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SYSTEMATICS

Reinstatement of the genus *Psorodendron* and related systematic novelties as revealed from phylogenetic analyses of the tribe Amorpheae (Leguminosae, Papilionoideae)

Revalidación del género *Psorodendron* y novedades sistemáticas relacionadas a partir de análisis filogenéticos de la tribu Amorpheae (Leguminosae, Papilionoideae)

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ABSTRACT

The legume tribe Amorpheae comprises eight genera and ca. 240 species exclusive to the New World. We performed parsimony and maximum likelihood phylogenetic analyses based on sequence data from the nuclear gene CNGC4, the chloroplast *trnK/matK* genes and the nuclear ribosomal ITS regions. Our goal was to infer the generic-level phylogenetic relationships of the tribe with an expanded sampling on *Dalea*, a genus that comprises nearly 70 % of the species of the tribe. We corroborated that the tribe Amorpheae is formed by the Daleoid clade, comprising *Dalea*, *Marina,* and *Psorothamnus*, and the Amorphoid clade comprising *Amorpha, Apoplanesia, Errazurizia, Eysenhardtia,* and *Parryella*. Additionally, *Errazurizia* resulted polyphyletic given that one of its species (*E. rotundata*) clusters with *Parryella* in the most inclusive combined datasets (CNGC4 + ITS, ITS + *matK*/*trn*K, and CNGC4 + ITS + *matK*/*trn*K); thus, we reinstate the existing name *Parryella rotundata* to render these two genera as monophyletic. We also corroborate that *Psorothamnus* is paraphyletic, with species falling into two non-sister subclades, one of them sister to *Dalea* + *Marina*, and the other corresponding to the former genus *Psorodendron*, making imperative the reinstatement of the latter. *Dalea* is also corroborated as paraphyletic given that *D. filiciformis* results sister to *Marina*; thus, this species is transferred to *Marina* in order to render monophyly of these two genera. Finally, the relationships of the Colombian species remain uncertain due to the incongruence between ITS alone versus *matK/trnK* and the combined ITS + *matK/trnK* datasets.

Keywords: Colombian legumes, *Dalea, Errazurizia, Marina*, *Parryella*, *Psorothamnus*, molecular systematics.

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RESUMEN

La tribu de leguminosas Amorpheae comprende ocho géneros y ca. 240 especies exclusivas del Nuevo Mundo. Realizamos análisis filogenéticos por parsimonia y máxima verosimilitud de secuencias del gen nuclear CNGC4, los genes del cloroplasto *matK/trnK*, y la región nuclear ribosomal ITS. Nuestro objetivo fue inferir las relaciones filogenéticas a nivel genérico de la tribu con un muestreo ampliado en *Dalea*, un género que comprende casi el 70 % de las especies de la tribu. Corroboramos que la tribu Amorpheae está formada por el clado Daleoide, con los géneros *Dalea*, *Marina* y *Psorothamnus*, y el clado Amorphoide, con *Amorpha, Apoplanesia, Errazurizia, Eysenhardtia* y *Parryella*. Además, *Errazurizia* resulta polifilético dado que una de sus especies (*E. rotundata*) resulta hermana de *Parryella* en los análisis combinados más incluyentes (CNGC4 + ITS, ITS + *matK*/*trn*K, and CNGC4 + ITS + *matK*/*trn*K); como resultado, revalidamos el nombre previo *Parryella rotundata* a fin de reestablecer la monofilia de estos dos géneros. A la vez, corroboramos que *Psorothamnus* es parafilético, con sus especies agrupadas en dos clados no hermanos, uno de ellos hermano de *Dalea* + *Marina*, y el otro corresponde al género previamente descrito como *Psorodendron*, por lo que se hace imperativa su revalidación. *Dalea* también es corroborado como parafilético ya que *D. filiciformis* resulta ser la especie hermana de *Marina*; como resultado, esta especie es transferida a *Marina* a fin de mantener la monofilia de estos dos géneros. Finalmente, las relaciones filogenéticas de las especies colombianas continúan inciertas debido a la incongruencia entre ITS versus *matK/trnK* y los marcadores combinados ITS + *matK/trnK*.

Palabras clave: *Dalea, Errazurizia*, *Marina*, *Parryella*, *Psorothamnus*, leguminosas de Colombia, sistemática molecular.

INTRODUCTION

The exclusively New World tribe Amorpheae (Leguminosae: Papilionoideae) comprises eight genera and approximately 240 species (Barneby 1977, Piñeros-Urrego and González 2019, 2020). Based on morphological traits, Barneby (1977) proposed two generic groups, the first with *Dalea* Lucanus*, Errazurizia* Phil.*, Marina* Liebm. and *Psorothamnus* Rydb.*,* and the second with *Amorpha* L.*, Apoplanesia* C.Presl.*, Eysenhardtia* Kunth and *Parryella* Torr. & A. Gray. In addition, Barneby (1977) proposed five subgenera within *Dalea,* namely *Asprolea, Dalea, Parosela, Psoropteris,* and *Theodora*. Previous phylogenetic analyses based on morphological and molecular data have shown that the tribe is monophyletic and conformed by two subclades, namely the Daleoids, comprising *Dalea*, *Marina* and *Psorothamnus*, and the Amorphoids comprising *Amorpha, Apoplanesia, Errazurizia, Eysenhardtia,* and *Parryella* (McMahon and Hufford 2004, McMahon 2005). These authors stated that *Psorothamnus* should be treated in its narrow sense, i.e. including the type species *P. emoryi* and the species of the subclade sister to (*Dalea* + *Marina*), whereas the remaining species were informally treated as the *Psorodendron* clade, in reference to Rydberg's (1919) genus *Psorodendron*. In addition, McMahon and Hufford (2004) and McMahon (2005) concluded that *Dalea* is paraphyletic with respect to *Marina,* and that these two genera are sister to a paraphyletic *Psorothamnus*. The paraphyly of *Psorothamnus* was also corroborated by Cardoso *et al.* (2013). The sampling of *Dalea* in these analyses was focused primarily on North American and Mexican species, which prevent any detailed conclusion regarding species-level phylogenetic relationships of the Andean species, including those present in Colombia.

