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Phylogenetic Relationships in *Echinocereus* (Cactaceae, Cactoideae)

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Abstract—*Echinocereus* is the third most species-rich genus in the Cactaceae. It is distributed in North America from Mexico to the central U. S. A. Previous molecular phylogenetic studies have indicated that the genus is polyphyletic, but incomplete taxon sampling and unclear resolution have hindered the formal re-evaluation of generic and infrageneric circumscriptions. To address this problem, we analyzed six plastid regions (*matK*, *rbcL*, *psbA-trnH*, *trnQ-rps16*, *rpl16*, and *trnL-F*) using maximum parsimony and Bayesian inference criteria for 59 species, including all previously proposed infrageneric entities and representing the full range of morphological variation known in the genus. Our results support the monophyly of *Echinocereus* if *E. pensilis* is excluded and reestablished as the monotypic genus *Morangaya*. Two additional morphological characters, erumpent flower buds and green stigma lobes, further support the circumscription of *Echinocereus* sensu stricto. Phylogenetic analyses recovered nine main clades in *Echinocereus* s. s., one of which corresponds to the *Triglochidiati* section; the remaining clades did not correspond to any other recognized sections. We suggest a re-evaluation of previously proposed infrageneric entities.

Keywords—Bayesian inference, cpDNA, erumpent floral bud, *Morangaya*, parsimony.

Echinocereus Engelm. (Cactoideae, Cactaceae) is a genus that includes between 44 and 71 species (Taylor 1985, 1993; Blum et al. 1998; Hunt et al. 2006). It is distributed from the central U. S. A. (South Dakota) to southern Mexico (Oaxaca) (Taylor 1985), where it has diversified in xeric scrubland, and in pine-oak and deciduous tropical forests. *Echinocereus* is morphologically heterogeneous, as seen in its growth forms, stem thickness, root types, and flower size and shape (Fig. 1).

Engelmann (1848) described the genus *Echinocereus* as including species with short, single or branched stems, few to several ribs, lateral and diurnal flowers, a medium-length receptacular tube with trichomes and spines, and black and tuberculate seeds, assigning *E. viridiflorus* Engelm. as the species type. The classification of *Echinocereus* within the Cactoideae subfamily has been unstable. Schumann (1899) placed *Echinocereus* in the tribe Echinocacteae, composed of South American and North American genera. Britton and Rose (1922) classified *Echinocereus* in the subtribe Echinocereinae, while Berger (1926) placed it in the Nyctocerei group within the tribe Cereeae. Buxbaum (1958) grouped *Echinocereus*, *Bergerocactus* Britton & Rose, *Machaerocereus* Britton & Rose, *Rathbunia* Britton & Rose, and *Wilcoxia* Britton & Rose in the tribe Echinocereeae based on their cylindrical or globose stems and their diurnal flowers with scales and spines on the pericarpel and receptacular tube. Phylogenetic analyses derived from molecular data suggest that *Echinocereus* is in tribe Pachycereeae (sensu Gibson and Horak, 1978; Echinocereeae sensu Hunt et al. 2006) and sister to the clade composed of *Escontria* Rose, *Myrtillocactus* Console, *Polaskia* Backeb., and *Stenocereus* (A. Berger) Riccob. (Wallace 2002; Wallace and Gibson 2002; Arias et al. 2005; Hernández-Hernández et al. 2011).

The circumscription of *Echinocereus* has changed since it was described by Engelmann (1848). This genus was originally thought to include species in both North and South America (Lemaire 1868; Rümpler 1886), but Schumann (1899) later defined the genus as being limited to North America. Subsequently, Purpus (1908) transferred *Cereus pensilis* K. Brandegee to *Echinocereus* based on flower similarity. Britton and Rose (1909) separated *E. poselgeri* Lem. as the genus *Wilcoxia* Britton & Rose, but agreed with Purpus's proposal and retained *E. pensilis* in *Echinocereus* (Britton and Rose 1922). In contrast, Rowley (1974) separated *E. pensilis* (K. Brandegee) J. A. Purpus and proposed the monotypic genus *Morangaya* G.D. Rowley. The recognition of *Morangaya* and *Wilcoxia* as independent genera has been supported by various authors (Moran 1977; Bravo-Hollis 1978; Bravo-Hollis and Sánchez-Mejorada 1991). However, Taylor (1985) recognized them as sections of *Echinocereus*, a proposal that has been accepted in recent literature (Blum et al. 1998; Anderson 2001; Guzmán et al. 2003; Hunt et al. 2006). The generic circumscription proposed by Taylor (1985) was corroborated by phylogenetic analysis (Wallace and Fourquer 1995) inferred from restriction enzymes and few taxa, where *E. pensilis* was recovered as the sister taxon to the remaining *Echinocereus* species. Recently, using a single marker (*trnK-matK*), Bárcenas et al. (2011) recovered *E. pensilis* as related to *Stenocereus*, *Polaskia*, *Myrtillocactus*, and *Escontria*. Finally, using *rpl16* and *trnL-F*, Barba (2012) recovered *E. pensilis* as a member of *Echinocereus*.

The recognition and comparison of the morphological diversity of *Echinocereus* have generated various infrageneric classification proposals since the end of the 19th century (Table 1). With a reduced sample, Miller (1988) analyzed the systematic value of the floral pigments in *Echinocereus*; however, he concluded that these characters only allow close species from certain sections to be grouped (sensu Taylor 1985). Presently, there are no studies that confirm whether the infrageneric entities proposed for *Echinocereus* are monophyletic (Bárcenas et al. 2011). Within this context, the most recent treatment of Cactaceae (Hunt et al. 2006) included 65 species of *Echinocereus* in eight sections (Table 1). This classification, based on morphological comparisons, represents a useful hypothesis to test the monophyly of the genus and sections proposed through phylogenetic analysis of a large number of molecular characters.

Phylogenetic studies based on molecular characters have contributed to the classification of subfamilies, tribes and genera of Cactaceae (Butterworth et al. 2002; Nyffeler 2002; Arias et al. 2003; Crozier 2004; Arias et al. 2005; Edwards et al. 2005; Ritz et al. 2007; Griffith and Porter 2009; Hernández-Hernández et al. 2011; Bárcenas et al. 2011;

Fig. 1. Morphology of selected *Echinocereus* species based on sections proposed by Hunt et al. (2006) (Table 1). A. *Echinocereus pensilis* (Sect. *Morangaya*; *Arias 1295*, MEXU). B. *E. engelmannii* (Sect. *Erecti*; *Arias 1813*, MEXU). C. *E. maritimus* (*Arias 1799*, MEXU). D. *E. acifer* (Sect. *Triglochidiati*; *Sánchez 51*, MEXU). E. *E. scheeri* (Sect. *Triglochidiati*; *Sánchez 36*, MEXU). F. *E. stramineus* (Sect. *Costati*; *Arias 2049*, MEXU). G. *E. mapimiensis* (Sect. *Echinocereus*; *Sánchez 84*, MEXU). H. *E. knippelianus* (Sect. *Echinocereus*; *Arias 1938*, MEXU). I. *E. bristolii*; *Arias 1836*, MEXU). J. *E. rigidissimus* (Sect. *Reichenbachii*; *Arias 2021*, MEXU). K. *E. leucanthus* (Sect. *Wilcoxia*; *Arias 2011*, MEXU). L. *E. pulchellus* (Sect. *Pulchellus*; *Arias 1442*, MEXU).

Table 1. Historical infrageneric classification in *Echinocereus*.

Author	Infrageneric entities
Schumann (1899)	Four series: *Graciles* Engelm., *Subinermes* (K. Schum.), *Prostrati* K. Schum., *Erecti* K. Schum.
Taylor (1985, 1988, 1989)	Eight sections: *Morangaya* (G. D. Rowley) N. P. Taylor, *Erecti* (K. Schum.) Bravo, *Costati* (Engelm.) N. P. Taylor, *Echinocereus, Triglochidiati* Bravo, *Reichenbachii* N. P. Taylor, *Wilcoxia* (Britton & Rose) N. P. Taylor, *Pulchellus* N. P. Taylor
Bravo-Hollis and Sánchez-Mejorada (1991)	Six sections: *Subinermes, Scheera* Backeb., *Triglochidiati, Prostrati, Echinocereus, Erecti*
Taylor (1993)	Eight sections: *Morangaya, Erecti, Costati, Echinocereus, Triglochidiati, Reichenbachii, Wilcoxia, Pulchellus*
Blum et al. (1998)	Three subgenera: *Morangaya* (G. D. Rowley) Lange, *Triglochidiati* (Bravo) W. Blum, Mich.Lange & Rutow, *Echinocereus* (seven sections): *Erecti, Costati, Subinermes, Echinocereus, Reichenbachii, Wilcoxia, Pulchellus*
Hunt et al. (2006)	Eight sections: *Morangaya, Erecti, Triglochidiati, Costati, Echinocereus, Reichenbachii, Wilcoxia, Pulchellus*

Vázquez-Sánchez et al. 2013), but studies at the infrageneric level are still scarce (Butterworth and Wallace 2004; Demaio et al. 2011; Korotkova et al. 2011; Majure et al. 2012). This study uses six coding and non-coding chloroplast molecular markers to obtain the best possible resolution at different taxonomic levels. These markers have proven their usefulness in phylogenetic studies within Cactaceae. The *matK* and *rbcL* coding regions, combined with other chloroplast markers, were previously used by Vázquez-Sánchez et al. (2013) to infer the phylogeny of tribe Cacteae. Korotkova et al. (2011) and Calvente (2012) demonstrated the usefulness of the *psbA-trnH* and *trnQ-rps16* intergenic spacers (IGS), in combination with other chloroplast markers, to resolve phylogenetic relationships in *Rhipsalis* (Cactaceae). The *rpl16* intron has been used often in phylogenetic studies of Cactaceae (e.g. Butterworth et al. 2002; Arias et al. 2005), and the region composed of the *trnL* intron and the *trnL-trnF* IGS (referred to here as *trnL-trnF*) has been widely used in phylogenetic reconstruction in Cactaceae due to a high percentage of informative sites (e.g. Nyffeler 2002; Arias et al. 2003, 2005; Edwards et al. 2005).

