillate flowers (summarized in Table 1). The four genera have small hermaphroditic flowers that usually have one functional sex (Fig. 6). They are trimerous, actinomorphic, and hypogynous, with six imbricate perianth segments that are sometimes reflexed at anthesis in the staminate flowers (e.g., Fig. 6A, i and iii). The pistillode of the staminate flowers ranges from inconspicuous to prominent in *Beaucarnea*, and it is unilocular or trilocular (Fig. 6A, i). In *Calibanus* and *Dasylirion* the pistillode is mostly inconspicuous (Fig. 6A, ii and iv), and in *Nolina* it is mostly prominent and trilocular (Fig. 6A, iii). In *Beaucarnea*, *Calibanus*, and *Dasylirion* the perianth segments are crenulate (Fig. 6B, i, ii, and iv), whereas in *Nolina* they are apically papillate (Fig. 6B, iii). Papillate apices of perianth segments in *Nolina* are diagnostic (Fig. 8). The gynoecium in *Beaucarnea* and *Calibanus* is syncarpous, fleshy, smoth and thick-walled (Fig. 6C, i–ii). In *Beaucarnea* it is mostly 3-winged, and in *Calibanus* it lacks wings (Fig. 6C, i and ii). In *Nolina* the gynoecium is semecarpous, fleshy, granular and thin-walled, and lacks wings (Fig. 6C, iii), and in *Dasylirion* it
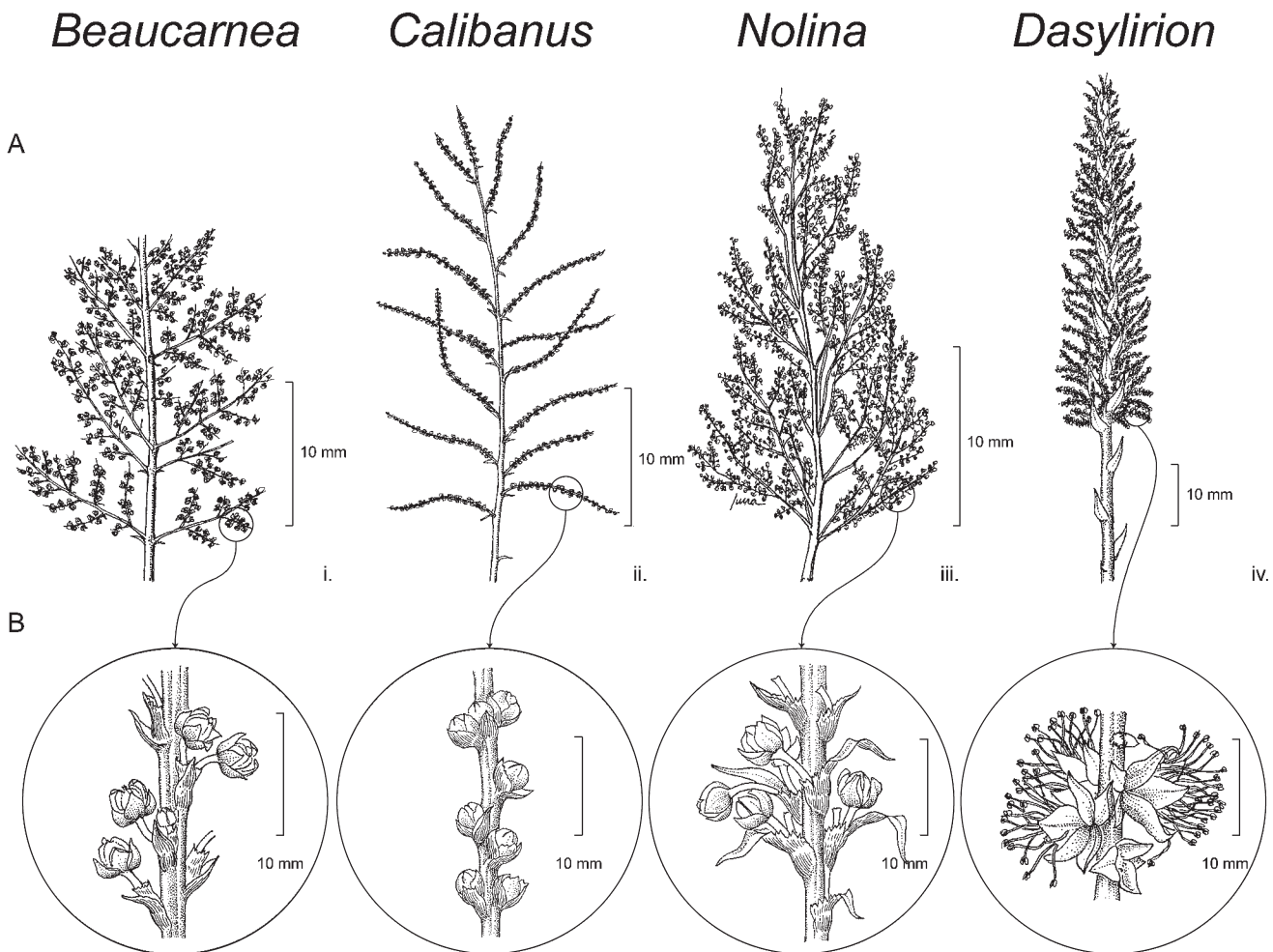

Fig. 5. Representative inflorescences of *Beaucarnea*, *Calibanus*, *Nolina*, and *Dasylirion*. **A,** general inflorescence morphology; **B,** detail of the floriferous portions of the inflorescences.
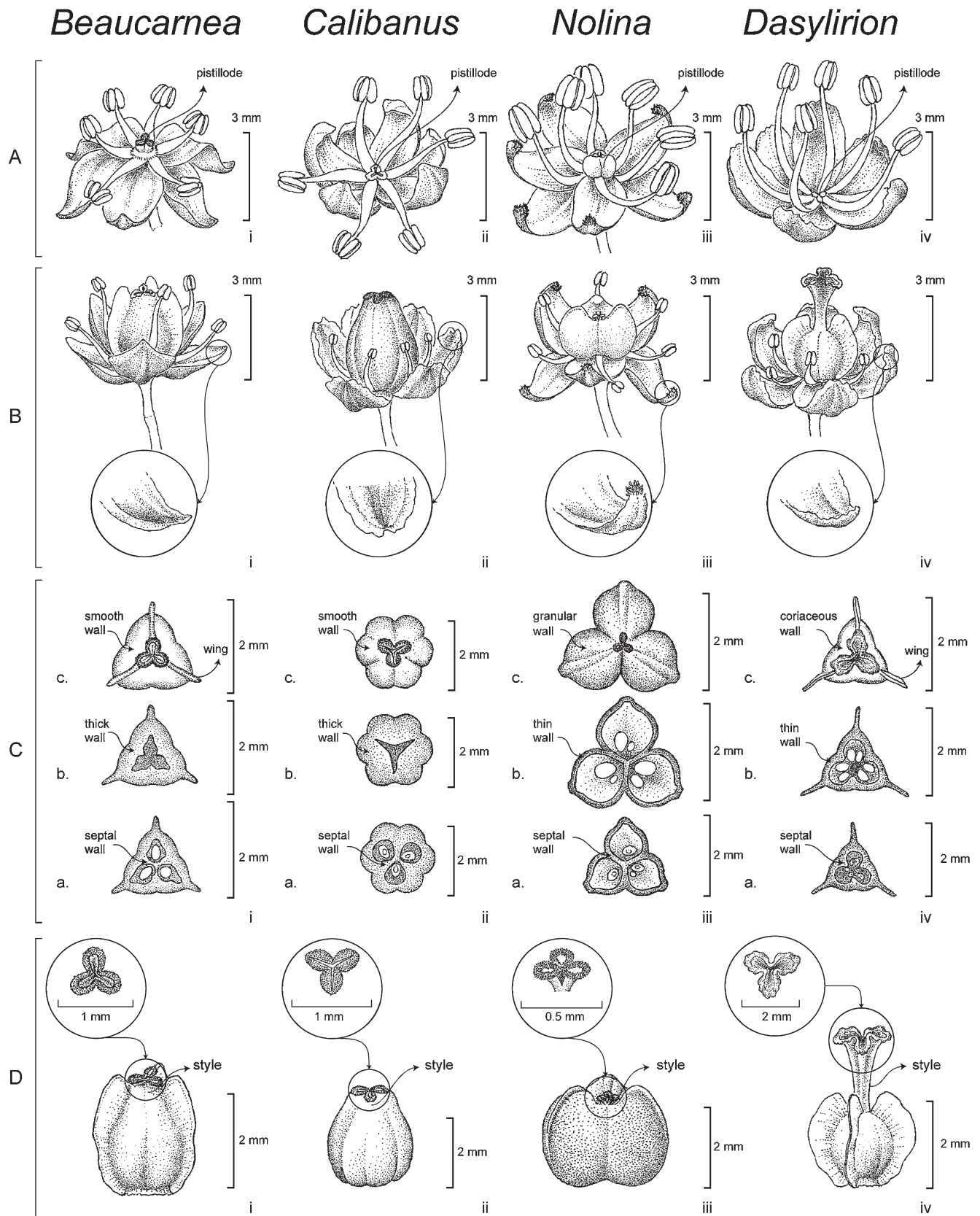
Fig. 6. Reproductive structures of *Beaucarnea*, *Calibanus*, *Nolina*, and *Dasylirion*. **A,** staminate flowers; **B,** pistillate flowers with a detail of a perianth segment; **C,** apical views of the gynoecium: **a,** cross section near ovary base, **b,** cross section at the midsection, and **c,** apex; **D,** gynoecium with a detail of the stigma.