Our aims in the present study are (1) to revisit the classification within the tribe Amorpheae based on phylogenetic analyses with an expanded sampling including the Colombian species of *Dalea* (namely *D. carthagenensis* (Jacq.) J.F. Macbr.*, D. coerulea* (L.f.) Schinz & Thell., *D. cuatrecasasii* Barneby*, D. foliolosa* (Aiton) Barneby and the recently described *D. wilsonii* Piñeros-Urrego & González); and (2) to assess whether the Colombian species are more closely related to North and Central America taxa or to their South American congeners.

MATERIALS AND METHODS

DNA extraction, amplification and sequencing

DNA of 20 samples collected in the field was extracted using the MO-BIO Power Plant Isolation Kit Cat No. 13400-S kit. The chloroplast *trnK/matK* gene, the nuclear ribosomal marker ITS (ITS1+5.8S+ITS2), and the nuclear gene CNGC4 were amplified. Because of its large size, the *matK/trnK* region was amplified in two fragments using the primers *matK*1221F and *matK*2340R (fragment one), and *matK*2025F and *trnK*2R (fragment two). Polymerase chain reaction (PCR) was conducted using the following profile: four minutes at 94 °C, 35 cycles of one minute at 94 °C, one minute at 45 °C or 48 °C (fragments one and two, respectively) and two minutes at 72 °C, followed by a final extension of five minutes at 72 °C. The ITS region was amplified using the primers ITS/5.8S N-nc18s1 (forward) y C26A (reverse). The primers and the PCR profiling for these markers followed McMahon and Hufford (2004). A PCR "touchdown" profile was used for amplification as follows: four minutes at 94 °C, five cycles of one minute at 94 °C, one minute at 52 °C y two minutes at 72 °C decreasing the temperature by 1 °C in each cycle, followed by 30 cycles of one minute at 94 °C, one minute at 48 °C and two minutes at 72 °C, with a final extension of five minutes at 72 °C. The nuclear region CNGC4 was amplified using the primers CNGC4Fwd y CNGC4Rev (McMahon 2005) and the following PCR profile: four minutes at 94 °C, 35 cycles of one minute at 94°C, one minute at 58 °C and one minute at 72 °C, with a final extension of five minutes at 72 °C. The PCR products were cleaned with the "ExoSAP-IT PCR Product Cleanup" protocol. Sequencing was performed at the Centro Nacional de Secuenciación Genómica, Sede de Investigación Universitaria (SIU), Universidad de Antioquia, Medellín.

Phylogenetic analyses

Twelve sequences of four Colombian species of *Dalea* were newly generated for the present research (Table 1; voucher specimens were deposited at the Herbario Nacional Colombiano, Universidad Nacional de Colombia, COL). Additional sequences from extra-Colombian *Dalea*