In addition to including several plastid regions, this study is also the first to include a broad sampling of the species recognized in *Echinocereus* that encompass the morphological variation observed in the genus. Therefore, the objectives of this work are as follows: (1) to test the monophyly of *Echinocereus*, (2) to resolve the relationship between *E. pensilis* and the other Stenocereinae genera (*Escontria, Myrtillocactus, Polaskia, Stenocereus*), and (3) to test whether the infrageneric entities recognized by Hunt et al. (2006) represent natural groups within *Echinocereus*.

Materials and Methods

Taxon Sampling—The *Echinocereus* sampling included representatives from the eight sections recognized by Hunt et al. (2006). We sampled 59 of the 65 species of *Echinocereus* recognized by Hunt et al. (2006), Baker (2006a, 2006b), and Sánchez et al. (2013), as well as 10 representative species of *Escontria, Myrtillocactus, Polaskia,* and *Stenocereus* because a possible relationship with all of these genera was suggested by Arias et al. (2005), Hernández-Hernández et al. (2011), and Bárcenas et al. (2011). The analyses included a total of 81 terminals. The ingroup consisted of 71 individuals; whenever possible, a second sample for each species of *Echinocereus* with two subspecies was included in the phylogenetic analyses (Appendix 1). The functional outgroup consisted of 10 individuals that include representatives of other genera of Echinocereeae and Hylocereeae. The analyses included 459 new DNA sequences of *Echinocereus*, as well as 25 sequences that were previously deposited in GenBank by Arias et al. (2005), Butterworth and Wallace (2005), Hernández-Hernández et al. (2011), and Korotkova et al. (2011). Voucher information and the GenBank accession numbers of the samples used in this study are provided in Appendix 1.

DNA Extraction, Amplification, and Sequencing—Samples from 1 cm^3 stems were silica gel-dried, frozen and pulverized. The extraction was achieved using the DNeasy plant mini kit (Qiagen, Inc., Valencia, California). The total DNA was stored at -20°C. The sequences were PCR-amplified in volumes of 25 μL. The following primers and profiles of thermal cycles were used. For *matK*, we used the primers KIM3F and KIM1R (CBOL Plant Working Group 2009), with a reaction profile of 94°C for 2 minutes; 30 cycles of 94°C for 30 sec, 48°C for 40 sec, and 72°C for 40 sec; and a final extension of 72°C for 7 minutes. For *psbA-trnH*, we used the primers psbA (Sang et al. 1997) and trnH (Tate and Simpson 2003), with a reaction profile of 94°C for 2 minutes; 29 cycles of 94°C for 30 sec, 52°C for 30 sec, and 72°C for 2 minutes; and a final extension of 72°C for 7 minutes. For *rbcL*, we used the primers rbcLA-F and rbcLA-R (CBOL Plant Working Group 2009), with a reaction profile of 94°C for 2 minutes; 29 cycles of 94°C for 1 minute, 48°C for 1 minute, and 72°C for 2 minutes and 30 sec; and a final extension of 72°C for 7 minutes. For *rpl16*, we used the primers rpl161R and rpl163F (Hernández-Hernández et al. 2011), and for *trnL-F* we used the primers c, d, e, and f (Taberlet et al. 1991). For these two markers we used a reaction profile of 94°C for 2 minutes; 30 cycles of 94°C for 1 minute, 50–55°C for 30 sec, and 72°C for 1 minute and 30 sec; and a final extension of 72°C for 7 minutes. Finally, for *trnQ-rps16*, we used the primers trnQ2 and rps16X1 (Korotkova et al. 2010) with a reaction profile of 95°C for 2 minutes; 33 cycles of 95°C for 30 sec, 55°C for 1 minute, and 72°C for 1 minute; and a final extension of 72°C for 10 minutes. The PCR products were sequenced at the High Throughput Genomics Unit at the University of Washington (http://www.htseq.org).

Phylogenetic Analyses—The sequences for each marker were assembled using Sequencher v. 4.8 (Gene Codes Corporation, Ann Arbor, MI, USA). The matrices were pre-aligned with Muscle (Edgar 2004) using MEGA 5 (Tamura et al. 2011) and manually adjusted afterward with Mesquite v. 2.75 (Maddison and Maddison 2010). Insertion-deletion events (indels) were identified (Ochoterena 2009) and coded using the simple coding method proposed by Simmons and Ochoterena (2000). A concatenated matrix including the six markers and indels was created for the phylogenetic analyses. A maximum parsimony (MP) analysis was performed with TNT v. 1.1 (Goloboff et al. 2008), using only parsimony-informative characters from the concatenated matrix. A heuristic search was conducted with 100,000 random-addition sequence replicates, retaining 10 trees from each replicate, exchanging branches using "TBR" (tree-bisection-reconnection). Branch support values were calculated by bootstrap (BS) (Felsenstein 1985) and jackknife (JK) resampling with 10,000 replicates (Farris et al. 1996) following the same search strategy used in the MP analysis with TNT (Goloboff et al. 2008). For the Bayesian analysis (BI), three molecular partitions were generated from the concatenated matrix. DNA evolution models for partitions were estimated using the Akaike information criterion (AIC) in jModelTest v. 0.1.1 (Posada 2008), resulting in a TIM1 + Γ model for the coding marker partition (*matK* and *rbcL*), a GTR + Γ model for the non-coding marker partition (*psbA-trnH*, *rpl16*, *trnL-F*, and *trnQ-rps16*), and an Mkv model (Lewis 2001) for the indels partition. A partitioned BI analysis was performed in MrBayes v. 3.2 (Ronquist and Huelsenbeck 2003) and consisted of two runs of four chains for five million iterations, saving one tree every 100 generations, and beginning with one random tree. The burn-in parameter was fixed at generation 750,000 using Tracer v. 1.5 (Rambaut and Drummond 2007). With the remaining trees, a 50% majority-rule consensus tree was generated. The trees obtained from the MP and BI analyses were edited using FigTree v. 1.3.1 (Rambaut 2009). To identify the contribution of INDELs to the tree resolution and support of branches, we performed additional MP and BI analyses with a concatenated matrix that did not include the previously coded INDELs. Analyses were performed with identical parameters as described above. The combined matrix and trees are available from TreeBASE (study accession number 13983).

Ancestral States Reconstruction—The strict consensus tree from the MP analysis of the concatenated data was used for assessing character evolution in *Echinocereus*. Some of these characters have been used in the most comprehensive taxonomic treatments (Taylor 1985, 1988, 1989; Blum et al. 1998) to circumscribe the genus and sections. The character state assignments were based on our field study, the examination of herbarium specimens, and the literature (Moran 1977; Taylor 1985, 1993; Blum et al. 1998; Arias and Terrazas 2006; Vázquez-Sánchez et al. 2012). The following characters were analyzed: 1) growth form: globose, globose-depressed, broadly cylindrical, narrowly cylindrical, and phylloclade; 2) root type: fibrous, taproot, and tuberous; 3) floral bud origin: non-erumpent and erumpent; 4) stigma lobe color: white, pale yellow, and green; and 5) flower shape: funnel-shaped, broadly funnel-shaped, and tubular funnel-shaped. The likelihood ancestral state reconstruction method was implemented in Mesquite v. 2.75 (Maddison and Maddison 2010) using the unordered states assumption and the Mk1 model for discrete morphological characters. This analysis estimates the proportional likelihood (P) of the morphological states on each node of a given topology. The *p* value ranges from 0–1, where a value near 1 is more likely to have been the ancestral state.

Results

Data Matrices—The complete matrix with six markers included 4,995 bases, of which only 305 were parsimony informative. We coded 44 informative INDELs that included single sequence repetitions, deletions, and inversions (Ochoterena 2009). Sequence statistics for each marker are given in Table 2.

Phylogenetic Analyses—The MP analysis that included informative sites and indels had 349 characters and resulted in 36 equally parsimonious trees with a length of 768 steps (Fig. 2). The BI analysis included 5,039 characters including INDELs (Fig. 3). The MP strict consensus and BI majority-rule consensus trees were congruent in their topologies. However, the MP strict consensus tree was less resolved in terms of species relationships than the BI majority-rule consensus tree. The MP strict consensus tree showed a grade for the clades V, VI, and a polytomy between VII, VIII, and IX, while the BI majority-rule consensus tree showed a polytomy for the clades V, VI, VII, and VIII + IX (Figs. 2, 3). Moreover, the position of *E. longisetus* is somewhat uncertain; in the MP strict consensus tree, this species is a poorly supported sister taxon of clades V through IX, while in the BI majority-rule consensus tree, *E. longisetus* plus clade IV are sister to clades V through IX. The MP and BI analyses calculated using the matrix without INDELs resulted in trees with lower branch support (results not shown).

Both the MP and BI consensus trees revealed two significant results. The relationships between *Echinocereus pensilis*, *Escontria*, *Myrtillocactus*, *Polaskia*, and *Stenocereus* are strongly supported (Figs. 2, 3; 97% MP BS / 99% MP JK, 1.00 BI PP). Our results also indicate that *E. pensilis* is sister to *Stenocereus eruca*, *Escontria chiotilla*, *S. montanus*, *S. alamosensis*, *S. pruinosus*, *Polaskia chichipe*, *Myrtillocactus schenckii*, *M. cochal*, and *M. geometrizans*. This clade of 10 species is defined in this work as the *Stenocereus* group.

The remaining species of *Echinocereus* form a well-supported clade (*Echinocereus* s. s.) that is sister to the *Stenocereus* group (Figs. 2, 3; 100% MP BS / 100% MP JK, 1.00 BI PP). Two main groups are recovered within the *Echinocereus* s. s. Group A has 11 taxa with weak to moderate support (<50% MP BS / 52% MP JK, 0.94 BI PP), while group B includes the remaining 49 taxa, supported by <50% MP BS / 62% MP JK, 1.00 BI PP. The affinities of *E. longisetus* are unresolved, as it is the only species that differs in its placement in the MP and BI trees. The nine clades in both groups A and B are well supported in the BI majority-rule consensus tree (Fig. 3); but, in the MP strict consensus tree, the same clades receive from strong (e.g. clade III, 99% MP BS / 99% MP JK; Fig. 2) to weak branch support (e.g. clade IX, 65% MP BS / 70% MP JK; Fig. 2). These nine clades do not correspond to the sections recognized by Hunt et al. (2006), with the exception of clade IX in which all of the species from the *Triglochidiati* section are grouped.