is syncarpous, coriaceous, thin-walled, and 3-winged (Fig. 6C, iv). The thin- and granular-walled semecarpous gynoecium is diagnostic for *Nolina*, and in *Dasylirion* the coriaceous gynoecium is diagnostic (Fig. 8). The ovary in *Beaucarnea* and *Calibanus* is unilocular with septal walls basally fused (Fig. 6C, ia, iia) and sometimes remaining well developed the length of the

ovary, but never fused (Fig. 6C, ib and iib). In *Nolina* the ovary is trilocular and 3-lobed with well-developed septal walls that are fused the length of the ovary (Fig. 6C, iii). In *Dasylirion* the ovary is unilocular with septal walls that are reduced and thin and never fused (Fig. 6C, iv). The trilocular ovary with well-developed septal walls that remain fused the length of the ovary
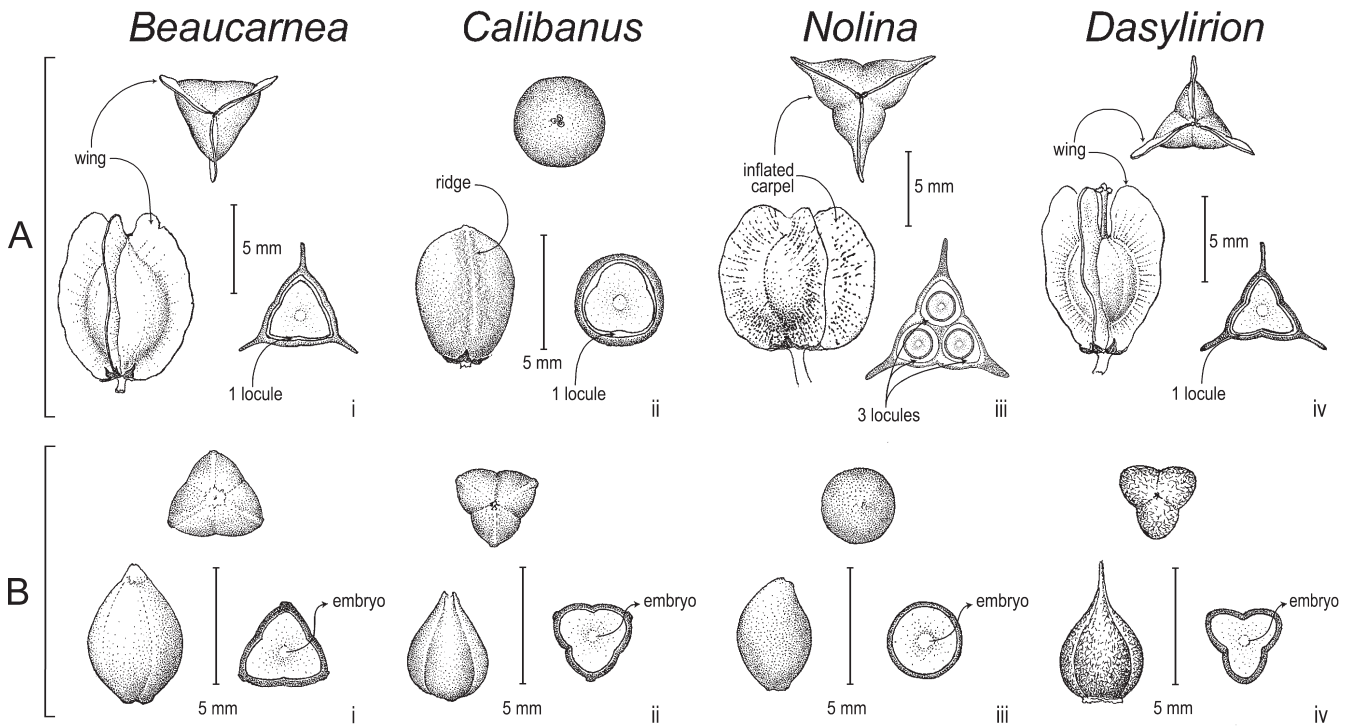

Fig. 7. A, representative fruits of each genus: lateral and apical views, cross sections; **B,** representative seeds of each genus: lateral and apical views, cross section.
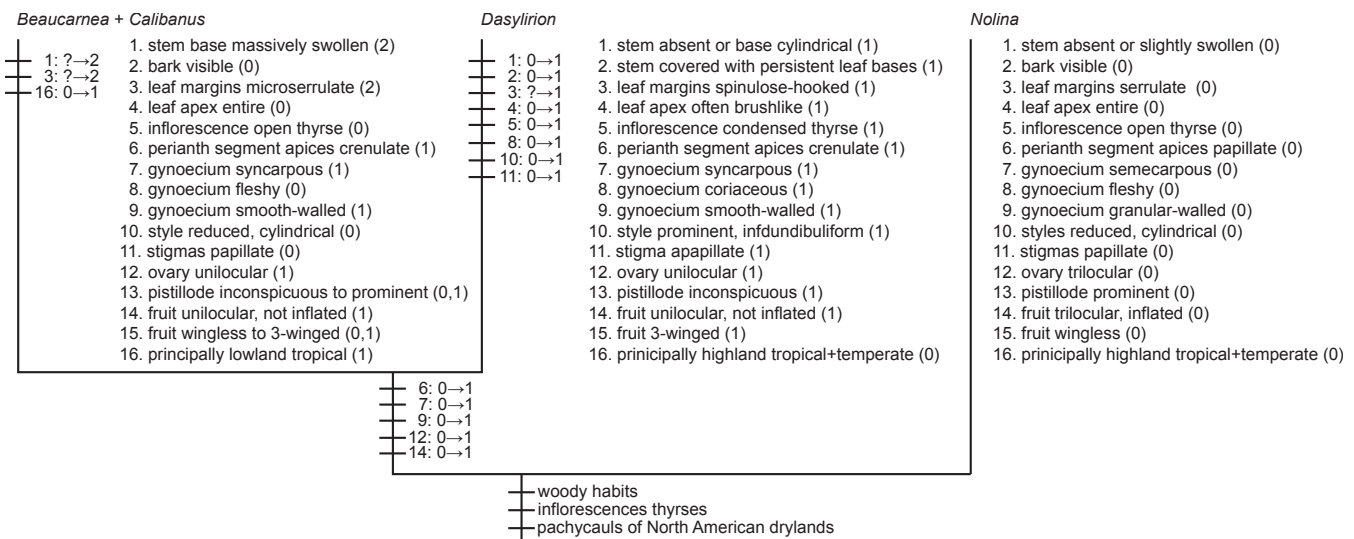

Fig. 8. Phylogenetic distribution of diagnostically important morphological characters in *Beaucarnea* (including *Calibanus*), *Dasylirion*, and *Nolina*. The horizontal lines indicate the character state transformations that characterize the clades and genera, with character number corresponding to the lists given under each generic name. The arrows indicate the directionality of change between states. The lists summarize the combinations of features diagnostic of each genus. Full details of character mapping may be found in the Electr. Suppl.: Fig. S4.

is diagnostic for *Nolina* (Fig. 8). Placentation in the four genera is basal and axile Fig. (6C, a). The style in *Beaucarnea* and *Calibanus* is short to slightly elongate, fleshy, and bears a 3-lobed papillate stigma (Fig. 6D, i and ii); in *Nolina* it is short, with each carpel having its own papillate stigma (Fig. 6D, iii); and in *Dasylirion* the style is prominent, hollow infundibuliform, hyaline, and bears a 3-lobed stigma that lacks papillae (Fig. 6D, iv). The prominent and infundibuliform style lacking papillae is diagnostic for *Dasylirion* (Fig. 8). Table 1 summarizes the comparative attributes of the flowers of the four genera.

Fruits. — The fruits in the four genera are capsules with delayed dehiscence (Fig. 7). *Beaucarnea* and *Dasylirion* have 3-winged fruits (Fig. 7A, i, iv), with the wings sometimes being narrow (*B. compacta*). The fruits of *Calibanus* and *Nolina* lack wings, but in *Calibanus* each carpel bears a longitudinal ridge medially (Fig. 7A, ii), and in *Nolina* each carpel is inflated (Fig. 7A, iii). The fruits in *Beaucarnea*, *Calibanus*, and *Dasylirion* are unilocular (Fig. 7A, i, ii, iv), and in *Nolina* they are trilocular (Fig. 7A, iii). Trilocular and inflated fruits in *Nolina* are diagnostic (Fig. 8). The seeds of *Beaucarnea*, *Calibanus*, and *Dasylirion* are 3-lobed and mostly single (Fig. 7B, i, ii, iv), whereas *Nolina* usually develops three spherical seeds (Fig. 7B, iii). The embryo in the four genera is cylindrical (Fig. 7B). Table 1 summarizes the comparative attributes of the fruits and seeds of the four genera under study.