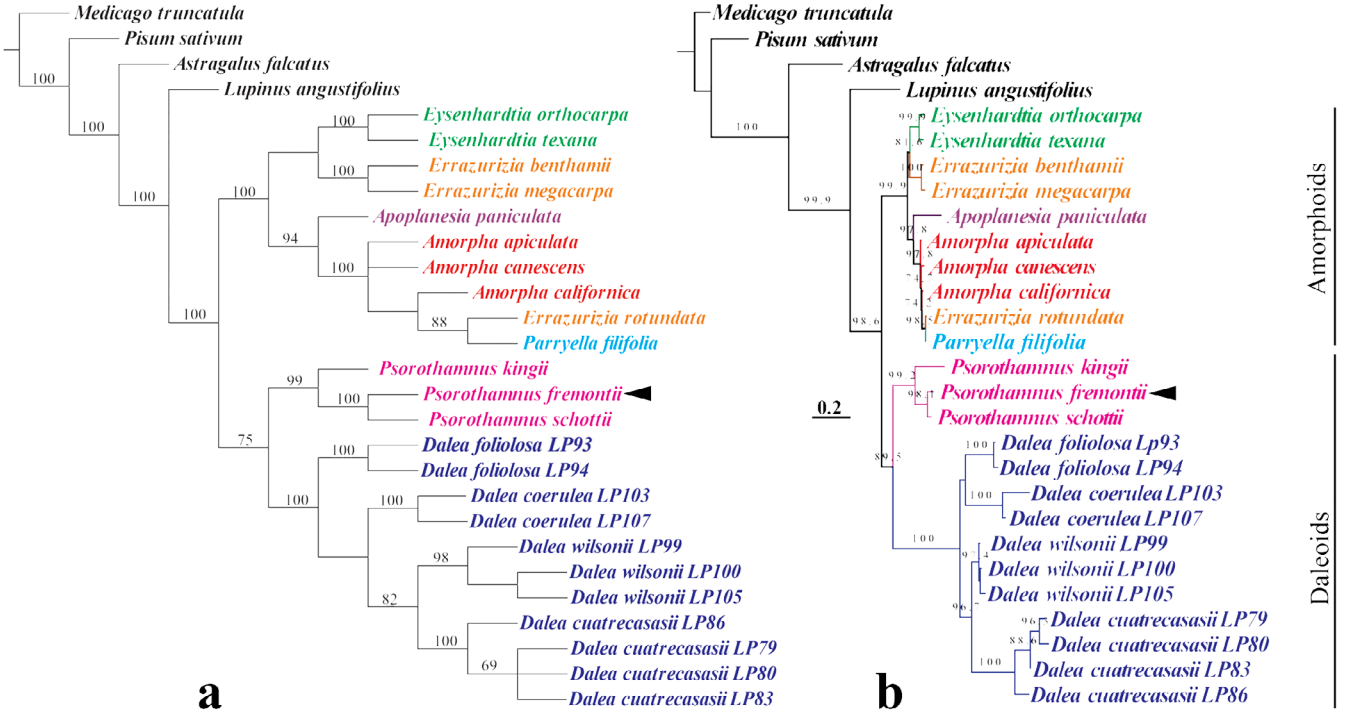

Figure 1. Phylogenetic trees calculated from the combined ITS + CNGC4 dataset. **a.** Strict consensus tree of 4 MPTs (L = 1487, CI = 0.61 and RI = 0.79); **b.** Maximum Likelihood tree. Note the monophyly of the Amorphoids (*Amorpha*, *Apoplanesia*, *Errazurizia*, *Eysenhardtia and Parryella*), and the Daleoids (*Dalea* and *Psorothamnus*), and the polyphyly of *Errazurizia*. Arrowhead points to the type species of former genus *Psorodendron* (*P. fremontii;* see text). Details for terminal codes are given in Table 1. Numbers above branches are bootstrap percentages greater than 50%.

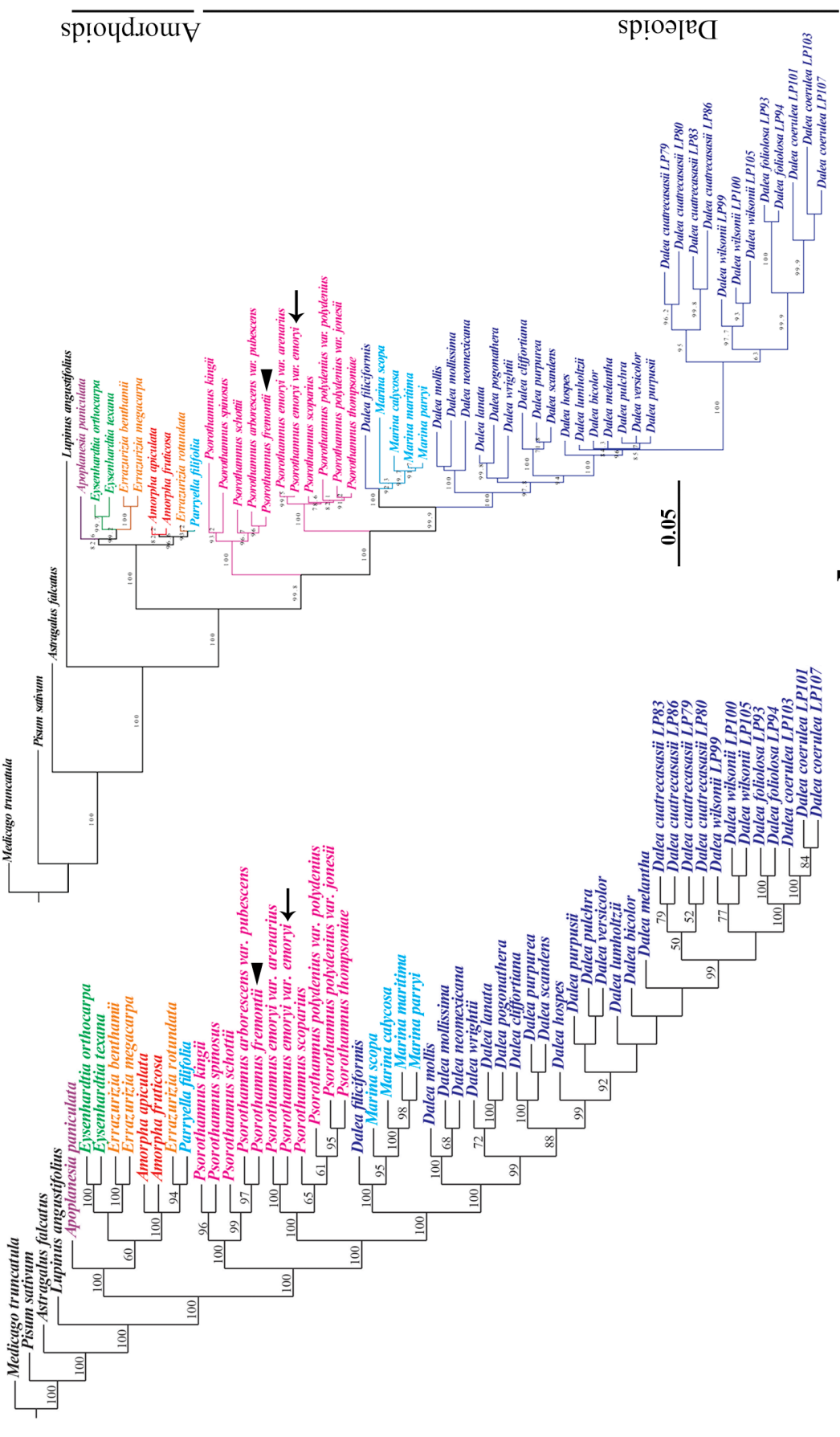

Figure 2. Phylogenetic trees calculated from the combined ITS + *matK/trnK* dataset. **a.** Strict consensus tree of two MPTs (L = 3279, CI = 0.53 and RI = 0.77); **b.** Maximum Likelihood tree. Note the monophyly of the Amorphoids (*Amorpha*, *Apoplanesia*, *Errazurizia*, *Eysenhardtia*, and *Parryella*), and the Daleoids (*Dalea*, *Marina*, and *Psorothamnus*), the polyphyly of *Errazurizia*, the paraphyly of *Psorothamnus* with respect to *Dalea* + *Marina*, and the paraphyly of *Dalea* with respect to *Marina*. Arrow points to the type species of *Psorothamnus* (*P. emoryi*); arrowhead points to the type species of former genus *Psorodendron* (*P. fremontii*; see text). Details for terminal codes are given in Table 1. Numbers above branches are bootstrap percentages greater than 50%.

species and the remaining genera of the tribe Amorpheae (*Amorpha, Apoplanesia, Errazurizia, Eysenhardtia, Marina, Parryella,* and *Psorothamnus*) were downloaded from the GenBank, and from McMahon and Hufford (2004) and McMahon (2005) (Table 1). Orthologs from *Astragalus falcatus* Lam., *Lupinus angustifolius* L., *Medicago truncatula* Gaertn., and *Pisum sativum* L. were used as outgroup taxa (Table 1). All sequences were compiled using BioEdit6. Nucleotide sequences were aligned using the online version of MAFFT V7 (Katoh *et al.* 2019) with a gap open penalty of 5.0 and an offset value of 1.0. All other default settings were used without further modification.