Ancestral States Reconstruction—Parsimony optimization of six morphological characters on the MP consensus tree is shown in Figs. 4 and 5. The narrowly cylindrical growth form is the ancestral state for *Echinocereus* s. s., with a reduction to globose and globose-depressed stems that can be found throughout *Echinocereus* s. s. lineages (Fig. 4A). Fibrous roots are ancestral for *Echinocereus* s. s., whereas taproots have arisen independently six times in *Echinocereus*, one time within group A (*E. knippelianus*) and five within group B (*E. chisosensis*, *E. palmeri*, *E. pulchellus*, *E. schmollii*, and *E. sciurus*) (Fig. 4B). The erumpent origin of the floral bud is an apomorphy of *Echinocereus* s. s.; however, within group A, a reversal occurred in a subclade that includes five species with non-erumpent floral buds (Figs. 4C, 6). Green stigma lobes clearly represent an apomorphy for the *Echinocereus* s. s. clade; this feature has long been diagnostic for this genus (Figs. 1 B–L, 4D). Figure 5 shows the reconstruction of floral shape, where funnel-shaped was inferred to be the plesiomorphic state in *Echinocereus* s. s.

Discussion

Relationships of Echinocereus Within the Subtribe Echinocereinae—The MP and BI topologies confirm that *Echinocereus* s. s. (excluding *E. pensilis*) is sister to the genera comprising the *Stenocereus* group (Figs. 2, 3). The molecular phylogenies inferred here are consistent with Wallace (2002), Arias et al. (2005), Hernández-Hernández et al. (2011), and Bárcenas et al. (2011). Results of these studies are similar to the evolutionary relationships suggested by Berger (1926) and Buxbaum (1958), who recognized a certain "affinity" between *Echinocereus* and *Stenocereus* (e.g. *Machaerocereus*, *Rathbunia*) due to the shared presence of a low columnar growth form and the presence of diurnal flowers with scales and spines on the pericarpel and receptacular tube; however,

Table 2. Summary description of the various datasets and parsimony tree statistics.

	matK	*psbA-trnH*	*rbcL*	*rpl16*	*trnL-F*	*trnQ-rps16*	Combined
Length	800	530	579	1,240	1,191	655	4,995
Constant characters	696	395	483	954	920	515	3,963
Variable characters	104	135	96	286	271	140	1,032
Informative characters	32	44	25	86	80	38	305
% informative characters	4.00	8.30	4.31	6.93	6.71	5.80	6.10
Indels	-	10	2	10	16	6	44

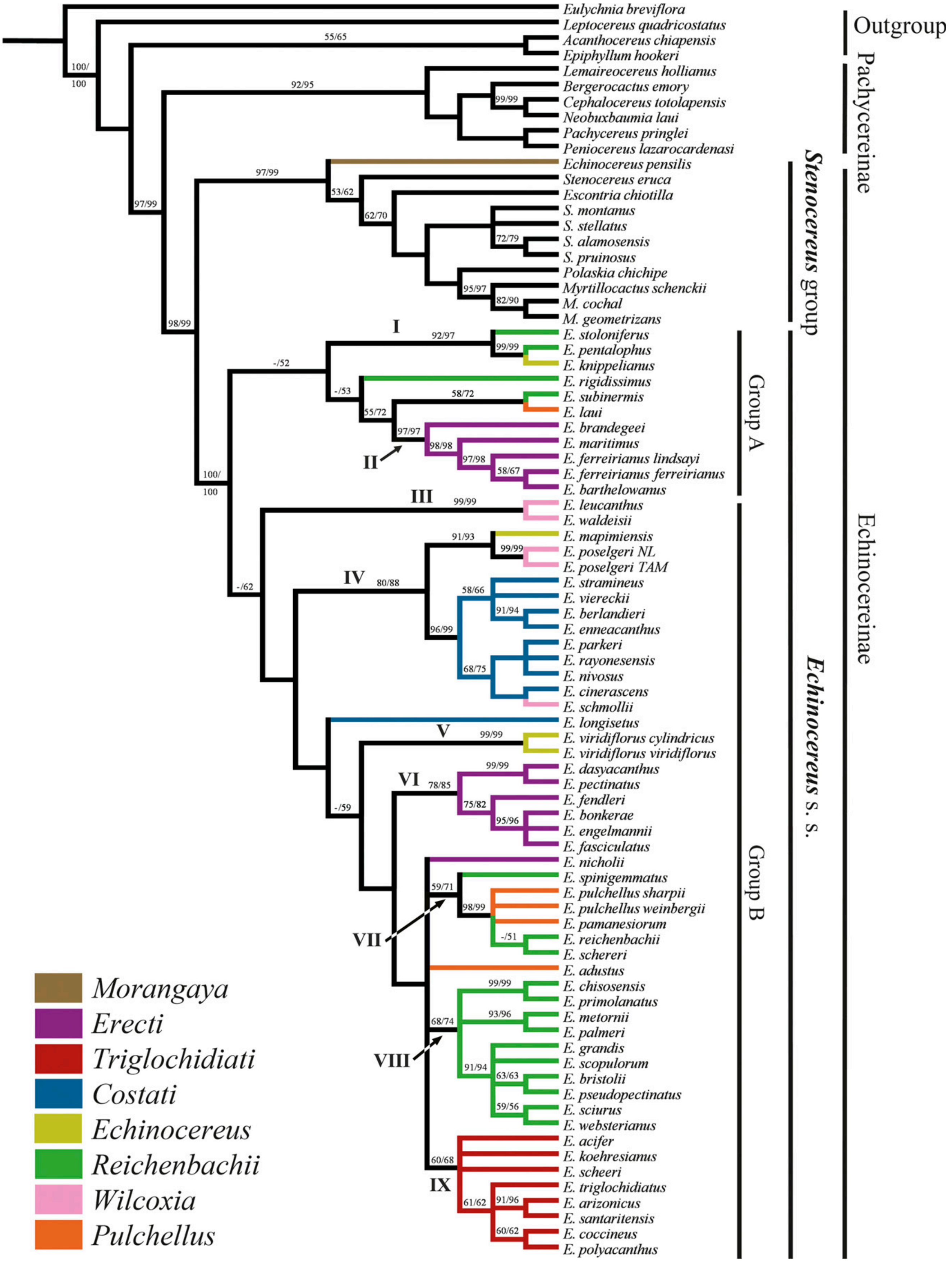

FIG. 2. Strict consensus cladogram of 36 most parsimonious trees resulting from concatenated sequences of *matK*, *rbcL*, *psbA-trnH*, *trnQ-rps16*, *rpl16*, *trnL-F*, and INDELs. Numbers above branches are maximum parsimony bootstrap/jackknife values. Tree length = 774; CI = 0.55; RI = 0.80. Different colors represent sections according to Hunt et al. (2006).

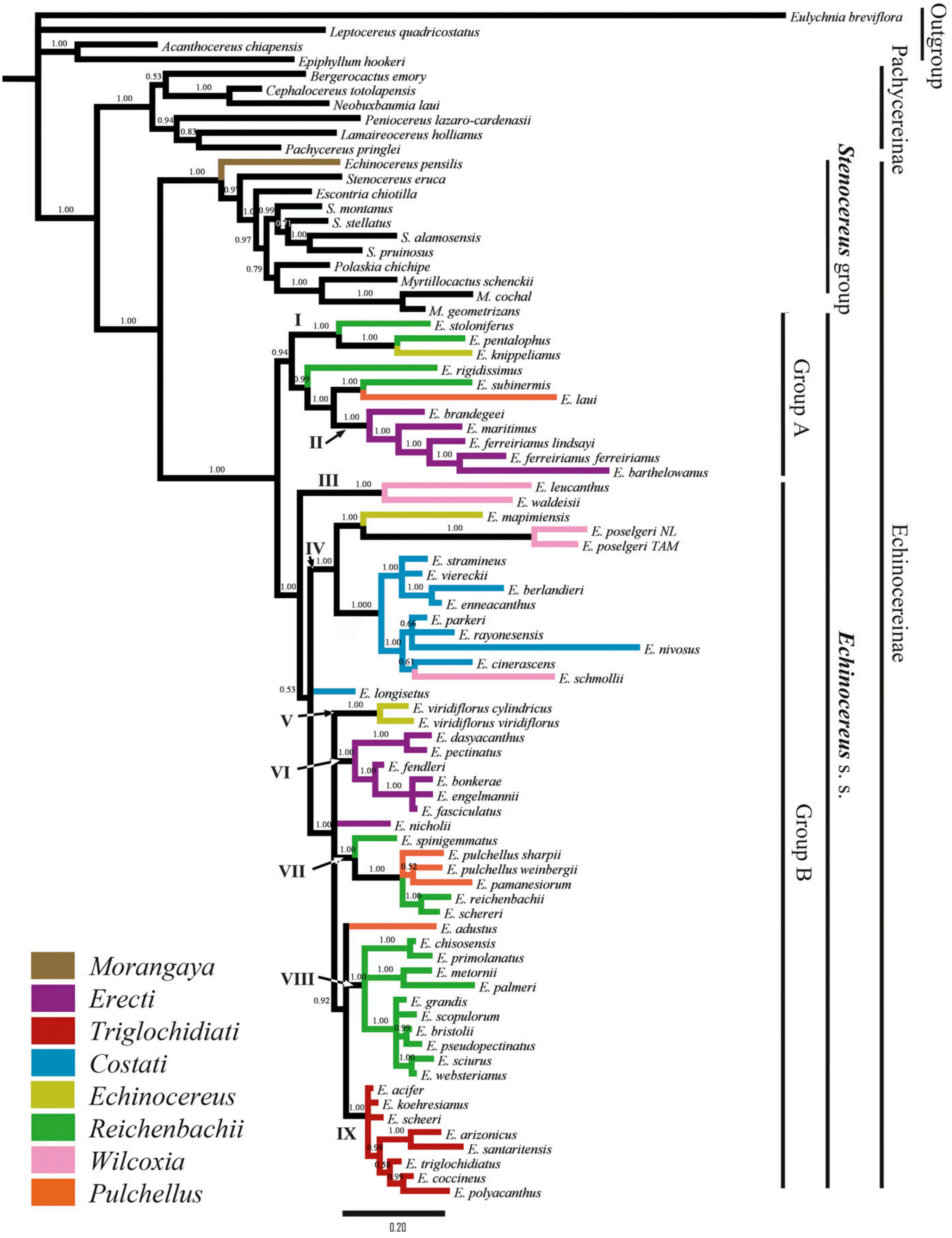

FIG. 3. Majority-rule consensus tree of 42,500 trees resulting from Bayesian analysis of concatenated sequences of *matK*, *rbcL*, *psbA-trnH*, *trnQ-rps16*, *rpl16*, *trnL-F*, and INDELs. Numbers above branches correspond to Bayesian posterior probabilities. Different colors represent sections according to Hunt et al. (2006).