Habitat. — *Beaucarnea* covers the widest elevational range of the four genera, with species occurring from sea level to more than 2000 m above sea level in Mexico and northern Central America. However, most species occur at elevations below 1500 m in tropical deciduous forests. Species occurring at elevations above 1500 m, such as *B. purpusii*, *B. gracilis*, and *B. stricta*, occur in Mexican xerophytic scrubs. *Calibanus* also occurs in xerophytic scrubs at elevations between 1000 and 2300 m. *Nolina* and *Dasylirion* are mostly characteristic of elevations above 1500 m in the tropical areas where they broadly overlap with *Beaucarnea*. In tropical Mexico they grow in arid mountainous regions, but can reach into relatively low-lying areas in the northern parts of their range in the United States.

■ DISCUSSION

Generic-level analyses. — The controversy regarding the distinctness of *Beaucarnea* and *Nolina* is a century-old one, and has had repercussions on the conservation and management of these plants. It has also affected recent phylogenetic studies of the group. Our molecular phylogenetic analyses, with 24 samples including ten *Beaucarnea* species plus two putative species, and six species of *Nolina*, were consistent regarding the distinctness of these two genera, but also regarding the lack of distinctness between *Beaucarnea* and *Calibanus*. *Beaucarnea* plus *Calibanus* was supported as a clade sister to *Dasylirion*, and *Nolina* was supported as monophyletic (Figs. 2–3; Electr. Suppl.: Figs. S1–S2). Our results suggesting the mutual monophyly of these genera are therefore in agreement with previous studies based on molecular data that included more than one species of *Beaucarnea* and *Nolina* (Eguiarte & al., 1994; Bogler & Simpson, 1995, 1996; Eguiarte, 1995). Other phylogenetic studies, which considered *Beaucarnea* a synonym of *Nolina*, recovered *Nolina* as the sister taxon to either *Calibanus* or *Dasylirion* (Duvall & al., 1993; Chase & al., 1995, 2000; Rudall & al., 2000; Yamashita & Tamura, 2000). Because no sample other than "*Nolina recurvata*" (= *B. recurvata*) was included in these studies, the relationships between *Beaucarnea* and *Nolina* could not be confirmed.

Our morphological observations were in agreement with our molecular results and confirm the distinctness of *Beaucarnea* and *Nolina* (Figs. 4–8; Table 1). One of the reasons

Table 1. Reproductive attributes of *Beaucarnea* Lem., *Calibanus* Rose, *Nolina* Michx., and *Dasylirion* Zucc. useful for their identification.

	Perianth segments	Pistillate flowers							Fruits		
		Gynoecium									
						Ovary					
	Apex	Connation type	Style	Stigma	Append-ages	No. of locules	Septal walls	No. of locules	Append-ages	No. of seeds
Beaucarnea	crenulate	syncarpous	short to slightly elongate	3-lobed, papillate, and basally fused	0–3 wings	1	basally fused	1	3 wings	mostly 1
Calibanus	crenulate	syncarpous	short to slightly elongate	3-lobed, papillate, and basally fused	wings absent	1	basally fused	1	wings absent	mostly 1
Nolina	papillate	semecarpous	short	3, free, papillate	wings absent	3	fused the length of the ovary	3	wings absent	mostly 3
Dasylirion	crenulate	syncarpous	elongate	3-lobed, fused	3 wings	1	not fused	1	3 wings	mostly 1

why *Beaucarnea* has been considered a synonym of *Nolina* is the mistaken notion of *Beaucarnea* as having a trilocular ovary (Baker, 1872, 1881; Watson, 1879; Hemsley, 1882–1886). However, our observations confirm *Beaucarnea* as unilocular (Fig. 6C, ib). In addition to the unilocular vs. trilocular statuses of *Beaucarnea* and *Nolina*, we found other important reproductive differences between these two genera. For example, *Nolina* has a semecarpous gynoecium with three partly fused ovaries, each with its own stigma and style (Fig. 6C–D, iii), whereas *Beaucarnea* has a syncarpous gynoecium with three completely connate ovaries, styles, and stigmas (Fig. 6C–D, i). The gynoecium in *Nolina* is fleshy, thin- and granular-walled (Fig. 6C, iii), and the perianth segments have papillate tips (Fig. 6B, iii), whereas in *Beaucarnea* the gynoecium is fleshy, thick-, and smooth-walled (Fig. 6C, i), and the perianth segments have non-papillate tips (Fig. 6B, i). Fruits of *Nolina* are inflated, 3-lobed and lack wings (Fig. 7A, iii), whereas fruits of *Beaucarnea* are non-inflated and 3-winged (Fig. 7A, i). Finally, the seeds of *Nolina* are circular in cross section (Fig. 7B, iii), whereas in *Beaucarnea* they are 3-lobed in cross section (Fig. 7B, i). Our morphological observations in the context of our molecular hypotheses provide strong evidence to support *Beaucarnea* as an entity distinct from *Nolina* (Fig. 8). These results are of interest from the point of view of plant biogeography as well as on conservation and economic grounds. Our results highlight that *Beaucarnea*, whose species are all highly threatened, is a morphologically unique, highly geographically restricted lineage. Even though many of the plants commercialized come from greenhouses, many others are illegally extracted from habitat. Recognizing *Beaucarnea* as valid is the first step in the effective conservation and management of these species.

In contrast to the strong evidence supporting *Beaucarnea* as distinct from *Nolina*, we found no evidence to consider *Beaucarnea* and *Calibanus* as distinct. Our analyses recovered *Calibanus* nested within *Beaucarnea* (BP ≥ 74%; MLBP ≥ 83%; PP ≥ 0.95) (Figs. 2–3, Electr. Suppl.: Figs. S1–S2). These findings were supported by our morphological observations. The gynoecium in both genera is semecarpous with three partly fused ovaries, each with its own stigma and style (Fig. 6C–D, i–ii). It is also unilocular, has thick but smooth walls, and the septal walls are basally fused (Fig. 6C, i–ii). Also, the perianth segments in both genera are entire and do not have papillate tips (Fig. 6B, i–ii). The general morphology of *Beaucarnea compacta* and *Calibanus glassianus* is also very similar (Fig. 1B–C). The main morphological difference we found between *Beaucarnea* and *Calibanus* was the 3-sided ovary of *Beaucarnea* vs. the 6-lobed ovary of *C. hookeri* (Fig. 6C, i–ii), and the fruit ornament. Unlike *Beaucarnea*, *Calibanus* has fruits that lack wings, though *C. glassianus* has fruits with ridges (Hernández & Zamudio, 2003). These ridges likely represent reduced wings that are simply further reduced in *C. hookeri* (Fig. 7A). See Fig. 8 for the unique combination of character states that diagnose the B-C complex.

Based on our molecular results and morphological observations, we formally include *Calibanus* in *Beaucarnea*. Maintaining both genera would require recognition of manifestly paraphyletic groups. Alternatively, we would need to consider

the erection of multiple genera, at least one from each of the major clades within the *Beaucarnea-Calibanus* clade. By far the simplest way of resolving this paraphyly is to include *Calibanus* in *Beaucarnea* (see the Taxonomy section).

With respect to *Dasylirion*, we found it to be monophyletic with high support values, and recovered it as sister to the *Beaucarnea-Calibanus* complex in all partitions except for the plastid *ycf1* (Figs. 2–3; Electr. Suppl.: Figs. S1–S2). The genus is readily recognized given that at least 8 of 16 morphological features examined here are diagnostic for *Dasylirion* (Fig. 8).

Species-level analyses. — The present study contributes the first phylogenetic hypothesis of *Beaucarnea* based on molecular data. One previous phylogenetic hypothesis has been proposed based on morphological characters, though it was never published (Hernández, 1993a). Also, two sections of *Beaucarnea* have been proposed based on broad morphological characters (Trelease, 1911). We will contrast these two previous proposals with the results obtained in this study. Unless specified, we base our further discussion on the concatenated analysis derived from the maximum likelihood (ML) analysis, which differed from the Bayesian hypothesis only in the position of *B. stricta* (Fig. 3), and from the parsimony hypothesis in the unresolved position of some clades (Electr. Suppl.: Fig. S2).

Within the *Beaucarnea-Calibanus* complex, we recovered six major clades, the species of which grow mainly in two contrasting habitat types, relatively dry and relatively moist. The "southern" and the "recurvata" clades are found in moister and less extreme environments than the other four clades. The species of the "southern" and "recurvata" clades share some morphological characters, which may be adaptations to their relatively moist environments. For example, they have slender stems and branches, smooth bark, recurvate green leaves, shallowly sunken stomata, and glabrous leaf grooves. These tall habits, ample leaf area, and relatively exposed stomata seem congruent with their relatively moist forest habitat. The other four clades, the "gracilis", "calibanus", "purpusii", and "stricta" clades, grow in drier environments, such as xerophytic scrubs and tropical deciduous forests. These species share some morphological characters that may be adaptations to drier environments with more marked extremes of temperature and drought. For example, they tend to have robust stems and branches, thick and tesselated bark, nearly straight glaucous leaves, papillate grooves, and deeply sunken stomata. Most of these features would plausibly seem to reduce water loss during prolonged dry seasons.