The three individual markers (CNGC4, ITS and *trnK/matK*) as well as combined sets of all three markers and two-markers (ITS-*trnK/matK*, ITS-CNGC4, and *trnK/matK*-CNGC4) were analyzed under Maximum Parsimony (MP), and Maximum Likelihood (ML). The two-marker combined analyses (ITS-*trnK/matK*, ITS-CNGC4, and *trnK/matK*-CNGC4) were performed in order to evaluate species relationships using a broader sampling (53 terminals, 24 terminals, and 23 terminals, respectively) available of Amorpheae. In particular, the combined ITS-*trnK/matK* dataset allowed to significantly increase sampling within the species-rich *Dalea*. The parsimony analyses were performed by using Nona (Goloboff 1999) through Winclada v1.00.08 (Nixon 2002). All characters were treated as non-additive. Gaps were treated as missing data. The uninformative traits were removed from the analyses. The Heuristic searches were performed using ten starting trees per replicate, 100 replicates, and 1000 trees hold in memory, and submitted to multiple TBR*. If needed, a strict consensus tree was also calculated. Bootstrap support values (BS) for individual and combined parsimony-based analyses were measured with NONA (Goloboff 1999) by conducting 1000 pseudoreplicas. For each replicate, 10 TBR searches were conducted, with one tree held after each replicate, and a total of 10 000 trees held in memory for the duration of the entire bootstrap analysis. The maximum likelihood (ML) analyses were performed using IQ-Tree through the W-IQ-TREE portal7 (Trifinopoulos *et al.* 2016). The molecular evolution model that best fit the data was calculated using the ModelFinder tool incorporated in IQ-TREE (Kalyaanamoorthy *et al.* 2017). The models calculated were: TIM3e+I+G4 for ITS; TVM+F+G4 for *trnK/matK*; TIM+F+G4 for CNGC4; TVM+F+ASC+G4 for ITS-CNGC4; TIM+F+G4 for ITS-*trnK/matK*; and K3Pu+F+G4 for *trnK/matK*-CNGC4 and the combined set of all three markers. Conventional Bootstrap of 1000 pseudoreplicas also implemented in

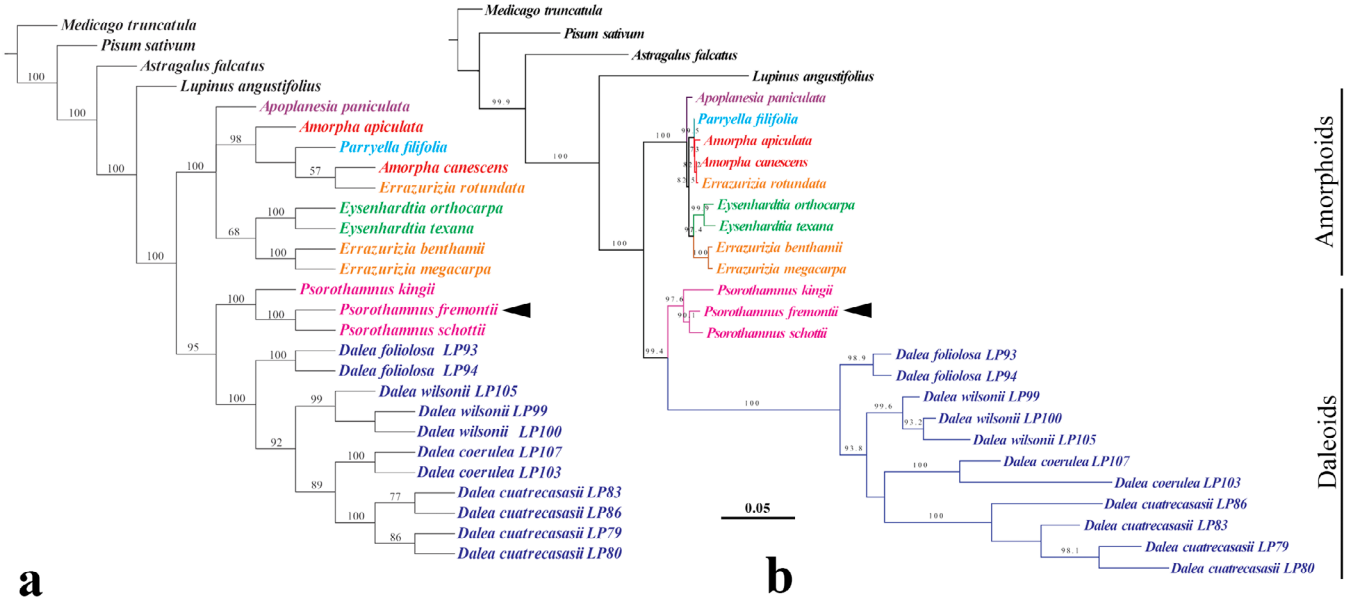

Figure 3. Phylogenetic trees calculated from the combined *matK/trnK* + CNGC4 dataset. **a.** Strict consensus tree of two MPTs (L = 1787, CI = 0.65 and RI = 0.78); **b.** Maximum Likelihood tree. Note the monophyly of the Amorphoids (*Amorpha*, *Apoplanesia*, *Errazurizia*, *Eysenhardtia*, and *Parryella*), and the Daleoids (*Dalea* and *Psorothamnus*), and the polyphyly of *Errazurizia*. Arrowhead points to the type species of former genus *Psorodendron* (*P. fremontii;* see text). Details for terminal codes are given in Table 1. Numbers above branches are bootstrap percentages greater than 50 %.