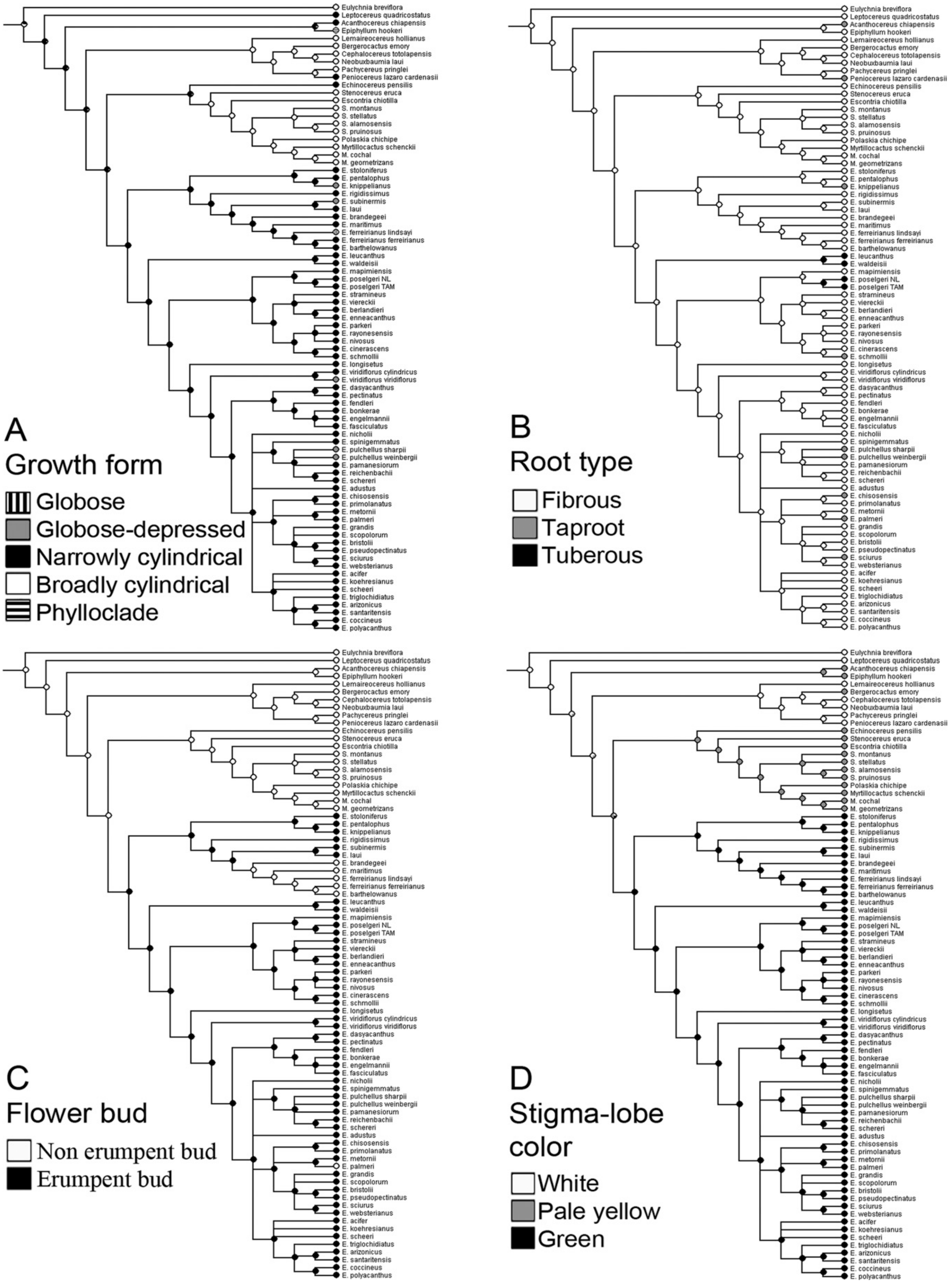

FIG. 4. Likelihood ancestral state reconstruction on the MP strict consensus tree. A: growth form; B: root type; C: type of flower bud; D: stigma lobe color.

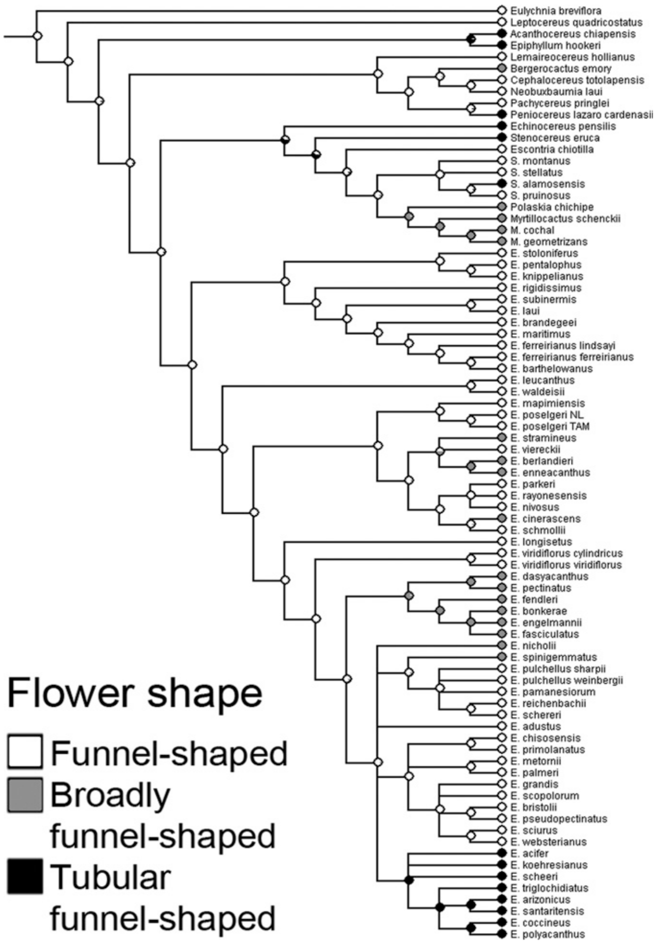

FIG. 5. Likelihood ancestral state reconstruction of flower shape on the MP strict consensus tree.

Berger (1926) and Buxbaum (1958) did not discuss the relationships of *Echinocereus* and *Stenocereus* to the remaining genera. Later, Gibson and Horak (1978) proposed a close relationship for *Escontria, Myrtillocactus, Polaskia*, and *Stenocereus*, based on stem anatomy, triterpene chemistry, and tannins in funicular cells. Anatomical observations (unpublished data) allow us to confirm the presence of tannins (ovules, funicles, and stamens) in all *Echinocereus* species examined. Triterpene chemistry has not been addressed in *Echinocereus*, and its support for the relationships in the *Stenocereus* group remains unconfirmed. Despite this, in accordance with the ICBN principle of priority, the major clade that includes *Echinocereus* s. s. + the *Stenocereus* group is referred to here as subtribe Echinocereinae (Figs. 2, 3).

Echinocereus pensilis and Its Relationships—The placement of *E. pensilis* as sister to the remaining taxa of the *Stenocereus* group is consistent with Bárcenas et al. (2011). However, this phylogenetic relationship differs from the results of Wallace and Fourquer (1995), who suggest that *E. pensilis* is the earliest taxon to diverge within the genus *Echinocereus*. The study by Wallace and Fourquer (1995) included fewer taxa and was based on 12 chloroplast DNA restriction enzymes, while the present study includes a broader sampling of *Echinocereus* and related genera, and includes six chloroplast DNA markers.