Based on some of these morphological characters, Trelease (1911) proposed two infrageneric divisions for *Beaucarnea*, *Beaucarnea* sect. *Beaucarnea* and *Beaucarnea* sect. *Papillatae* (Trel.) Thiede. In the section *Beaucarnea* Trelease (1911) placed *B. recurvata*, *B. inermis*, *B. pliabilis*, *B. guatemalensis*, and *B. goldmanii*. In the section *Papillatae* Trelease (1911) placed *B. stricta*, including *B. purpusii*, and *B. gracilis*. Below, we contrast each clade recovered in the present study with Trelease's subdivisions to determine whether each should be considered valid. We also contrast our results with those of Hernández (1993a).

The "southern" clade. — Made up of *B. goldmanii*, *B. pliabilis*, and *B. guatemalensis*, the "southern" clade is a

well-defined group. We recovered this clade with high support values in the nuclear, plastid, and concatenated analyses (Figs. 2–3; Electr. Suppl.: Figs. S1–S2). These findings are in agreement with Hernández (1993a), who recovered this group as monophyletic based on vegetative and reproductive characters (Electr. Suppl.: Fig. S5), but in disagreement with Trelease (1911). Trelease (1911) placed the species of the southern clade, along with *B. recurvata* and *B. inermis*, in *Beaucarnea* sect. *Beaucarnea*, because of their similar morphology. They all have slender branches, recurvate green leaves, and glabrous grooves, except for *B. guatemalensis*, which has papillate blades, though its papillae are shorter and sparser than those of the species of drier environments. Despite their gross similarity, neither molecular nor geographical information indicate a close association between *B. recurvata* (including *B. inermis*; Hernández, 1993a) and the species of the "southern" clade. *Beaucarnea recurvata* occurs from southern Tamaulipas to central Veracruz (Trelease, 1911; Hernández, 1993a), and Oaxaca (Hernández-Sandoval & al., 2012), and the species of the "southern" clade occur from south-east Mexico to Central America. The distribution of the morphological features in the "southern" and "recurvata" clades, suggest that these vegetative traits may have emerged more than once in the group, and cannot be used to reconstruct the relationships among *Beaucarnea* species. Instead, they seem more likely similar adaptive responses to similar environmental conditions. We conclude that *Beaucarnea* sect. *Beaucarnea* should not be considered a valid subdivision of *Beaucarnea*.

The "recurvata" clade. — The "recurvata" clade, made up of *Beaucarnea recurvata*, *B. sanctomariana*, and the putative species *B.* sp1, is a well-supported group (Electr. Suppl.: Table S3), but it awaits more detailed study. *Beaucarnea sanctomariana* was described from the Santa María Chimalapa area on the Atlantic slope of the Isthmus of Tehuantepec in Oaxaca (Hernández, 2001). Another name, "*B. congesta*" (Hernández, 1993a), has been proposed for *B.* sp1, which are much larger plants collected in hills southwest of Santa María Chimalapa, on the Pacific rather than the Gulf slope, but this name was never formally published. Some specimens collected at these Pacific slope localities have also been labeled as *B. stricta*, and all of these specimens have, at one time or another, also been determined as *B. recurvata* (Hernández-Sandoval & al., 2012). We are confident that these specimens do not belong to *B. stricta*. The Isthmian specimens have very long, pendent green leaves with smooth grooves, whereas *B. stricta* has much shorter, straight glaucous-green leaves with papillate grooves (Lemaire, 1861; Hernández, 1993a). They also differ in habit, with *B. stricta* being more gracile, rarely exceeding a meter in diameter, and the Isthmian plants being very massive, often 3 m or more in diameter with the swollen portion 2 m tall and abundantly branched from the apex of the trunk. Also, our sample collected in the Isthmus of Tehuantepec, *B.* sp1, was recovered as sister to *B. sanctomariana*, and these two as sister to *B. recurvata*, but never as related to *B. stricta* (Figs. 2–3; Electr. Suppl.: Figs. S1–S2). Based on morphology, Hernández (1993a; Electr. Suppl.: Fig. S5) recovered *B. sanctomariana*, *B. recurvata*, and "*B. congesta*" in a grade as succesive sister

taxa, with "*B. congesta*" as sister to the "southern" clade. However, our results suggest that the "recurvata" and "southern" groups are not closely related.

The "gracilis" clade. — The different population samples of *B. gracilis* made up the "gracilis" clade. This clade emerged as sister to the "recurvata" clade (Figs. 2–3). Our results are in disagreement with Trelease (1911), who placed *B. gracilis* and *B. stricta* alone in their own section *Papillatae*, and with Hernández (1993a), who, based on morphological characters, recovered *B. gracilis* as sister to the rest of *Beaucarnea*, except for *B. stricta* and *B. purpusii*, which he recovered as sister taxa. The environmental pressures in this group seem likely to determine many of the vegetative features of the species. *Beaucarnea gracilis* grows in drier environments whereas *B. recurvata* grows in moister environments, suggesting that the morphological similarity is convergent and should not be used as phylogenetic characters. Geographically, though, both *B. gracilis* and *B. recurvata* are found in the general region of the eastern Sierra Madre, so the grouping could make sense geographically.

The "calibanus" clade. — The discovery of *Beaucarnea compacta* and *Calibanus glassianus* and their morphological and geographical proximity provided strong evidence for a close phylogenetic relationship between these species, and thus between the two genera. Our molecular analyses support this close association. *Calibanus* was nested within *Beaucarnea*, and *B. compacta* and *C. glassianus* formed a well-supported group (Figs. 2–3). We recovered this group with high support values in each partition and in the combined data (Electr. Suppl.: Table S2). The lack of resolution within the *B. compacta*–*C. glassianus* group may indicate that the time from speciation between them has been short. We did not observe nucleotide divergence between any molecular partition (see Electr. Suppl.: Table S1), but found vegetative and reproductive differences between *B. compacta* and *C. glassianus* that are consistent with their status as distinct species.

The "purpusii" and "stricta" clades. — We tested the taxonomic circumscription of *B. purpusii* because its status as distinct from *B. stricta* is unclear. Trelease (1911) synonymized *B. purpusii* with *B. stricta*, but later Hernández (1993a) and Rivera-Lugo & Solano (2012) suggested that *B. purpusii* is an independent species. Today some important botanical databases still regard *B. purpusii* as synonym of *B. stricta* (Espejo & López-Ferrari, 2008; The Plant List: http://www.theplantlist.org, accessed 2014; Tropicos: http://tropicos.org, accessed 2014). Here we tested the circumscription of *B. purpusii* by including three samples of *B. purpusii* and three samples of *B. stricta*, and recovered them as separate (Figs. 2–3; Electr. Suppl.: Figs. S1–S2). *Beaucarnea purpusii* emerged as sister to *B. hiriartiae*, and these two as sister to *B.* sp2. Rather than close to *B. purpusii*, *B. stricta* emerged as sister to the rest of *Beaucarnea* minus the "southern" clade (Fig. 3). Moreover, we found conspicuous inflorescence differences between *B. purpusii* and *B. stricta*. For example, *B. purpusii* has very short internodes between rhipidia, and the bracteole of each node tends to be thicker and longer than in *B. stricta*. In contrast, in *B. stricta* the internodes are conspicuously longer than in *B. purpusii*, and the

bracteole of each node tends to be thinner than in *B. purpusii*. Also, the inflorescence of *B. stricta* usually has three branching orders, whereas in *B. purpusii* the inflorescence has usually two branching orders. More study is needed, especially of the reproductive characters of these two species. However, based on our molecular results and morphological observations, we conclude that *B. purpusii* should be considered a separate species (see Taxonomy section).

With respect to the ambiguous position of *B. stricta*, which was recovered as sister to *B.* sp2 in the nuclear analyses (Fig. 2), and as sister to *Beaucarnea* minus the "southern" clade in the ML concatenated analysis (Fig. 3), it could plausibly be the product of hybridization of *B. stricta* with *B.* sp2, followed by repeated backcrossing of the hybrid with one of its parents. Virtually nothing, though, is known regarding the pollination biology of these or any other *Beaucarnea* species.

Regarding the plants collected in southwestern Puebla, here referred to as *B.* sp2, we found them to be morphologically and molecularly distinct from other *Beaucarnea* species. They have greatly swollen bases that abruptly taper into a slender, sparingly branched stem. The bark is gray and smooth, the leaves are green, straight, and short, and the plants are short, reaching no more than 4 m. The general morphology of these plants resembles *B. hiriartiae* but with a more distinctly swollen base. After analyzing the material morphologically and molecularly, we concluded that it could represent a new species. A detailed analysis of this material is in progress.

■ TAXONOMY

The description of *Beaucarnea* is updated here to reflect the inclusion of *Calibanus* as a result of our molecular analyses, morphological observations, and literature reviewed. We present a list of *Beaucarnea* species including one new combination. The types for *B. gracilis*, *B. stricta*, and *B. recurvata* were not designated (Lemaire, 1861). The literature reviewed and the examination of herbarium specimens carried out in this study suggests a lack of holotypes for these species. According to Art. 9.12 of the *ICN* (McNeill & al., 2012) an illustration may be used as a lectotype when no isotypes, syntypes, isosyntypes or paratypes are extant. Lemaire (1861) published an illustration of *B. recurvata* in its protologue, so we designate that illustration as a lectotype for *B. recurvata*. Regarding *B. gracilis* and *B. stricta* we refrain from designating neotypes for the time being, pending a detailed search of European herbaria to be sure that there are indeed no holotypes. According to Fournier (1872: 48), the library of Lemaire was sold and the collections dispersed. The search for this material could provide useful information regarding the type specimens or living plants Lemaire used for his descriptions. For example, Baker (1872) stated that the original plant on which Lemaire based his description of *B. recurvata* was from the living collection of Wilson Saunders or from the cactus house at Kew. Perhaps specimens survive there. Clearly some information is available to go on, but the matter will require detailed botanical detective work. Regarding *B. hookeri*, we designate as lectotype

a specimen from Kew that was made in 1873 from a living plant cultivated at the cactus house. Hooker described this species from living plants he received at Kew (Hooker, 1859), though with the misapplied name *Dasylirion hartwegianum*. This specimen likely belongs to one of the plants that Hooker analyzed when he described the species, as we can testify from Baker (1872: 327).