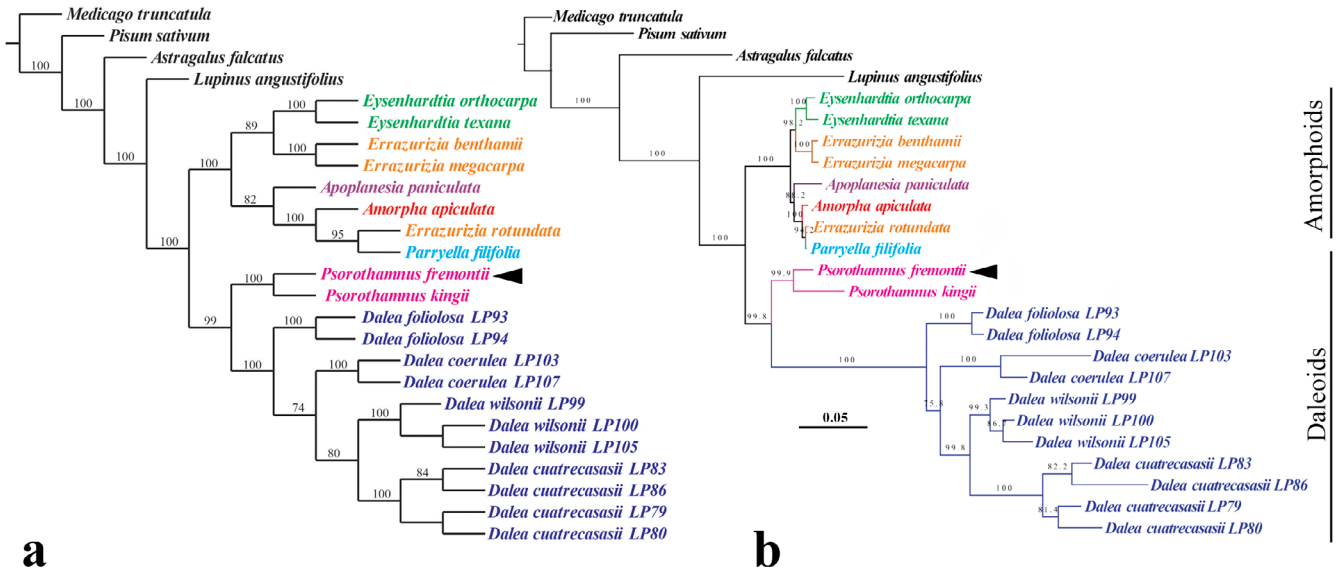

Figure 4. Phylogenetic trees calculated from the combined ITS + CNGC4 + *matK/trnK* dataset. **a.** Single MPT (L = 2572, CI = 0.63 and RI = 0.78); **b.** Maximum Likelihood tree. Note the monophyly of the Amorphoids (*Amorpha*, *Apoplanesia*, *Errazurizia*, *Eysenhardtia*, and *Parryella*), and the Daleoids (*Dalea* and *Psorothamnus*), and the polyphyly of *Errazurizia*. Arrowhead points to the type species of former genus *Psorodendron* (*P. fremontii*; see text). Details for terminal codes are given in Table 1. Numbers above branches are bootstrap percentages greater than 50%.

IQ-TREE were used to calculate branch support values on the ML trees (Hoang *et al.* 2018). Phylogenetic trees obtained were visualized and edited on FigTree8 and labeled in Photoshop Illustrator CC 2019.

RESULTS

The most inclusive combined datasets (CNGC4 + ITS, ITS + *matK*/*trn*K, and CNGC4 + ITS + *matK*/*trn*K; Figs. 1-4) show that the tribe Amorpheae is formed by the Daleoid clade, comprising *Dalea*, *Marina* and *Psorothamnus*, and the Amorphoid clade comprising *Amorpha, Apoplanesia, Errazurizia, Eysenhardtia,* and *Parryella*. Additionally, *Errazurizia* resulted polyphyletic given that one of its species (*E. rotundata*) clusters with *Parryella*. We also corroborate that *Psorothamnus* is paraphyletic, with species falling into two non-sister subclades, one of them sister to *Dalea* + *Marina*, and the other corresponding to the former genus *Psorodendron*. Finally, *Dalea* is shown to be paraphyletic given that *D. filiciformis* results sister to *Marina* (Figs. 1-4).

ITS. The analyses of the ITS (ITS1, ITS2 and 5.8S) region included 70 terminals and an average length of 931 base pairs (bp). The parsimony (MP) analysis resulted in 88 most parsimonious trees (MPTs) of length (L) = 1607, consistency index (CI) = 0.45, and retention index (RI) = 0.79. A total of 384 sites (41.24 %) resulted phylogenetically informative (Table 2). Eleven clades collapsed in the strict consensus tree (Suppl. Fig. 1a). The two major clades of the tribe Amorpheae, namely the Amorphoids (*Amorpha, Apoplanesia, Errazurizia, Eysenhardtia,* and *Parryella*), and the Daleoids (*Dalea*, *Marina,* and *Psorothamnus*) received, respectively, BS values of 100 % and 89 % in the MP analysis (Suppl. Fig. 1a), and 99.5 % and 95.8 %, in the ML analysis (Suppl. Fig. 1b). Within the Amorphoids, *Apoplanesia* resulted sister to the subclade formed by all species of *Eysenhardtia* plus two species of *Errazurizia* (*E. benthamii* (Brandegee) I.M.Johnst. and *E. megacarpa* (S. Watson) I.M.Johnst.; BS 76.6 % in the ML analysis); *Eysenhardtia* is the only genus recovered as monophyletic in both the MP (BS 96 %) and the ML (BS 97.9 %) analyses; *Errazurizia* resulted polyphyletic, as a third species (*E. rotundata* (Wooton) Barneby) comes out as sister to *Parryella filifolia* A. Gray (BS 92 % and 98.4 % in the MP and the ML analyses, respectively); the latter two species are nested in the paraphyletic *Amorpha* in the ML analysis (BS 86 %). Within the Daleoids, *Psorothamnus* results paraphyletic with respect to the *Dalea* + *Marina* clade. One of the *Psorothamnus* subclades comprises *P. arborescens* (A. Gray) Barneby, *P. fremontii* (A. Gray) Barneby, *P. kingii* (S. Watson) Barneby, *P. schottii* (Torr.) Barneby, and *P.*