Previously, the circumscription and relationships of *E. pensilis* were examined using morphological characters. Rowley (1974) proposed the monotypic genus *Morangaya* for *E. pensilis* (= *Cereus pensilis*), and Moran (1977) argued that *E. pensilis* should be excluded from *Echinocereus* because it does not share the typical characters (e.g. erumpent floral buds and shoots, green stigma lobes; Figs. 1, 6). Moreover, *E. pensilis* has long stems (up to 4 m), may be a climber or low-growing plant, has vestigial leaves at the apex of the stem, exhibits the generation of new spines in both young and old stems, and forms adventitious roots, which do not exist in *Echinocereus* s. s. However, Taylor (1985) considered these to be non-specialized attributes without phylogenetic significance, so this taxon was kept within the genus *Echinocereus*. Our results are consistent with those proposed by Rowley (1974) and Moran (1977), and, therefore, *E. pensilis* should be excluded from *Echinocereus*. In addition, Loza-Cornejo and Terrazas (2003) found that *E. pensilis*, like all of the *Stenocereus* species, have silica bodies. This character was considered to be a synapomorphy for *Stenocereus* and allowed for *Rathbunia* to be incorporated into the genus *Stenocereus* (Taylor and Gibson 1994; Terrazas and Loza-Cornejo 2002). In a phylogenetic analysis of molecular (*rpl16*, *trnL-F*) and morphological characters, Arreola (2006) shows that *E. pensilis* is sister to the rest of the *Stenocereus* species. However, our results are inconclusive with regard to the relationship between *E. pensilis* and the *Stenocereus* group because

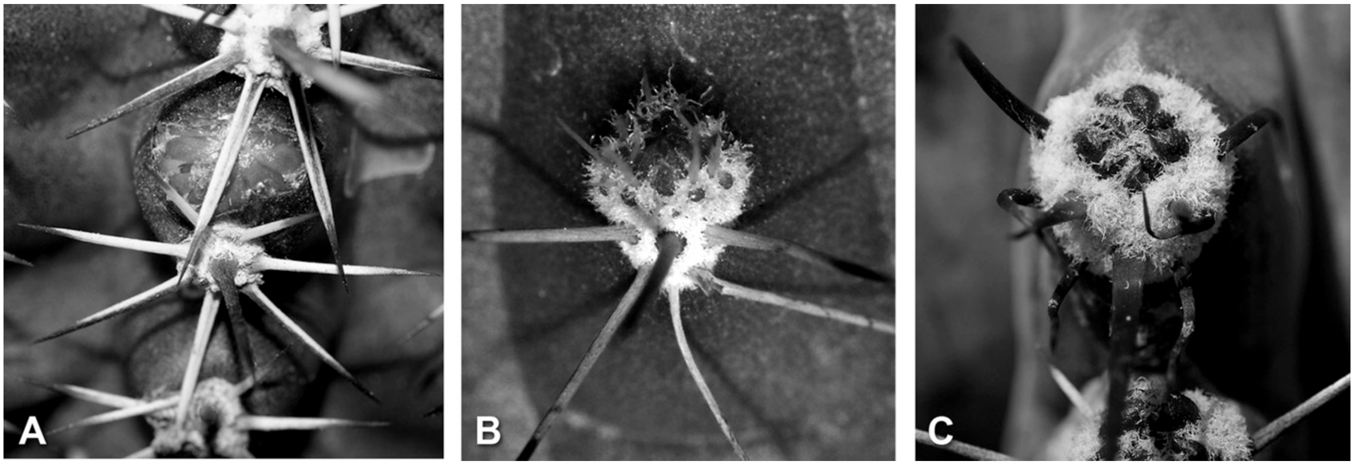

FIG. 6. Floral bud origin in some Echinocereinae species. A. *Echinocereus fendleri* (erumpent; *Arias 2023*). B. *Echinocereus pensilis* (non-erumpent; *Arias 1295*). C. *Stenocereus pruinosus* (non-erumpent; UNAM-*Jardin Botanico C-08–110*).

our sample includes only five of the 29 recognized taxa (Gibson and Nobel 1986; Terrazas and Loza-Cornejo 2002; Arreola 2006). Based on this phylogenetic study and the morphological evidence that has been discussed, we propose excluding *E. pensilis* from *Echinocereus* and re-establishing the monotypic genus *Morangaya* (Rowley 1974) for this taxon.

***Circumscription of Echinocereus* s. s. *and Its Infrageneric Relationships*—**The genus *Echinocereus* may be recognized as monophyletic if *E. pensilis* is excluded. Based on the present study, *Echinocereus* s. s. consists of species that show two main characters: erumpent floral buds (with a reversion in *E. barthelowanus*, *E. brandegeei*, *E. ferreirianus*, and *E. maritimus*, clade II) and green stigma lobes (Britton and Rose 1922; Moran 1977; Taylor 1985; Blum et al. 1998; Hunt et al. 2006). Our results also recovered nine major clades within *Echinocereus* s. s., of which only clade IX represents a named infrageneric entity (section *Triglochidiati*). In the remaining clades, few informal taxonomic groups are recognized according to the infrageneric classification proposed by Taylor (1985, 1988, 1989, 1993) and Blum et al. (1998) (Figs. 2, 3; clades I – IX).

Clade I—This clade containing three species is highly supported (92% MP BS / 97% MP JK, 1.00 BI PP), but does not correspond to any taxonomic section according to Hunt et al. (2006), although *E. stoloniferus* and *E. pentalophus* are part of the *E. subinermis* group of *Reichenbachii* according to Taylor (1993). *Echinocereus stoloniferus and E. pentalophus* subsp. *leonensis* share the presence of subterranean stems (rhizomes), funnel-shaped flowers (Blum et al. 1998), and a receptacular tube with a large quantity of long trichomes. The relationship between *E. pentalophus* and *E. knippelianus* was strongly supported by the molecular characters (99% MP BS / 99% MP JK, 1.00 BI PP). The few (five to seven) broad ribs are potential characters that could have phylogenetic significance. However, the morphology of the *E. knippelianus* flower is different from the rest of the species in the clade. The distribution of these species is disjunct, given that *E. stoloniferus* is found in northwestern Mexico, especially in the Sierra Madre Occidental, while *E. knippelianus* and *E. pentalophus* are native to northeastern and central Mexico, in the Sierra Madre Oriental and the region adjoining the Mexican Plateau.

Clade II—This clade is composed of five species, is highly supported (97% MP BS / 97% MP JK, 1.00 BI PP), and partially belongs to *Erecti* (Hunt et al. 2006). The species in clade II share highly angled, cylindrical stems, flattened central spines, and funnel-shaped flowers (Blum et al. 1998). In addition, in this clade the floral buds emerge as non- erumpent (Fig. 6), which appears to be the ancestral state for this clade (P = 0.992; Fig. 4C). The two subspecies of *E. ferreirianus* do not form a monophyletic group because *E. ferreirianus* subsp. *ferreirianus* is sister to *E. barthelowanus* based on two molecular apomorphies. The placement of these taxa is consistent with Hunt et al. (2006), and, according to Taylor (1985), they share bicolored perianth and pale green stigmas. Therefore, the taxa should be re-evaluated using a comparative study that includes multivariate and molecular analyses to recognize species (e.g. Baker and Butterworth 2013). All of the species that are recovered in this clade are endemic to Baja California and Baja California Sur, Mexico, which allows us to hypothesize that the diversification of the clade began after the Oligocene epoch (30 Ma), at the beginning of the separation and displacement of a southwestern portion of North America, currently the Baja California Peninsula (Ferrusquía-Villafranca, 1998).

Clade III—This clade of *E. leucanthus* and *E. waldeisii* is strongly supported (99% MP BS / 99% MP JK, 1.00 BI PP). Both species share slender stems, tuberous roots, elongated fruit (Taylor 1985, 1989; Blum et al. 1998, 2008; Hunt et al. 2006), and fibrous secondary xylem (Loza-Cornejo and Terrazas 2003). These morphological characters are also present in *E. poselgeri*, which is why they were grouped in *Wilcoxia* (Taylor 1985, 1989, 1993; Blum et al. 1998, 2008; Hunt et al. 2006). In this analysis, *E. poselgeri* is nested within clade IV, suggesting that these characters were acquired independently (e.g. tuberous roots, Fig. 4B). Our results support the proposal by Blum et al. (2008) to recognize *E. waldeisii* as a distinct species from *E. poselgeri* based on their differences in spination and flower color. This clade has a disjunct distribution, given that *E. leucanthus* is endemic to the coastal region of northwestern Mexico (Sinaloa, Sonora), whereas *E. waldeisii* only inhabits a narrow strip of northeastern Mexico (San Luis Potosi, Tamaulipas). Based on the phylogenetic hypothesis and the disjunct distribution, we estimate that this lineage could have experienced early diversification.

Clade IV—This clade of 11 species has moderate support (80% MP BS / 88% MP JK, 1.00 BI PP) and is comprised of two groups. The first includes *E. poselgeri* (with two samples from different locations) and *E. mapimiensis* (91% MP BS / 93% MP JK, 1.00 BI PP), and the second includes the majority of the species from the *Costati* section (Hunt et al. 2006) plus *E. schmollii* (96% MP BS / 99% MP JK, 1.00 BI PP). This result is consistent with the molecular phylogenies presented by Arias et al. (2005), Hernández-Hernández et al. (2011), and Barba (2012) in which *E. poselgeri* is recovered as sister to members of *Costati*. A more detailed analysis of the morphology is required to postulate characters that corroborate the relationship between *E. poselgeri* and *E. mapimiensis*; however, both taxa show similarities in the types of environments where they are found, given that both prefer plains with sandy soils. They also have relatively small seeds (1.0–1.5 mm in length) in comparison to the other taxa in the genus. The remaining *Costati* taxa have erect stems that are generally branched and funnel-shaped or broadly funnel-shaped flowers (Blum et al. 1998) that are fuchsia-colored and turn brown when they are placed in an alcohol-formalin solution (Taylor 1985). In addition, many species in the clade have spines or bristles on the receptacular tube, a character that is also shared by *E. schmollii*. The *E. cinerascens* group, sensu Taylor (1993), is not recovered as monophyletic. Our results confirm that *E. berlandieri*, *E. enneacanthus*, *E. stramineus*, and *E. viereckii* form a monophyletic group, and this relationship is consistent with studies by Moore (1967) and, in particular, Miller (1988) that recover *E. enneacanthus* and *E. stramineus* as sister taxa. The taxa from this clade are widely distributed in Mexico (Hidalgo, Querétaro, Guanajuato, San Luis Potosi, Zacatecas, Durango, Nuevo León, Tamaulipas, Coahuila, and Chihuahua) and the U. S. A. (New Mexico, Texas).