Beaucarnea Lem. in Ill. Hort. 8: Misc. 59. 1861 − Type: *B. recurvata* Lem.
= *Calibanus* Rose in Contr. U.S. Natl. Herb. 10: 90. 1906, **syn. nov.** − Type: *C. caespitosus* (Scheidw.) Rose (≡ *Dasylirion caespitosum* Scheidw.).

Plants hermaphroditic, dioecious, or polygamodioecious, with massively swollen bases and sparse (or no) erect branches, habit arborescent to caespitose, <60 cm to 10(–18) m tall, base conic to globose, bark smooth or squamose, branching pseudodichotomous. Leaves perennial, acicular to ensiform, rosulate, mostly terminal, straight and terminally erect to recurvate and pendent, caniculate to striate, glabrous to minutely papillate, green to glaucous blue-green, sometimes with persistent old leaves covering the branches, margin microcrenulate to microserrulate; stomata tetracytic under stomatal crypts. Inflorescence a thyrse, branching orders primary, secondary, and sometimes tertiary, decreasing in size acropetally, last unit of the inflorescence a reduced rhipidium. Inflorescence bracts lanceolate, triangular to widely triangular, apex acuminate to long caudate, membranaceous. Bracts subtending rhipidia ovate to lanceolate, basally coriaceous. Bracteoles per flower 1, sometimes enclosing the subtended flowers, ovate, obovate, or orbicular, apex acute, truncate to rounded, margin entire to praemorse. Pedicels articulate. Flowers actinomorphic, hypogynous, perianth segments 6, basally fused, imbricate, the outer three mostly smaller, erect to reflexed, ovate to obovate, whitish to slightly tinged purple or red, midvein evident. Pistillate flowers 2–5 per rhipidium, perianth segments not reflexed at anthesis, ovary superior, pyriform, ovoid to ellipsoid, 3-lobed, sometimes 6-lobed, mostly 3-winged, 3-carpellar, unilocular, septum prominent to reduced, basally fused, ovules 6, 2 per carpel, placentation basally axile, style slightly elongate to reduced, stigma 3-lobed, papillate, exserted at anthesis, staminodes 6, sometimes exserted at anthesis. Staminate flowers 2–9 per rhipidium, perianth segments sometimes reflexed at anthesis, stamens 6, basally epitepalous, filamentous, narrowly conic, anthers versatile, dehiscence longitudinal, pistillode inconspicuous to prominent. Capsules with delayed dehiscence, ellipsoidal, orbicular or obovoid, wings present or absent. Seeds 1 per fruit, globose, 3-lobed, yellow to brown, testa rugose, embryo cylindrical.

Beaucarnea compacta L.Hern. & Zamudio in Brittonia 55: 226–228, fig. 1a–i. 2003 – Holotype: Mexico, Guanajuato, Mun. Atarjea, 6.5 km al SE de El Guamúchil, la brecha a Atarjea, 1400 m, 12 Sep 1997, *S. Zamudio, E. Pérez-Cálix & L. Hernández 10465* (IEB barcode IEB000164898!; isotypes: CHAPA n.v., ENCB n.v., MEXU No. 1195814!, QMEX n.v.).

Beaucarnea glassiana (L.Hern. & Zamudio) V.Rojas, **comb. nov.** ≡ *Calibanus glassianus* L.Hern. & Zamudio in Brittonia 55: 228–231, fig. 2a–i. 2003 – Holotype: Mexico, Guanajuato, Mun. Xichú, 10 km al NE de Xichú, por la brecha a Atarjea, 1000 m, 12 Sep 1997, *E. Pérez-Cálix, S. Zamudio & L. Hernández 3719* (IEB barcode IEB000164900!; isotypes: CHAPA n.v., ENCB n.v., MEXU No. 1346691!, QMEX n.v.).

Beaucarnea goldmanii Rose in Contr. U.S. Natl. Herb. 12: 261–262, pl. 20. 1909 – Holotype: Mexico, Chiapas [Mpio. La Trinitaria, Had. de] San Vicente, 4000 ft., 26 Apr 1904, *E. Goldman 887* (US No. 566461 [barcode 00433505]!; isotype: US No. 566560 [barcode 00433507]!).

Beaucarnea gracilis Lem. in Ill. Hort. 8: Misc. 61. 1861 ≡ *Dasylirion gracile* (Lem.) J.F.MacBr. in Contr. Gray Herb., n.s., 56: 17. 1918, non (Brongn.) Zucc. 1845 ≡ *Nolina gracilis* (Lem.) Cif. & Giacom., Nomencl. Fl. Ital. 1: 136. 1950 – Type: Not designated.
= *B. oedipus* Rose in Contr. U.S. Natl. Herb. 10: 88, pl. 23. 1906 – Holotype: Mexico, Puebla, hills near Tehuacán, 30 Aug–8 Sep 1905, *J.N. Rose & J.H. Painter 10157* (US No. 453660 [barcode 00433509; photos: F No. 1668419 MEXU No. 453660]!; isotype: US No. 1405977 [barcode 00955529]!).

Beaucarnea guatemalensis Rose in Contr. U.S. Natl. Herb. 10: 88, fig. 1. 1906 – Holotype: Guatemala, in a rocky ravine on the south side of the Sierra de las Minas, opposite El Rancho, Guatemala, 600 m, 10 Mar 1905, *W.A. Kellerman 4320* (US No. 474781 [barcode 00433508]!; isotypes: F No. 220674 [barcode V0045987F]!, LL barcode LL00370295!, MEXU No. 49251!, MICH barcode MICH1002507B!, TEX barcode TEX00370294!, UC barcode UC1228022!).

Beaucarnea hiriartiae L.Hern. in Acta Bot. Mex. 18: 25–27, fig. 1. 1992 – Holotype: Mexico, Guerrero, 12 km al S de Mezcala, 03 Ene 1986, *L. Hernández & M. Martínez 1629* (MEXU not found; isotypes: TEX barcode 00370296!, UAT n.v.).

Beaucarnea hookeri (Lem.) Baker in J. Bot. 10: 327. 1872 ≡ *Dasylirion hartwegianum* Hook. in Bot. Mag. 85: t. 5099. 1859, non Zucc. 1845 ≡ *Dasylirion hookeri* Lem. in Ill. Hort. 6: Misc. 24. 1859 ≡ *Calibanus hookeri* (Lem.) Trel. in Proc. Amer. Philos. Soc. 50: 426–427. 1911 – **Lectotype (designated here):** Royal Botanical Gardens, Kew, Cactus House, 1873 (K barcode K000524953!).
This specimen comes from a living plant cultivated at the cactus house at Kew, and is likely one of the specimens that Hooker analyzed when he described the species, though with the misapplied name *Dasylirion hartwegianum.*

= *Dasylirion caespitosum* Scheidw. in Wochenschr. Vereines Beförd. Gartenbaues Königl. Preuss. Staaten 4: 286. 1861 ≡ *Calibanus caespitosus* (Scheidw.) Rose in Contr. U.S. Natl. Herb. 10: 90–91, pl. 24–25, fig. 4. 1906 – **Lectotype (designated here):** Mexico, Hidalgo, near Ixmiquilpan, 1905, *Rose 8954* (US No. 452434 [barcode 00908027]!).

Beaucarnea pliabilis (Baker) Rose in Contr. U.S. Natl. Herb. 10: 89. 1906 ≡ *Dasylirion pliabile* Baker in J. Linn. Soc., Bot. 18: 240. 1880 ≡ *Nolina pliabilis* (Baker) Lundell in Bull. Torrey Bot. Club. 66: 587. 1939 – Holotype: Mexico, Yucatán, Sisal, *Schott 892* (BM barcode BM00055136!; isotypes: MO Nos. 3266850 [barcode MO-102016]! & 3265872 [barcode MO-102017]!).
= *Dracaena petenensis* Lundell in J. Washington Acad. Sci. 25: 230. 1935 ≡ *Beaucarnea petenensis* (Lundell) Lundell in Bull. Torrey Bot. Club 66: 586. 1939 – Holotype: Guatemala, Petén, Monte Hiltun, 17 May 1933, *C.L. Lundell 3271* (MICH barcode MICH1218166!; isotype: LL barcode LL00370293!).
= *Beaucarnea ameliae* Lundell in Bull. Torrey Bot. Club 66: 585, fig. 1. 1939 – Holotype: Mexico, Yucatán, Progreso, Merida road, km 29, denuded limestone flats bordering cienega, 26 Jul 1938, *C.L. Lundell & A.A. Lundell 8128* (MICH barcode MICH1192204!; isotypes: CAS barcodes CAS0001018! & CAS0001019!; F barcodes F0045086!, F0045985F! & F0045986F!, GH Nos. 351625! & 351626!, LL barcodes LL00373252! & LL00370292!, MEXU Nos. 53009! & 53010!).