spinosus (A. Gray) Barneby (BS 89 % and 99.5 % in the MP and the ML analyses, respectively), all of them members of the former genus *Psorodendron*. These results were consistently found in both the Parsimony (Suppl. Fig. 1a) and the Maximum Likelihood analyses (Suppl. Fig. 1b). The second *Psorothamnus* subclade comprises the remaining species of the genus (BS 100 % and 99.5 % in the MP and the ML analyses, respectively), including its type species *P. emoryi* (A.Gray) Rydb. Finally, *Dalea* results paraphyletic with respect to *Marina* (BS 100 % and 99.5 % in the MP and the ML analyses, respectively), as *D. filiciformis* B.L. Rob. & Greenm. comes out as sister to *Marina* (BS 95 % and 95.3 % in the MP and the ML analyses, respectively).

As for the Colombian species, *Dalea foliolosa* results in a polytomy (in the strict consensus tree from MP analysis), along with three subclades that in total comprise 20 additional *Dalea* species (Suppl. Fig. 1a, b). One of these subclades is exclusive to the Andes and comprises the Colombian *D. coerulea* plus the Peruvian *D. myriadenia* Ulbr. and *D. weberbaueri* Ulbr. in the ML analysis (BS 99.8 %). The Colombian endemic *D. cuatrecasasii* resulted clustered with *D. bicolor* Willd., from Mexico, and *D. versicolor* Zucc., from S United States, Mexico and Guatemala in the ML analysis (BS 75 %). Finally, *D. wilsonii* is recovered as sister to *D. cartagenensis* in the ML tree (BS 89 %; Suppl. Fig. 1b).

MatK/trnK. The *matK/trnK* analyses included 58 terminals with an average length of 3055 base pairs (bp). The parsimony analysis resulted in 788 MPTs of L = 2387, CI = 0.71, and RI = 0.89. A total of 661 sites (21.63 %) resulted phylogenetically informative (Table 2). A total of 18 nodes collapsed in the strict consensus tree (Suppl. Fig. 2a). The two major clades of the tribe Amorpheae, namely the Amorphoids (*Amorpha, Apoplanesia, Errazurizia, Eysenhardtia* and *Parryella*), and the Daleoids (*Dalea* and *Marina*, and *Psorothamnus*) are both recovered with BS values of 99.5-100 % in the MP and the ML analyses (Suppl. Fig. 2). Within the Amorphoids, *Apoplanesia* resulted sister to the remaining Amorphoid genera (BS 96 % in both the MP and ML analyses); *Eysenhardtia,* the only genus recovered as monophyletic (BS 100 % and 98.6 % in the MP and the ML analyses, respectively), is recovered (with a BS of 99 % and 96.2 % in the MP and the ML analyses, respectively) as sister to *Errazurizia benthamii* plus *Errazurizia megacarpa* (BS 100 % in both, the MP and the ML analyses). Thus, *Errazurizia* resulted polyphyletic, as its third species (*E. rotundata*) clusters with *Amorpha fruticosa* L. (BS 95% and 77.4 % in the MP and the ML analyses, respectively), which, in turn, are part of a polytomy along with *A. apiculata* Wiggins and *Parryella filifolia* (BS 99 % and 94.6 % in the MP and the ML analyses, respectively).

Within the Daleoids, *Psorothamnus* results paraphyletic with respect to the *Dalea* + *Marina* clade. One of the *Psorothamnus* subclades comprises *P. arborescens, P. fremontii, P. kingii, P. schottii*, and *P. spinosus* (BS 100 % in both the MP and the ML analyses), all of them members of the former genus *Psorodendron*. The second *Psorothamnus* subclade comprises the remaining species of the genus (BS 100 % and 99.9 % in the MP and the ML analyses, respectively), including its type species *P. emoryi*. Finally, *Dalea* results paraphyletic with respect to *Marina* (BS 100 % and 96.6 % in the MP and the ML analyses, respectively), as *D. filiciformis* comes out as sister to *Marina* (BS 100 % and 99.7 % in the MP and the ML analyses, respectively). Finally, *matK-trnK* does not provide an accurate phylogenetic signal for the Colombian species of *Dalea* except for the clustering of all *D. coerulea* accessions in the strict consensus tree (Suppl. Fig. 2).

CNGC4. The matrix for the analyses of this nuclear marker included 28 sequences with an average of 929 bp. In the Parsimony analysis, 574 sites (61.78 %) were phylogenetically informative. Three MPTs were obtained, with L= 611, CI = 0.62 and RI = 0.76 (Table 2). Three nodes collapsed in the strict consensus tree (Suppl. Fig. 3a). Unlike the previous markers, CNGC4 is the only one that does not recover the monophyly of Amorphoids and Daleoids, as the three species of *Psorothamnus* sampled resulted sister to the clade formed by the Amorphoid genera plus *Dalea*. However, the BS value for this clustering is negligible in both analyses (51 % and 52.8 % in MP and ML trees, respectively; Suppl. Fig. 3). Within the Amorphoids, CNGC4 also uncovers the polyphyly of *Errazurizia* and the closer relationship of *E. rotundata* either with *Amorpha* or with *Parryella* (BS 93 % and 93.4 % in the MP and the ML analyses, respectively) than to the remaining species of *Errazurizia*. As for the Colombian species, CNGC4 supports the clustering of the two or more accessions for each of the sampled species (*D. coerulea, D. cuatrecasasii, D. foliolosa,* and *D. wilsonii)* (Suppl. Fig. 3).