Clade V—This clade represents a group of two subspecies of *E. viridiflorus* (99% MP BS / 99% MP JK, 1.00 BI PP) included in the section *Echinocereus* (Hunt et al. 2006; Blum et al. 2012) (Figs. 2, 3). Although Hunt et al. (2006) consider the two taxa that were recovered in this clade to be subspecies of *E. viridiflorus*, they can be recognized as separate species, as proposed by Blum et al. (2012), because the size and shape of the stem, number of ribs, and spination are different. In addition, *E. viridiflorus* subsp. *viridiflorus* has two molecular autapomorphies, whereas *E. viridiflorus* subsp.

cylindricus has three autapomorphies. Both taxa share small (3 cm long) funnel-shaped flowers that are yellow with brown borders (Blum et al. 1998). *Echinocereus chloranthus* and *E. russanthus* could not be included in this analysis, but they do share certain significant morphological characters with the two taxa in clade V, such as the shape and variation in flower color; therefore, we predict that they belong to this clade. The distribution of both taxa in clade V extends from Mexico (Chihuahua, Coahuila) to the U. S. A. (Colorado, Kansas, New Mexico, and Texas).

Clade VI—Six species with moderate support (78% MP BS / 85% MP JK, 1.00 BI PP) are grouped and partially represent the section *Erecti* (Hunt et al. 2006). This clade is made up of *E. engelmannii*, *E. fasciculatus*, the *E. fendleri* group (*E. bonkerae* and *E. fendleri*; Blum et al. 1998), and the *E. pectinatus* group (*E. dasyacanthus* and *E. pectinatus*; Blum et al. 1998). The species in this clade have erect stems and broad, funnel-shaped flowers, a thick and rigid receptacular tube with few trichomes, as well as fleshy, slightly protruding tepals at the base (Taylor 1985; Blum et al. 1998). The inclusion of *E. engelmannii* in this clade is also supported by the presence of certain floral pigments that it shares with *E. fendleri* (Miller 1988). However, our results do not confirm the proposal by Taylor (1993) and Blum et al. (1998) who suggested a close relationship between *E. engelmannii*, *E. brandegeei*, *E. barthelowanus*, *E. ferreirianus*, and *E. maritimus* (clade II). The phylogenetic position of *E. nicholii* from section *Erecti* is uncertain in our analyses. Taylor (1985) considered it a subspecies of *E. engelmannii*, which is inconsistent with our results. Interestingly, Parfitt (1987) recognizes *E. nicholii* as an independent species because it has a different ploidy level, pale pink flowers, and small seeds with distinctive papillae. The taxa in clade VI are widely distributed across northern Mexico (San Luis Potosi and Tamaulipas to Sonora and Baja California) and the U. S. A. (Texas to California).

Clade VII—This clade contains six taxa with varying levels of support (59% MP BS / 71% MP JK, 1.00 BI PP). It partially includes the *Reichenbachii* and *Pulchellus* sections. *Echinocereus spinigemmatus* is recovered as sister to the remaining taxa, which form a group with higher support (98% MP BS / 99% MP JK, 1.00). The similarity and possible relationship between these two sections and *Wilcoxia* (clades III, IV; Figs. 2, 3) were mentioned by Taylor (1993) and Blum et al. (1998), although without much evidence. The species included in clade VII (except *E. spinigemmatus*) have erect stems, funnel-shaped flowers, a nectary that is generally less than 1 mm long, flexible and slender tepals, and fruits with little pulp, which are dry when mature. The placement of *E. rigidissimus* between clades I and II (group A), is surprising, as it has the short cylindrical stem, linear-elliptic areoles, pectinate radial spines, funnel-shaped flower, thin and bicolored perianth segments of the *E. reichenbachii* group (sensu Taylor, 1985). On the other hand, the two subspecies of *E. pulchellus* analyzed here are placed in clade VII, but share two molecular autapomorphies that could suggest a rapid lineage diversification within this species. Therefore, a re-evaluation of the four subspecies currently included in *E. pulchellus* (sensu Hunt et al. 2006) should be conducted, including specimens from distinct populations and combining morphometric and nuclear DNA analyses. The species that make up this clade are mainly distributed in Mexico (Oaxaca to Coahuila and Nuevo León) and extend into the U. S. A. (Colorado to Texas).

Clade VIII—This clade is made up of ten species that have medium to strong support (68% MP BS / 74% MP JK, 1.00 BI PP); these species were all previously placed in section *Reichenbachii* (Hunt et al. 2006). Blum et al. (1998) recognized the informal *E. sciurus* group with six species (*E. bristolii*, *E. grandis*, *E. pseudopectinatus*, *E. sciurus*, *E. scopolorum*, and *E websterianus*), which is maintained as a monophyletic group with strong support (91% MP BS / 94% MP JK, 1.00 BI PP). The species in clade VIII are distinguished by their short stems, which branch very rarely, areoles with short and numerous spines, funnel-shaped flowers, flexible and slender tepals, a nectary between 1–4 mm long, and seeds that are 1–1.5 mm in length (Taylor 1985; Blum et al. 1998). These species are mainly distributed in a wide swath between northern and northwestern Mexico (Coahuila to Sonora and Baja California Sur), extending into contiguous zones in the southern U. S. A. (Texas to Arizona). In particular, the *E. sciurus* group mentioned above appears to have diversified in the Sonoran Desert, including the islands of the Gulf of California.

Clade IX—This clade includes all of the species that were classified in *Triglochidiati* (Hunt et al. 2006), although it is recovered with varying levels of support (60% MP BS / 68% MP JK, 1.00 BI PP). The number of species included in this section differs in each study (Taylor 1993; Blum et al. 1998), but our previous results support the recognition of nine species, six of which are present in Mexico (Sánchez et al. 2013) and five in the U. S. A. (Baker 2006b). This section includes species with basal branching and red, tubular and funnel-shaped flowers, a receptacular tube that is as long as or longer than the perianth, and internal stamens that are longer than the external stamens (Bravo-Hollis 1973; Blum et al. 1998; Sánchez et al. 2013). In addition, the species in this clade consistently share the hummingbird pollination syndrome, as suggested by Taylor (1985) and Cota (1993). Bravo-Hollis and Sánchez-Mejorada (1991) divide the members of this clade into two sections, *Triglochidiati* and *Scheera*, mainly based on the flower tube length; however, our results do not allow these groups to be recognized. According to the evolutionary hypothesis put forth by Blum et al. (1998), *E. scheeri* retains the highest number of plesiomorphic attributes, while *Triglochidiati* represents the sister group of the rest of the *Echinocereus* species. However, our results reveal that group A (clades I and II) is the earliest diverging clade within *Echinocereus*. The species in clade IX are generally distributed in high elevation and temperate regions from west to northwest and northern Mexico (Guanajuato and Jalisco to Chihuahua and Baja California), as well as in central, south, and southwestern U. S. A. (from Wyoming to Texas and California).

***Ancestral State Reconstruction in Echinocereus* s. s.**—The characters evaluated here are the most distinctive for delimiting taxonomic groups within *Echinocereus* s. s. With regard to growth form (Figs. 1, 4A), *Echinocereus* s. s. can vary from globose, globose-depressed to narrowly cylindrical (Bravo-Hollis and Sánchez-Mejorada 1991; Hunt et al. 2006). The ancestral state reconstruction shows that the narrowly cylindrical growth form is ancestral in the genus (P = 0.998). Additionally, this study shows that there is a tendency toward reducing the cylindrical stem in several lineages within *Echinocereus* s. s., given that most of the species have stems of less than 30 cm in length. In group A, the short stem evolved to globose (e.g. *E. ferreirianus* subsp. *lindsayi*) and globose-depressed (e.g. *E. knippelianus*; Fig. 1H), as also occurred in group B (e.g. *E. viridiflorus* subsp. *viridiflorus* and *E. pulchellus*; Fig. 1L).

According to Taylor (1985), the tuberous root is a character shared by three species of section *Wilcoxia* (*E. leucanthus*, *E. waldeisii*, and *E. poselgeri*), but, interestingly, the analyses presented here show that *Wilcoxia* is not a monophyletic group; therefore, tuberous roots are homoplasious, while taproots appear to have evolved independently in clades I (*E. knippelianus*), IV (*E. schmollii*), VII (*E. pulchellus*), and VIII (*E. chisosensis*, *E. palmeri*, and *E. sciurus*) as a strategy to store reserves. Our analysis shows that both the tuberous root and the taproot evolved from the fibrous root (Fig. 4B) ($P = 0.999$).

In the majority of cacti, floral buds appear in the upper section of the areole (Gibson and Nobel 1986), but Britton and Rose (1922) and subsequently Taylor (1985), Bravo-Hollis and Sánchez-Mejorada (1991), Blum et al. (1998), and Hunt et al. (2006) argue that in *Echinocereus* they are erumpent, breaking the epidermis above the areole.

We found that erumpent flower buds represent the ancestral state in *Echinocereus* s. s. ($P = 0.977$), with a reversal to non-erumpent floral buds in the species in clade II (*E. maritimus*, *E. brandegeei*, *E. ferreirianus*, and *E. barthelowanus*, Fig. 4C). Taylor (1985) had already recognized the existence of this same group of species (clade II), which maintains "primitive" characteristics in the development of the floral and shoot buds. The adaptive significance of erumpent flower buds is not completely clear, but this trait may protect the buds from damage caused by low temperatures when *Echinocereus* evolved in regions with constant frost and temperatures below 0°C in the winter. However, further research is needed to understand the ontogenetic processes involved in this modification and its relationship to protection at lower temperatures (Sánchez et al. in mss.).

Stigma lobes in cacti are usually colored and have a papillose texture. The green color is a synapomorphy for *Echinocereus* s. s. (Fig. 4D, $p = 0.988$). It has been documented that green stigma lobes are practically invariant within *Echinocereus* s. s. (Cota 1993); however, it is possible to observe variation in green tones in certain species (e.g. *E. adustus*, *E. ferreirianus*, and *E. knippelianus*).