Beaucarnea purpusii Rose in Contr. U.S. Natl. Herb. 10: 89. 1906 – Holotype: Mexico, Puebla, Tehuacán, near Tehuacán, 30 Aug–8 Sep 1905, *Rose 10156* (US No. 453695 [barcode 00433506]!; isotypes: MEXU No. 7576 [barcode MEXU00007576]!, NY s.n.!, US No. 1405976 [barcode US00955530]!).

Beaucarnea recurvata Lem. in Ill. Hort. 8: Misc. 59. 1861 ≡ *Nolina recurvata* (Lem.) Hemsl., Biol. Cent.-Amer., Bot. 3: 372. 1884 ≡ *Dasylirion recurvatum* (Lem.) J.F.MacBr. in Contr. Gray Herb., n.s., 56: 17. 1918 – **Lectotype (designated here):** [illustration] "Beaucarnea recurvata Ch.Lem." in Ill. Hort. 8: Misc. [58]. fig. 1. 1861. — For an image of the lectotype, see Electr. Suppl.: Fig. S6.
According to Art. 9.12 of the *ICN* (McNeill & al., 2012) if there are no isotypes, syntypes, isosyntypes or paratypes extant, the lectotype must be chosen from among the paratypes if such exist. If no cited specimens exist, the lectotype must be chosen from among the uncited specimens and cited and uncited illustrations that comprise the remaining original material, if such exist. In this case, the uncited illustration in the protologue of *Beaucarnea*, which corresponds to *B. recurvata*, is designated here as the lectotype of this species.

= *Dasylirion inerme* S.Watson in Proc. Amer. Acad. Arts 26: 157. 1891 ≡ *Beaucarnea inermis* (S.Watson) Rose in Contr. U.S. Natl. Herb. 10: 88, fig. 2. 1906 – **Lectotype (designated here):** Mexico, San Luis Potosí, Las Palmas, 27 Jun 1890, *Pringle 3108* (GH barcode 00035098!; isolectotypes: F Nos. 105210 [barcode V0046007F]! & 263377 [barcode V0046008F]!, LL barcode LL00370297!, MO

No. 3270469!, K barcode K000524954!, MICH barcode 1192205!, MEXU barcode MEXU 00007575!, NY barcode 00277836!, US barcodes 00091923! & 00091924!).

Beaucarnea sanctomariana L.Hern. in Novon 11: 50. 2001 – Holotype: Mexico, Oaxaca, Mpio. Santa María Chimalapa, afloramientos de roca en la cresta S del cañón del Río Corte, ca. 4 km al N de Sta. María, cerca de la vereda al Paso de la Cueva, 28 Apr 1988, *T. Wendt 5914* (MEXU not found; isotypes: CHAPA n.v., LL not found, MO not found, UAT n.v.).

Beaucarnea stricta Lem. in Ill. Hort. 8: Misc. 61. 1861 ≡ *Beaucarnea recurvata* var. *stricta* (Lem.) Baker. in J. Linn. Soc., Bot. 18: 234. 1880 ≡ *Dasylirion strictum* (Lem.) J.F.MacBr. in Contr. Gray Herb., n.s., 56: 17. 1918 ≡ *Nolina stricta* (Lem.) Cif. & Giacom., Nomecl. Fl. Ital. 1: 136. 1950 – Type: Not designated.

Excluded names

Beaucarnea congesta L.Hern., ined., invalid.
Beaucarnea glauca Roezl. in Belgique Hort. 33: 138. 1883., nom. nud.
Beaucarnea tuberculata Roezl. in Belgique Hort. 33: 138. 1883., nom. nud.
Pincenectitia glauca Hort., nom. nud., pro. syn.
Pincenectitia gracilis Hort., nom. nud., pro. syn.
Pincenectitia tuberculata Hort., nom. nud., pro. syn.

Key to the species of *Beaucarnea*

1. Leaf papillae present ……………………………… 2
1. Leaf papillae absent ……………………………… 9
2. Habit caudiciform, plants 1 m or less tall; perianth segments purplish ……………………………………… 3
2. Habit arborescent, plants 2 m or more tall; perianth segments whitish ………………………………………… 5
3. Stem usually subterranean; leaves in fascicles scattered on the upper stem surface, 0.5 cm or less wide .. ***B. hookeri***
3. Stem aboveground; leaves borne on branches emerging from the upper surface of the swollen stem base, 0.5 cm or more wide ………………………………………… 4
4. Gynoecium and fruits winged; branching starts at 80–100 cm above base of inflorescence ……… ***B. compacta***
4. Gynoecium and fruits not winged; branching starts at 20–25 cm above base of inflorescence …… ***B. glassiana***
5. Leaves linear, usually 1 cm or less wide, rigidly concave …………………………………………***B. gracilis***
5. Leaves lanceolate or linear-lanceolate, usually 1 cm or more wide, flat or only flexible concave …………………… 6
6. Gynoecium 2.0 mm or less in length; style elongate; perianth segments longer than gynoecium; fruit without apical notch; Guerrero …………………………… ***B. hiriartiae***
6. Gynoecium 2.0 mm or more in length; style short; perianth segments shorter than the gynoecium; fruit with apical notch; Puebla, Oaxaca, and Central America ………… 7

7. Rhipidium bracts lanceolate, usually twice the length of the bracteoles; fruits 1.5 cm or more long; leaf papillae short, found mostly on the underside of the leaf; Central America ………………………………**B. guatemalensis**
7. Rhipidium bracts ovate to triangular, usually the same length as the bracteoles; fruits less than 1.5 cm long; leaf papillae long, on both leaf surfaces; Puebla and Oaxaca ………………………………………………… 8
8. Distalmost order branches of the inflorescence with congested rhipidia; rhipidium bracts 3.0–4.0 mm long; bracteole 3.0–5.5 mm ………………………………**B. purpusii**
8. Distalmost order branches of the inflorescence with non-congested rhipidia; riphidium bracts 2.0–3.0 mm long; bracteole 2.0–2.5 mm long …………………… **B. stricta**
9. Leaves 1–2 cm wide at the middle; rhipidium bracts almost as long as the bracteoles ……………………………… 10
9. Leaves 2 cm or more wide at the middle; rhipidium bracts twice or more as long as bracteoles; Chiapas, Yucatan Peninsula, Belize, Guatemala, Honduras, El Salvador ……11
10. Plants intricately branched, branches slender and relatively flexible; branching usually starting at 1 m or below; adults 3–6 m tall (usually 3–4 m); Santa María Chimalapa, Oaxaca ………………………………… **B. sanctomariana**
10. Plants laxly branched, branches thick and relativey rigid; branching usually starting at 2 m or above; adults always more than 3 m tall (usually 5–10 m); San Luis Potosí, Tamaulipas, Veracruz, and northern Oaxaca …. **B. recurvata**
11. Plants sparingly branched; terminal rosettes with abundant leaves; plants growing at <100 m above sea level; Yucatan Peninsula, Guatemala, and Belize …………. **B. pliabilis**
11. Plants profusely branched; leaves in terminal rosettes relatively sparse; plants growing at >100 m above sea level; Chiapas, Guatemala, El Salvador, and Honduras ……… …………………………………………… **B. goldmanii**

■ ACKNOWLEDGEMENTS

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Appendix 1. List of taxa, localities (G, Guatemala; M, Mexico; U, United States of America), vouchers (all vouchers are deposited in MEXU) and GenBank accession numbers of the species sampled for this study. * indicates cultivated plants at the Botanical Garden, Instituto de Biología, UNAM; ‡ indicates herbarium specimens (MEXU).

Taxon, locality (country: state, municipality or district), *voucher*, ITS, *trnL-F*, *ycf1*