ITS + CNGC4. The combined analyses of these two markers were based on a matrix of 28 terminals and 1456 bp.

The analysis based on 540 parsimony-informative sites (37 %), produced four trees of L = 1487, CI = 0.61 and RI = 0.79 (Table 2). Two nodes are collapsed in the strict consensus tree (Fig. 1a). The resulting topologies recover the monophyly of Amorphoids (BS 100% in both the MP and the ML analyses, respectively) and Daleoids (BS 71% and 91.1% in the MP and the ML analyses, respectively) (Fig. 1). Within the former, *Errazurizia* resulted polyphyletic, with *E. rotundata* clustered with *Parryella filifolia* (BS 88 % and 99.3 % in the MP and the ML analyses, respectively), whereas the clade (*E. benthamii* + *E. megacarpa*) is sister to the clade (*Eysenhardtia orthocarpa* (A.Gray) S.Watson + *E. texana* Scheele; BS 60 % and 84.4 % in the MP and the ML analyses, respectively). As for the Colombian species of *Dalea*, this combined analysis supports the clustering of the two or more accessions for each individual species (namely, *D. coerulea, D. cuatrecasasii, D. foliolosa* and *D. wilsonii*), with maximum BS values except for the clustering of the three *D. wilsonii* accessions, which has a BS value of 98 % and 96.2 % in the MP and the ML analyses, respectively (Fig. 1).

ITS + *matK/trnK*. The combined analyses of ITS and *matK/trnK* were based on a matrix of 57 terminals and 3986 bp, 1028 (25.79 %) of which were informative under parsimony. The analysis resulted in two MP trees with L = 3279, CI = 0.53 and RI = 0.77 (Table 2). Only one node is collapsed in the strict consensus tree (Fig. 2a). The Amorphoids and the Daleoids are recovered as monophyletic, both with BS values ranging between 99.8 % and 100 % in both (MP and ML) analyses (Fig. 2). Within the Amorphoids, *Errazurizia* resulted polyphyletic, with *E. rotundata* clustered with *Parryella filifolia* (BS 94 % and 93.2 % in the MP and the ML analyses, respectively), whereas the clade *E. benthamii* + *E. megacarpa* (BS 100 % in both analyses) is sister to the clade (*Eysenhardtia orthocarpa* + *E. texana*; BS 97 % and 99.7 % in the MP and the ML analyses, respectively). Within the Daleoids, *Psorothamnus* results paraphyletic with respect to the *Dalea* + *Marina* clade. One of the *Psorothamnus* subclades comprises *P. arborescens*, *P. fremontii, P. kingii, P. schottii*, and *P. spinosus* (BS 100 % in both MP and ML analyses), all of them members of the former genus *Psorodendron*. The second *Psorothamnus* subclade comprises the remaining species of the genus (BS 100 % in both MP and ML analyses), including its type species *P. emoryi*. Finally, *Dalea* results paraphyletic with respect to *Marina*, given that *D. filiciformis* comes out as sister to *Marina* (BS 100 % in both analyses). The Colombian species are clustered together (BS 99 % and 100 % in the MP and the ML analyses, respectively); *D. cuatrecasasii* is recovered as sister to the moderately supported (BS 63 % in the ML analysis) subclade (*D. wilsonii*(*D. foliolosa*+*D. coerulea*)) (Fig. 2). Altogether, the Colombian species are sister to *D. melantha* S.Schauer, from S United States and Mexico in the MP analysis, although in the ML tree this Colombian clade is placed in a polytomy along with *D. lumholtzii* and a subclade comprising *D. bicolor, D. melantha, D. pulchra* Gentry*, D. purpusii* Brandegee, and *D. versicolor*.

***MatK/trnK* + CNGC4.** The combined analyses of these two markers were based on a matrix of 27 terminals and 3353 sites, of which 718 (21.41 %) were parsimony-informative. Two MP trees of L = 1787, CI = 0.65 and RI = 0.78 (Table 2) were obtained. One node is collapsed in the strict consensus tree (Fig. 3a). The Amorphoids and the Daleoids are recovered as monophyletic (BS 100% and 95% in the ML analysis, and 100 % and 99.4 % in the ML analysis; Fig. 3). Within the former, *Errazurizia* resulted polyphyletic, as *E. rotundata* clustered with *Amorpha canescens* Pursh (BS 57% and 99.5 % in the MP and the ML analyses, respectively), and the clade (*E. benthamii* + *E. megacarpa*) results sister to the clade (*Eysenhardtia orthocarpa* + *E. texana*); these two clades are supported with BS values of 100 % and 97.4 % in the MP and the ML analyses, respectively (Fig. 3). As for the Colombian species of *Dalea*, these combined analyses support the clustering of the two or more accessions for each individual species (namely, *D. coerulea, D. cuatrecasasii, D. foliolosa* and *D. wilsonii*; Fig. 3), with a minor topology variation within the four accessions of *D. cuatrecasasii* with respect to that obtained from the combined (CNGC4 + ITS) analysis. *D. cuatrecasasii* comes out as sister to *D. coerulea*, with a BS value of 89 % in the MP analysis (Fig. 3a) and a negligible support value (BS 23.4 %) in the ML analysis (Fig. 3b), and together they cluster with *D. wilsonii* (BS 92 % and 93.8 % in the MP and the ML analyses, respectively); in turn, *D. foliolosa* is sister to the remaining three species, with maximum BS values in both analyses)(Fig. 3).