Our results showed that the ancestral floral form was funnel-shaped (Fig. 5, $p = 0.994$) and that the remaining character states were derived from there (Fig. 5). This hypothesis is contrary to the one put forth by Blum et al. (1998), which suggested that the plesiomorphic character in *Echinocereus* is the tubular funnel-shaped flower. The broadly funnel-shaped flower appears to have evolved independently in clades IV (e.g. *E. stramineus*, Fig. 1F) and VI (e.g. *E. engelmannii*, Fig. 1B), wherein it turned out to be the ancestral state. The tubular funnel-shaped flower appeared only once in *Echinocereus* s. s. and represents the ancestral state of clade IX ($P = 0.999$) (e.g. *E. acifer* and *E. scheeri*, Fig. 1D, E). The funnel-shaped flower in *Echinocereus* is associated with a generalist pollination syndrome (Cota 1993), and, therefore, the shifts to another character state reflect a specialization tendency toward a certain pollination syndrome, for example, hummingbird pollination in *Triglochidiati* (clade IX). For this analysis, we only coded the general shape of the flower; however, there are changes in flower length, receptacular tube thickness, stamen length, and nectary length that provide greater diversity than the general shapes that are recognized here. A careful study of the morphological changes that are mentioned here and an exploration of their relationship with pollinators are in progress.

We conclude that the inclusion of a greater number of cpDNA markers generated a more robust hypothesis of phylogenetic relationships in *Echinocereus* s. l., allowing us to re-define the generic limits of *Echinocereus* s. s. and clarify its relationship with the *Stenocereus* group, which is best treated as part of an expanded Echinocereinae. By excluding *Echinocereus pensilis*, the generic delimitation of *Echinocereus* s. s. is supported by two morphological characters (erumpent flower buds and green stigma lobes). This study has also provided new insights into relationships within *Echinocereus* s. s., as most of the nine clades are robust. Section *Triglochidiati* was recovered as a monophyletic group, while the *Costati*, *Echinocereus*, *Erecti*, *Pulchellus*, *Reichenbachii*, and *Wilcoxia* sections must be re-circumscribed based on these results. A more thorough morphological revision will identify characters that will be useful for re-defining sections within *Echinocereus* s. s. It is also important to consider particular evolutionary factors that might influence the present phylogenetic hypothesis. Thus, it will be necessary to use nuclear DNA markers to confirm the relationships of taxa with uncertain positions (e.g. *E. longisetus*, *E. adustus*, and *E. nicholii*) and explore the possible hybrid origins of certain species (e.g. *E. laui*, *E. poselgeri*, and *E. schmollii*). Additional chromosome counts are also needed to better understand ploidy differences between taxa (e.g. diploid *E. arizonicus*, tetraploid *E. coccineus*, and hexaploid *E. yavapaiensis* in *Triglochidiati*; Baker 2006a, 2006b).

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APPENDIX 1. List of accessions sampled in this study, presented in alphabetical order, and following this format: Species, Provenance, Voucher (HERBARIUM ACRONYM), and Gen Bank numbers in the following order: matK/ rbcL/ psbA-trnH/ rpl16/ trnL-F/ trnQ-rps16. A dash (–) indicates that the locus was not sequenced for that specimen. Living voucher specimens are identified by their specimen number in cultivation at the Boon Botanical Garden (BBG), Desert Botanical Garden (DBG), and Huntington Botanical Gardens (HBG). Vouchers were collected in Mexico unless otherwise noted.

Acanthocereus chiapensis Bravo. Chiapas: *Guzmán 949* (MEXU) –/ KF783472/ KF783477/ DQ099985/ DQ099916/ KF783769; Chiapas: *Gómez 2100* (MEXU) HM041754/ –/ –/ –/ –/ –. ***Bergerocactus emoryi*** (Engelm.) Britton & Rose. Baja Cal.: *Arias 1307* (MEXU) KF783776/ KF783402/ KF783478/ DQ09999/ DQ099925/ KF783697. ***Cephalocereus totolapensis*** (Bravo & T. MacDoug.) Buxb. Oaxaca: *Terrazas 806* (CHAPA) KF783777/ KF783855/ KF783479/ KF783557/ KF783627/ KF783698. ***Echinocereus acifer*** (Otto ex Salm-Dyck) Jacobi. Zacatecas: *Sánchez 21* (MEXU) KF783779/ KF783404/ KF783480/ KF783559/ KF783629/ KF783700. ***Echinocereus adustus*** Engelm. Chihuahua: *Sánchez 23* (MEXU) KF783825/ KF783450/ KF783481/ KF783604/ KF783674/ KF783746. ***Echinocereus arizonicus*** Rose ex Orcutt. Chihuahua: *Sánchez 44* (MEXU) KF783780/ KF783405/ KF783482/ KF783560/ KF783630/ KF783701. ***Echinocereus barthelowanus*** Britton & Rose. Baja Cal. S.: *Sánchez-Mejorada 4393* (MEXU) KF783846/ KF783473/ KF783532/ KF783621/ KF783691/ KF783770. ***Echinocereus berlandieri*** (Engelm.) Haage. Nuevo León: *Arias 1454* (MEXU) KF783781/ / KF783406/ KF783483/ KF783561/ KF783631/ KF783702. ***Echinocereus bonkerae*** Thornber & Bonker. DBG 1991.0375, cult.: KF783782/ KF783407/ KF783484/ KF783567/ KF783632/ KF783703. ***Echinocereus brandegeei*** (J. M. Coult.) K. Schum. Baja Cal. S.: *Arias 1823* (MEXU) KF783783/ KF783408/ KF783485/ KF783562/ KF783633/ KF783704. ***Echinocereus bristolii*** W. T. Marshall. DBG 1994.0679, cult.: KF783784/ KF783409/ KF783486/ KF783563/ KF783634/ KF783705. ***Echinocereus chisosensis*** W. T. Marshall. Durango: *Sánchez 87* (MEXU) KF783848/ KF783475/ KF783534/ KF783623/ KF783693/ KF783772. ***Echinocereus cinerascens*** (D. C.) Lem. Hidalgo: *Arias 1732* (MEXU) KF783786/ KF783411/ KF783488/ KF783565/ KF783636/ KF783707. ***Echinocereus coccineus*** Engelm. Chihuahua: *Sánchez 64* (MEXU) KF783787/ KF783412/ KF783489/ KF783566/ KF783637/ KF783708. ***Echinocereus dasyacanthus*** Engelm. Chihuahua: *Sánchez 63* (MEXU) KF783788/ KF783413/ KF783490/ KF783568/ KF783638/ KF783709. ***Echinocereus engelmannii*** **(**Parry ex Engelm.) Lem. Baja Cal.: *Arias 1813* (MEXU) KF783789/ KF783414/ KF783491/ KF783570/ KF783639/ KF783710. ***Echinocereus enneacanthus*** Engelm. Durango: *Sánchez 74* (MEXU) KF783790/ KF783415/ KF783492/ KF783573/ KF783640/ KF783711. ***Echinocereus fasciculatus*** (Engelm. ex S. Watson) L. D. Benson. U. S. A. Arizona: *Anderson 6186* (DES) KF783791/ KF783416/ KF783493/ KF783571/ KF783641/ KF783712. ***Echinocereus fendleri*** (Engelm.) Rümpler. Sonora: *Arias 2031* (MEXU) KF783792/ KF783417/ KF783494/ KF783572/ KF783642/ KF783713. ***Echinocereus ferreirianus*** subsp. ***ferreirianus*** H. E. Gates. Baja Cal.: *Lindsay* s. n. (DES) KF783793/ KF783418/ KF783495/ KF783574/ KF783643/ KF783714. ***Echinocereus ferreirianus*** subsp. ***lindsayi*** (J.Meyrán) N. P. Taylor. Baja Cal.: *Arias 1814* (MEXU) KF783794/ KF783419/ KF783496/ KF783575/ KF783644/ KF783715. ***Echinocereus grandis*** Britton & Rose. Baja Cal.: *López* s.n. (MEXU) KF783795/ KF783420/ KF783497/ KF783576/ KF783645/ KF783716. ***Echinocereus knippelianus*** Liebner. Nuevo León: *Arias 2127* (MEXU) KF783796/ KF783421/ KF783498/ KF783577/ KF783646/ KF783717. ***Echinocereus koehresianus*** (G. Frank) W. Rischer. Sinaloa: *Sánchez 14* (MEXU) KF783797/ KF783422/ KF783499/ KF783578/ KF783647/ KF783718. ***Echinocereus laui*** G. Frank. Sonora: *Sánchez 33* (MEXU) KF783826/ KF783451/ KF783500/ KF783605/ KF783675/ KF783747. ***Echinocereus leucanthus*** N. P. Taylor. Sonora: *Terrazas 410* (MEXU) KF783827/ KF783452/ KF783501/ DQ100001/ DQ099932/ KF783748. ***Echinocereus longisetus*** (Engelm.) Lem. Coahuila: *Guzmán 1501* (MEXU) KF783798/ KF783423/ KF783502/ KF783579/ KF783648/ KF783719. ***Echinocereus mapimiensis*** Anderson. Durango: *Sánchez 84* (MEXU) KF783849/ KF783858/ KF783535/ KF783624/ KF783694/ KF783773. ***Echinocereus maritimus*** (M. E. Jones) K. Schum. Baja Cal. S.: *Arias 1804* (MEXU) KF783799/ KF783424/ KF783503/ KF783580/ KF783649/ KF783720. ***Echinocereus metornii*** G. Frank. Coahuila: *Sánchez 83* (MEXU) KF783851/ KF783476/ KF783536/ KF783626/ KF783696/ KF783775. ***Echinocereus nicholii*** (L. D. Benson) B. D. Parfitt. Sonora: *Arias 2029* (MEXU) KF783800/ KF783425/ KF783504/ KF783581/ KF783650/ KF783721. ***Echinocereus nivosus*** Glass & R. A. Foster. Coahuila: *Sánchez 88* (MEXU) KF783854/ KF783457/ KF783537/ KF783608/ KF783678/ KF783752. ***Echinocereus palmeri*** Britton & Rose. Chihuahua: *Sánchez 66* (MEXU) KF783801/ KF783426/ KF783505/ KF783582/ KF783651/ KF783722. ***Echinocereus pamanesiorum*** A. B. Lau. Zacatecas: *Arias 1879* (MEXU) KF783802/ KF783427/ KF783506/ KF783583/ KF783652/ KF783723. ***Echinocereus parkeri*** N. P. Taylor. San Luis Potosí: *Arias 2122* (MEXU) KF783803/ KF783428/ KF783507/ KF783584/ KF783653/ KF783724. ***Echinocereus pectinatus*** (Scheidw.) Engelm. San Luis Potosí: *Arias 1918* (MEXU) KF783804/ KF783429/ KF783508/ KF783569/ KF783654/ KF783725. ***Echinocereus pensilis*** (K. Brandegee) J. A. Purpus. Baja Cal. S.: *Arias 1295* (MEXU) KF783832/ KF783458/ KF783538/ KF783609/ KF783679/ KF783753. ***Echinocereus pentalophus*** (DC) Lem. Querétaro: *Arias 1737* (MEXU) KF783778/ KF783403/ KF783509/ KF783558/ KF783628/ KF783699. ***Echinocereus polyacanthus*** Engelm. Chihuahua: *Sánchez 24* (MEXU) KF783805/ KF783430/ KF783510/ KF783585/ KF783655/ KF783726. ***Echinocereus poselgeri*** Lem. Tamaulipas: *Arias 2000* (MEXU) KF783828/ KF783453/ KF783539/ KF783606/ KF783676/ KF783749. ***Echinocereus poselgeri*** Lem. Nuevo León: *Arias 1452* (MEXU) KF783829/ KF783454/ KF783540/DQ100004/ DQ099935/ -. ***Echinocereus primolanatus*** Fritz Shwarz ex N. P. Taylor. Coahuila: *Arias 1959* (MEXU) KF783806/ KF783431/ KF783511/ KF783586/ KF783656/ KF783727. ***Echinocereus pseudopectinatus*** (N. P. Taylor) N. P. Taylor. DBG 1994.0680, cult.: KF783807/ KF783432/ KF783512/ KF783587/ KF783657/ KF783728. ***Echinocereus pulchellus*** (Mart.) C. F. Först ex F. Seitz. Nuevo León: *Arias 1442* (MEXU) KF783808/ KF783433/ KF783513/ KF783588/ KF783658/ KF783729. ***Echinocereus pulchellus*** subsp. ***weinbergii*** (Weing.) N. P. Taylor. Zacatecas: *Sánchez 08* (MEXU) KF783809/ KF783434/ KF783514/ KF783589/ KF783659/ KF783730. ***Echinocereus rayonesensis*** N. P. Taylor. Nuevo León: *Arias 1947* (MEXU) KF783810/ KF783435/ KF783515/ KF783590/ KF783660/ KF783731. ***Echinocereus reichenbachii*** (Terscheck ex Walp.) Haage. Coahuila: *Arias 1956* (MEXU) KF783811/ KF783436/ KF783516/ KF783591/ KF783661/ KF783732. ***Echinocereus rigidissimus*** (Engelm.) Haage. Sonora: *Arias 2019* (MEXU) KF783812/ KF783437/ KF783517/ KF783592/ KF783662/ KF783733. ***Echinocereus santaritensis*** W. Blum & Rutow. U. S. A. Arizona: *Baker 13810* (DES) KF783813/ KF783438/ KF783518/ KF783593/ KF783663/ KF783734. ***Echinocereus scheeri*** (Salm-Dyck) Scheer. Chihuahua: *Sánchez 36* (MEXU) KF783814/ KF783439/ KF783519/ KF783594/ KF783664/ KF783735. ***Echinocereus schereri*** G. Frank. Durango: *Sánchez 72* (MEXU) KF783815/ KF783440/ KF783520/ KF783595/ KF783665/ KF783736. ***Echinocereus schmollii*** (Weing.) N. P. Taylor. Querétaro: *Arias 91* (MEXU) KF783831/ KF783456/ KF783521/DQ100005/ D099936/ KF783751. ***Echinocereus sciurus*** (K. Brandegee) Dams. Sinaloa: *Arias 1836* (MEXU) KF783785/ KF783410/ KF783487/ KF783564/ KF783635/ KF783706. ***Echinocereus scopulorum*** Britton & Rose. Sonora: *Arias 2017* (MEXU) KF783816/ KF783441/ KF783522/ KF783596/ KF783666/ KF783737. ***Echinocereus spinigemmatus*** A. B. Lau. Jalisco: *Arias 1874* (MEXU) KF783817/ KF783442/ KF783523/ KF783597/ KF783667/ KF783738. ***Echinocereus stoloniferus*** W. T. Marshall. Chihuahua: *Sánchez 32* (MEXU) KF783818/ KF783443/ KF783524/ KF783598/ KF783668/ KF783739. ***Echinocereus stramineus*** (Engelm.) Engelm. ex F. Seitz. Chihuahua: *Arias 2049* (MEXU) KF783819/ KF783444/ KF783525/ KF783599/ KF783669/ KF783740. ***Echinocereus subinermis*** (Salm-Dyck) Scheer. Sinaloa: *Guzmán 1312* (MEXU) KF783820/ KF783445/ KF783526/ KF783600/ KF783670/ KF783741. ***Echinocereus triglochidiatus*** Engelm. U. S. A. Arizona: *Earle* s.n. (DES), KF783821/ KF783446/ KF783527/