Beaucarnea compacta L.Hern. & Zamudio, M: Guanajuato, Xichú, *Rojas 31*, KC798443, KJ196034, KJ195992; *Beaucarnea compacta* L.Hern. & Zamudio, M: Guanajuato, Xichú, *Rojas 32*, KC798444, KJ196035, KJ195993; *Beaucarnea compacta* L.Hern. & Zamudio, M: Guanajuato, Xichú, *Rojas 33*, KC798445, KJ196036, KJ195994; *Beaucarnea goldmanii* Rose, M: Chiapas, Comitán de Dgz., *Olson 1103*, KC798461, KJ196052, KJ196010; *Beaucarnea goldmanii* Rose, M: Chiapas, Comitán de Dgz., *Olson 1104*, KC798462, KJ196053, KJ196011; *Beaucarnea goldmanii* Rose, G: Jalapa, Volcán Jumay, *Montero-Castro 1004*, KC798463, KJ196054, KJ196012; *Beaucarnea gracilis* Lem., M: Puebla, Tehuacán, *Rojas 9*, KC798439, KJ196030, KJ195988; *Beaucarnea gracilis* Lem., M: Puebla, Zapotitlán, *Rojas 11*, KC798440, KJ196031, KJ195989; *Beaucarnea gracilis* Lem., M: Oaxaca, Huajuapan, *Rojas 18*, KC798442, KJ196033, KJ195991; *Beaucarnea gracilis* Lem., M: Oaxaca, Cuicatlán, *Rojas 25*, KC798441, KJ196032, KJ195990; *Beaucarnea guatemalensis* Rose, G: Cobán, Chicoyoj, *Montero-Castro 1033*, KC798464, KJ196052, KJ196013; *Beaucarnea hiriartiae* L.Hern., M: Guerrero, Eduardo Neri, *Medina-Lemos E424*, KC798457, KJ196048, KJ196006; *Beaucarnea hiriartiae* L.Hern., M: Guerrero, Eduardo Neri, *Medina-Lemos E425*, KC798458, KJ196049, KJ196007; *Beaucarnea pliabilis* (Baker) Rose, M: Quintana Roo, Tulúm, *Cervantes 44*, KC798465, KJ196056, KJ196014; *Beaucarnea purpusii* Rose, M: Puebla, Zapotitlán, *Rojas 14*, KC798459, KJ196050, KJ196008; *Beaucarnea purpusii* Rose, M: Oaxaca, Santiago Chazumba, *Rojas 38*, KC798460, KJ196051, KJ196009; *Beaucarnea recurvata* Lem., M: Tamaulipas, Antiguo Morelos, *Rojas 28*, KC798436, KJ196027, KJ195985; *Beaucarnea sanctomariana* L.Hern., M: Oaxaca, Sta. María Chimalapa, *Salas SS7276*, KC798438, KJ196029, KJ195987; *Beaucarnea stricta* Lem., M: Oaxaca, Cuicatlán, *Rojas 21*, KC798452, KJ196043, KJ196001; *Beaucarnea stricta* Lem., M: Oaxaca, Cucatlán, *Rojas 22*, KC798453, KJ196044, KJ196002; *Beaucarnea stricta* Lem., M: Oaxaca, Cuicatlán, *Rojas 23*, KC798454, KJ196045, KJ196003; *Beaucarnea* **sp1,** M: Oaxaca, Juchitán, *Olson 1124*, KC798437, KJ196028, KJ195986; *Beaucarnea* **sp2,** M: Puebla, Acatlán, *Olson s.n.*, KC798456, KJ196047, KJ196005; *Beaucarnea* **sp2,** M: Puebla, Acatlán, *Rojas 37*, KC798455, KJ196046, KJ196004; *Calibanus glassianus* L.Hern. & Zamudio, M: Guanajuato, Xichú, *Rojas 34*, KC798446, KJ196037, KJ195995; *Calibanus glassianus* L.Hern. & Zamudio, M: Guanajuato, Xichú, *Rojas 35*, KC798447, KJ196038, KJ195996; *Calibanus glassianus* L.Hern. & Zamudio, M: Guanajuato, Xichú, *Rojas 36*, KC798448, KJ196039, KJ195997; *Calibanus hookeri* (Rose) Trel., M: Guanajuato, San Luis de la Paz, *Rojas 27*, KC798449, KJ196040, KJ195998; **Calibanus hookeri* (Rose) Trel., M: San Luis Potosí, *García-Mendoza 7836*, KC798450, KJ196041, KJ195999; **Calibanus hookeri* (Rose) Trel., M: Hidalgo, Zimapán, *García-Mendoza 7838*, KC798451, KJ196042, KJ196000; **Dasylirion acrotrichum* (Schiede) Zucc., M: Hidalgo, Ixmiquilpan, *García-Mendoza 7862*, KC798466, KJ196057, KJ196015; **Dasylirion berlandieri* S.Watson, M: San Luis Potosí, *García-Mendoza 5917*, KC798467, KJ196058, KJ196016; **Dasylirion longissimum* Lem., M: Tamaulipas, *Rojas s.n.*, KC798469, KJ196060, KJ196018; ‡*Dasylirion glaucophyllum* Hook., M: Hidalgo, Metztitlán, *García-Mendoza 7226*, KC798470, KJ196061KJ196061, KJ196019; **Dasylirion serratifolium* (Kraw. ex Schult.f) Zucc., M: Oaxaca, Huajuapan, *García-Mendoza 5816*, KC798468, KJ196059, KJ196017; ‡*Nolina cespitifera* Trel., M: Coahuila, Saltillo, *Hernández 2344*, KC798472, KJ196063, KJ196021; **Nolina durangensis* Trel., M: Durango, Canatlán, *García-Mendoza 5970*, KC798473, KJ196064, KJ196022; ‡*Nolina juncea* (Zucc.) J.F.MacBr., M: Durango, Nuevo Ideal, *López 107*, KC798474, KJ196065, KJ196023; ‡*Nolina lindheimeriana* (Scheele) S.Watson, U: Texas, Lampasas, *Webster 33296*, KC798475, KJ196066, KJ196024; ‡*Nolina longifolia* (Kraw. ex Schult.f.) Hemsl., M: Puebla, Lafragua, *Galván 1150*, KC798476, KJ196067, KJ196025; **Nolina parviflora* (Kunth) Hemsl., M: Oaxaca, Huajuapan, *García-Mendoza 7563*, KC798471, KJ196062, KJ196020; ‡*Ophiopogon planiscapus* Nakai, Japan, *Saiki 4452*, KC798477, KJ196068, KJ196026

Appendix 2. Specimens examined for morphology.

Beaucarnea compacta L.Hern. & Zamudio. MEXICO. Guanajuato: *Hernández 4600* (MEXU); *Zamudio 10465* (MEXU); *Zamudio 10469* (MEXU); *Zamudio 10787* (MEXU); *Zamudio 10791* (MEXU); *Zamudio 10792* (MEXU). *Beaucarnea goldmanii* Rose EL SALVADOR. *Reyna 1498* (F, NY), *Reyna 1500* (F, NY). GUATEMALA. Chiquimula: *Herández 1397H* (MEXU, F, NY, MO, US, MICH); *Steyermark 44117* (US, CHIC, F); Huehuetenango: *Maarten 5544* (MO); *Seyermark 51396* (F). MEXICO. Chiapas: *Breedlove 9043* (MEXU, CHIC); *Breedlove 28171* (MEXU, NY, MO, F, MICH); *Breedlove 39945* (MEXU, MICH); *Breedlove 40635* (MEXU, MO, NY); *Breedlove 47598* (NY); *Goldman 887* (MO); *Hernández 2431* (MEXU); *Hernández 2434* (MEXU); *Hernández 2563* (MEXU); *Martínez 20236* (MEXU); *Martínez 20237* (MEXU); *Martínez 22062* (MEXU); *Martínez 22391* (MEXU); *Matuda 1011* (MEXU, MO); *Miranda 7092* (MEXU, US); *Miranda 7660* (MEXU); *Miranda 7667* (MEXU); *Miranda 7715* (MEXU, US); *Téllez 6682* (MEXU, MO); *Zamudio 10* (MEXU). *Beaucarnea gracilis* Lem. MEXICO. Oaxaca: *Calzada 23193* (MEXU); *Castellanos 2457* (MEXU); *García-Mendoza 6593* (MEXU); *Martínez 33427* (MEXU). Puebla: *Calzada 22896* (MEXU); *Conzatti s.n.* (MEXU); *Gallardo 50* (MEXU); *García-Mendoza 2277* (NY, MEXU); *García-Mendoza 2278* (NY, MEXU); *Henrickson 2128* (MICH); *Hernández 2138* (MEXU); *Hernández 2140* (MEXU); *Hernández 2355* (MEXU); *Hernández 2368* (MEXU); *Hernández 2370* (MEXU); *Hernández 2510* (MEXU); *Hernández 2511* (MEXU); *Leuengerger 2558* (MEXU); *Martínez 21687* (MEXU); *Matuda 32292* (MEXU); *Mc Dougal 30, 51* (NY); *Mc Dougal 57* (NY); *Nolazco 4946* (MEXU); *O'Kane 3410* (MO); *Penell 196* (MEXU, NY); *Pringle 7017* (MICH); *Purpus 5860* (US, NY, MO, F, GH); *Reko 4240* (US); *Rose 10157* (MEXU, US); *Rose 11220* (GH, F, MO, NY); *Rzedowsky 19137* (MEXU, MICH, F); *Salinas 6958* (MEXU); *Salinas 7008* (NY); *Smith Jr. 4018* (US, CHIC); *Spetzman 1409* (MEXU); *Stevens 2535* (GH, MICH); *Taylor 25734* (NY); *Trelease s.n.* (MO); *Valiente 360* (MEXU). *Beaucarnea guatemalensis* Rose. GUATEMALA. Baja Verapaz: *Kellerman 4320* (MEXU, MO); *Kellerman 7029* (MEXU, CHIC, US, F). Guatemala: 1939, *Aguilar 401* (F); *Kellermen 6069* (US, F, MICH); *Morales 619* (US). Huhuetenango: *Herández 2545* (MEXU); *Molina 21408* (F); *Steyermark 51200* (US). Jalapa: *Herández 1396G* (MEXU, MO); *Kellerman 7038* (MICH, CHICAGO); *Steyermark 32302* (F). Progreso: *Herández 2546* (MEXU, MO). Sacatepéquez: *Castillo 2773* (NY). San Pedro Pimula: *Herández 1972* (MEXU); Zacapa: *Steyermark 43133* (GH, F). HONDURAS. *Martínez 12921* (MEXU). *Beaucarnea hiriartiae* L.Hern. MEXICO. Oaxaca: *Calzada 18289* (MEXU). Guerrero: *Dunn 20509* (MO, NY); *Gaona 15* (MEXU); *Franco 15* (MEXU); *Hernández 1631, 1632* (MEXU); *Hernández 2143* (MEXU); *Hernández 2463* (MEXU); *Lorea 2932* (MEXU); *Martínez 24088* (MEXU); *Miranda 4313* (MEXU); *Moore 4742* (MICH, GH); *Roe 1925* (NY); *Trejo 1865* (MEXU). *Beaucarnea pliabilis* (Baker) Rose. MEXICO. Campeche: *Chavelas ES-341* (MEXU, MICH); *Martínez 27056* (MEXU, NY); *Martínez 30581* (MEXU); *Martínez 30590* (MEXU); *Martínez 30892* (MEXU). Quintana Roo: *Álvarez 10918* (MEXU); *Davidse 20117* (MEXU, MO); *Lundell 7763* (MEXU, MICH); *Orellana 91* (MEXU); *Ramamoorthy 2070* (MEXU); *Téllez 1908* (MEXU). Yucatán: *Estrada E-92* (MEXU); *Estrada 392* (MEXU); *Estrada 394* (MEXU); *Estrada 395* (MEXU); *Estrada 400* (MEXU); *Estrada 401* (MEXU); *Gaumer 23520* (MO, NY, F, GH); *Gaumer 24327* (MO, MICH, F); *Goldman* no number (NY); *Herández 4291* (MEXU); *Herández 4321* (MEXU); *Lundell 7566* (MEXU, CHIC, MICH); *Lundell 8128* (MEXU, GH); *Matuda 37487* (MEXU); *Méndez 248* (MEXU, F, MO); *Miranda 8234* (MEXU); *Orellana 144* (MEXU); *Orellana 336* (MEXU); *Orellana 338* (MEXU); *Orellana 345* (MEXU); *Orellana 346* (MEXU); *Orellana 348* (MEXU); *Quero 2899* (MEXU); Sisal, Litoral near Sisal, *Schott 892* (MO); *Steere 1498* (F, MICH). *Beaucarnea purpusii* Rose. MEXICO. Oaxaca: *Calzada 23865* (MEXU); *García-Mendoza 7385* (MEXU). Puebla: *Chiang F-374* (MEXU); *García-Mendoza 6419* (MEXU); *García-Mendoza 6496* (MEXU); *Medrano F-717* (MEXU); *Ogden 5170* (MEXU, MICH); *Purpus 2397* (NY, MO, GH, F, US, GREY); *Rose* 10156 (NY, MEXU); *Valiente 933* (MEXU); *Villaseñor F-3133* (MEXU). *Beaucarnea recurvata* Lem. San Luis Potosí: *Palmer 644* (GH); *Pringle 3108* (MO); *Purpus* 5560 (US, GH, F). Tamaulipas: *Dressler 2038* (MEXU, MICH); *Gentry 12267* (MEXU); *González-Medrano 7284* (MEXU); *LeSueur 79* (F); *Lundell 7274* (MICH); *Martínez 3885* (MEXU, F); *Moore 3635* (MICH); *Rzedowsky 10344* (MEXU, MICH); *Rzedowsky 11109* (MEXU, MICH). Veracruz: *Castillo 146* (MEXU, NY); *Castillo 779* (MEXU, F); *Goldman 708* (US); *Hernández 2384* (MEXU); *Herández 4332* (MEXU); *Purpus 7615* (US, GH, MO); *Zola 862* (MEXU, F). *Beaucarnea stricta* Lem. MEXICO. Oaxaca: *Conzatti 1644* (F, US, MEXU); *Cruz-Espinoza 824* (MEXU); *Folsom 11201* (MEXU); *García 215* (MEXU); *García 644* (MEXU); *García-Mendoza 6590* (MEXU); *Hernández 2381* (MEXU); *Maldonado-Ruiz 1* (MEXU); *Maldonado-Ruiz 2* (MEXU); *Medrano F-889, F-890* (MEXU, MO); *Medrano F-1125* (MEXU); *Torres 134* (MEXU); *Torres 11279* (MEXU, MO). *Beaucarnea sanctomariana* L.Hern. MEXICO. Oaxaca: *Rojas 42* (MEXU); *Rojas 43* (MEXU). *Calibanus glassianus* (L.Hern. & Zamudio) Rojas. MEXICO. Guanajuato: *Hernández 4590* (MEXU); *Hernández 4591* (MEXU); *Pérez 3718* (MEXU); *Pérez 3564* (MEXU); *Pérez 3846* (MEXU, NY); *Zamudio 10780* (MEXU). *Calibanus hookeri* (Lem.) Trel. MEXICO. Guanajuato: *Carranza 5190* (MEXU). Hidalgo: *Purpus 1200, 4775* (MO). Querétaro: *Herández 4615* (MEXU); *Hernández 11160* (MEXU); *Moran 14759* (US); *Zamudio 7394* (MEXU); *Zamudio 7395* (MEXU). San Luis Potosí: *Alvarado s.n.* (MEXU); *Bonfil 1165* (MEXU); *Cabrera 444* (MEXU); *Gómez-Pompa 4893* (MEXU); *Lape 7655* (MEXU); *Martínez 22356* (MEXU); *Medrano s.n.* (MEXU). *Dasylirion acrotrichum* (Schiede) Zucc. MEXICO. Hidalgo: *García-Mendoza 7862* (MEXU); *Gómez-Pompa 31* (MEXU); *Rzedowski 17010* (MEXU); *Rzedowski 16725* (MEXU). *Dasylirion berlandieri* S. Watson. MEXICO. Monterrey: *Bogler 607* (MEXU); *Bogler 826* (MEXU). *Dasylirion leiophyllum* Engelm. Ex. Trel. U.S.A.. New Mexico: *Bogler 763* (MEXU); *Bogler 852* (MEXU). *Dasylirion palmeri* Trel. MEXICO. Tamaulipas: *Briones 2009* (MEXU). *Dasylirion serratifolium* (Karw. Ex Schult.f.) Zucc. MEXICO. Oaxaca: *García-Mendoza 6916* (MEXU). *Dasylirion simplex* Trel. MEXICO. Durango: *Bogler 699* (MEXU); *Bogler 886* (MEXU). *Dasylirion wheeleri* S. Watson ex Rothr. U.S.A.. New Mexico: *Bogler 859, 860* (MEXU); Texas: *Bogler 728* (MEXU); *Bogler 855* (MEXU). *Nolina beldingii* Trel. MEXICO. Baja California: *Gentry 11216* (MEXU); *Moran 7369* (CAS). *Nolina duranguensis* Trel. MEXICO. Durango: *Bogler 888* (MEXU); *García-Mendoza 6913* (MEXU); *Hernández 5585* (MEXU). *Nolina lindheimeriana* (Sheele) S. Watson. U.S.A.. Texas: *Lindheimer 1216* (MO); *Webster 33296* (TEX). *Nolina longifolia* (Karw. ex Schult.f.) Hemsl. MEXICO. Oaxaca: *García-Mendoza 4700* (MEXU); *Salas 6649* (MEXU). Puebla: *Galván 1150* (MEXU). *Nolina microcarpa* S. Watson. MEXICO. Sonora: *Gentry 22924* (MEXU). U.S.A.. Arizona: *Gentry 23684* (MEXU). Texas: *Gentry 9951*. *Nolina parryi* S. Watson. U.S.A.. California: *Gentry 23663* (MEXU). *Nolina parviflora* (Kunth) Hemsl. MEXICO. Hidalgo: *Galván 1350* (MEXU); *García-Mendoza 1424* (MEXU); *Rzedowski 31486* (MEXU). *Nolina texana* S. Watson. U.S.A.. Arizona: *Wentworth 2046* (MEXU). Texas: *Gentry 23193* (MEXU).

Appendix S3. Morphological characters and character states.

(1) **Stem bases:** 0 = absent or slightly swollen; 1 = absent or base cylindrical; 2 = massively swollen.
(2) **Stem outermost portion:** 0 = covered with visible bark; 1 = covered with persistent leaf bases.
(3) **Leaf margins:** 0 = serrulate; 1 = spinulose-hooked; 2 = microserrulate; 3 = entire.
(4) **Leaf apex:** 0 = entire; 1 = often brushlike.
(5) **Inflorescence:** 0 = open thyrse; 1 = condensed thyrse; 2 = raceme.
(6) **Perianth segment apices:** 0 = papillate; 1 = crenulate; 2 = entire.
(7) **Gynoecium fusion:** 0 = semecarpous; 1 = syncarpous.
(8) **Gynoecium consistency:** 0 = fleshy; 1 = coriaceous.
(9) **Gynoecium wall:** 0 = granular-walled; 1 = smooth-walled.
(10) **Styles:** 0 = reduced, cylindrical; 1 = prominent, infundibuliform; 2 = prominent, cylindrical.
(11) **Stigmas:** 0 = papillate; 1 = apapillate.
(12) **Ovary:** 0 = trilocular; 1 = unilocular.
(13) **Pistillode:** 0 = prominent; 1 = inconspicuous to slightly prominent; 2 = absent
(14) **Fruit locules:** 0 = trilocular, inflated; 1 = unilocular, not inflated.
(15) **Fruit appendages:** 0 = wingless; 1 = 3-winged.
(16) **Habitat:** 0 = principally highland tropical to temperate; 1 = principally lowland tropical.