DQ100006/ DQ099937/ KF783742. ***Echinocereus viereckii*** Werderm. Tamaulipas: *Arias 1996* (MEXU) KF783822/ KF783447/ KF783528/ KF783601/ KF783671/ KF783743. ***Echinocereus viridiflorus*** Engelm. subsp. ***viridiflorus***. U. S. A. New Mexico: *Baker 14479* (MEXU), KF783823/ KF783448/ KF783529/ KF783602/ KF783672/ KF783744. ***Echinocereus viridiflorus*** subsp. ***cylindricus*** (Engelm.) N. P. Taylor. Coahuila: *Sánchez 80* (MEXU) KF783847/ KF783474/ KF783533/ KF783622/ KF783692/ KF783771. ***Echinocereus waldeisii*** Haugg. San Luis Potosí: *Arias 2002* (MEXU) KF783830/ KF783455/ KF783530/ KF783607/ KF783677/ KF783750. ***Echinocereus websterianus*** G. E. Linds. Sonora: *Lindsay* s.n. (DES) KF783824/ KF783449/ KF783531/ KF783603/ KF783673/ KF783745. ***Epiphyllum hookeri*** Haw. Chiapas: *Bravo* s.n. (MEXU) KF783850/ KF783859/ KF783541/ KF783625/ KF783695/ KF783774. ***Escontria chiotilla*** (Weber ex K. Schum.) Rose. Oaxaca: *Arias 891* (MEXU) KF783833/ KF783459/ KF783542/ KF783610/ KF783680/ KF783754. ***Eulychnia breviflora*** Phil. HBG 78399, cult.: −/ KF783860/ KF783543/ KF783619/ KF783689/ KF783767; BBG 26764, cult./ FN669772/ −/ −/ −/ −/ −. ***Lemaireocereus hollianus*** (F. A. C. Weber ex J. M. Coult.) Britton & Rose. Puebla: *Arias 1373* (CHAPA) KF783834/ KF783460/ KF783544/ AY181603/ AY181623/ −. ***Leptocereus quadricostatus*** (Bello) Britton & Rose. PERU. Cabo Rojo: *Arias 1464* (MEXU) KF783845/ KF783471/ −/ KF783620/ KF783690/ KF783768. ***Leptocereus quadricostatus*** (Bello) Britton & Rose. ISU no ref., cult.: −/ −/ AY851582 (Butterworth and Wallace 2005)/ −/ −/ −. ***Myrtillocactus cochal*** (Orcutt) Britton & Rose. Baja Cal. S.: *Orduño* s. n. (MEXU) KF783835/ KF783856/ KF783545/ KF783611/ KF783681/ KF783755. ***Myrtillocactus geometrizans*** (Mart. ex Pfeiff.) Console. Puebla: *Arreola 1599* (CHAPA) KF783836/ KF783461/ KF783546/ KF783612/ KF783682/ KF783756. ***Myrtillocactus schenckii*** (J. A. Purpus) Britton & Rose. Puebla: *Terrazas 500* (CHAPA) KF783837/ KF783857/ KF783547/ AY181607/ AY181633/ KF783757. ***Neobuxbaumia laui*** (P. V. Heat) D. R. Hunt. Oaxaca: *Barba* s.n. (MEXU) KF783838/ KF783462/ KF783548/ KF783613/ KF783683/ KF783758. ***Pachycereus pringlei*** (S. Watson) Britton & Rose. Baja Cal. S.: *Arias 1348* (CHAPA) KF783839/ KF783463/ KF783549/ AY181589/ AY181642/ KF783759. ***Peniocereus lazaro-cardenasii*** (Contreras et al.) D. R. Hunt. Michoacán: *Contreras 20* (MEXU) KF783853/ KF783464/ KF783550/ DQ100021/ DQ099952/ KF783760. ***Polaskia chichipe*** (Gosselin) Backeb. Puebla: *Arias 1529* (MEXU) KF783840/ KF783465/ KF783551/ KF783614/ KF783684/ KF783761. ***Stenocereus alamosensis*** (J. M. Coult.) A. C. Gibson & K. E. Horak. Sinaloa: *Arias 1838* (MEXU) KF783841/ KF783466/ KF783552/ KF783615/ KF783685/ KF783762. ***Stenocereus eruca*** (Brandegee) A. C. Gibson & K. E. Horak. Baja Cal. S.: *Arreola 1614* (CHAPA) KF783842/ KF783467/ KF783556/ KF783616/ KF783686/ KF783763. ***Stenocereus montanus*** (Britton & Rose) Buxb. Sonora: *Arias 2004* (MEXU) KF783852/ KF783468/ KF783553/ KF783617/ KF783687/ KF783764. ***Stenocereus pruinosus*** (Otto ex Pfeiff.) Buxb. Puebla: *Arias 750* (MEXU) KF783843/ KF783469/ KF783554/ KF783618/ KF783688/ KF783765. ***Stenocereus stellatus*** (Pfeiff.) Riccob. Puebla: *Arias 1375* (MEXU) KF783844/ KF783470/ KF783555/ AY181590/ AY181640/ KF783766.