ITS + *matK/trnK* + CNGC4. The combined analyses of all three markers were based on a matrix of 25 terminals and 4511 sites, of which 1015 (22.5 %) were parsimony-informative, resulted in one MP tree of L = 2572, CI = 0.63 and RI = 0.78 (Table 2; Fig. 4a). The Amorphoids and the Daleoids are recovered as monophyletic with respective

BS values of 100 % and 99 %, respectively, in both analyses (Figs. 4a, 4b). Within the former, *Errazurizia* resulted polyphyletic, with *E. rotundata* clustered with *Amorpha apiculata* (BS 100 %), whereas the clade (*E. benthamii* + *E. megacarpa*) is sister to the clade (*Eysenhardtia orthocarpa* + *E. texana*); these two clades are supported with the maximum BS values in both (MP and ML) analyses. As for the Colombian species of *Dalea*, these combined analyses support the clustering of the two or more accessions for each individual species (namely, *D. coerulea, D. cuatrecasasii, D. foliolosa* and *D. wilsonii*), with a negligible topology variation within the four accessions of *D. cuatrecasasii* with respect to that obtained from the combined (CNGC4 + ITS) analysis. *D. cuatrecasasii* results to be sister to *D. wilsonii* (BS 80 % and 99.8 % in the MP and the ML analyses, respectively), and together they cluster with *D. coerulea* (BS 74 % and 75.8 % in the MP and the ML analyses, respectively); in turn, *D. foliolosa* is sister to the remaining three species, with maximum BS values in both (MP and ML) analyses (Fig. 4).

DISCUSSION

Upon expansion of sampling within *Dalea* implemented in the present study, all the partitioned and the combined datasets analyzed under MP and ML corroborate the results reported by McMahon and Hufford (2004), and McMahon (2005) as follows:

1. The tribe Amorpheae is formed by two monophyletic groups, namely the Daleoids, comprising *Dalea*, *Marina*, and *Psorothamnus*, and the Amorphoids, comprising *Amorpha, Apoplanesia, Errazurizia, Eysenhardtia*, and *Parryella*. The bootstrap values that support these two main clades range from 89 % (in the ML analysis of the combined CNGC4-ITS dataset) to 100 % (in the ML analysis of the *matK*/*trn*K dataset, and the combined ITS + *matK*/*trn*K, CNGC4 + *matK*/*trn*K, and CNGC4 + ITS + *matK*/*trn*K datasets).

2. *Errazurizia* is polyphyletic given that one of its species (*E. rotundata*) clusters with *Parryella* in the most inclusive combined analyses performed of the CNGC4 + ITS, the ITS + *matK*/*trn*K, and the CNGC4 + ITS + *matK*/*trn*K datasets. The bootstrap values that support this result range from 93 % (in the ML analysis of the combined ITS + *matK*/*trn*K dataset) to 98 % (in the ML analysis of the combined CNGC4 + ITS dataset). Additional evidence for the close relationship between *E. rotundata* and *Parryella* species comes from their similar pollen morphology (Ferguson 1990). Thus, the name *P. rotundata* is here reinstated in order to render reciprocal monophyly between these two genera:

Parryella rotundata Wooton, Bull. Torrey Bot. Club 25(8): 457 (1898).

Homotypic synonym= Errazurizia rotundata (Wooton) Barneby.

This transference adds a second species to *Parryella*, until now conformed by *P. filifolia*, and reduces from four to three the number of species of *Errazurizia*, namely *E. benthamii*, *E. megacarpa* and *E. multifoliolata* (Clos) I.M.Johnst.

3. *Psorothamnus* is paraphyletic, with species falling into two non-sister clades. One of the *Psorothamnus* subclades, including the type species of the genus (*P. emoryi*), results sister to *Dalea* + *Marina*, a result that receives the highest (100 %) bootstrap value in the partitioned ITS and the *matK/trnK* analyses, and the combined ITS + *matK/trnK* dataset. Altogether, this trigeneric assemblage is recovered as sister to a second *Psorothamnus* subclade with *P. arborescens, P. fremontii, P. kingii*, *P. schottii*, and *P. spinosus*. The bootstrap values that support the latter subclade range from 99 % in the ITS-based analysis to 100 % in the *matK/trnK* and the combined ITS + *matK/trnK* analysis. All these species are former members of *Psorodendron*, a genus described as such in 1919 based on the type species *P. johnsonii* (=*P. fremontii*), making imperative its reinstatement. The genus *Psorodendron* was proposed originally by Rydberg (1919) as distinct from *Psorothamnus* based on the presence of pedicellate flowers and exserted pods in the former, *versus* sessile flowers and inserted pods in the latter. An updated description of the genus is here provided, based on all the species assigned to it, and described by Rydberg (1919, 1928a, 1928b), and Barneby (1977, under *Psorothamnus* sect. *Capnodendron* Barneby, *P.* sect. *Xylodalea* (S. Wats.) Barneby, and *P.* sect. *Winnemucca* Barneby).

Psorodendron Rydb., N. Amer. Fl. 24(1): 41 (1919). Type: *Dalea johnsonii* S. Wats.

Stoloniferous herbs, shrubs or trees to 7(-10) m tall. Branches often spinescent; stems glabrous or sparsely strigulose or vestured with ascending, appressed indument. Leaves pinnate or simple, caducous or persistent at anthesis. Inflorescences loosely racemose or spicate, the axis becoming spiniform during or after blooming. Flowers subtended by a deciduous bract and two small subulate bracteoles at the base of the short pedicels. Petals glabrous, with or without glands. Apex of the connective with or without a gland. Ovules 2-7 per ovary. Pods to 1 cm long, inserted to exserted.

Psorodendron, as reinstated here, comprises five species widespread in desert basins of Arizona, Baja California, California, Nevada, and Utah (United States). Full synonymy of all five species (based on Barneby, 1977) is given below; names marked with asterisk correspond to *Psorodendron* binomials treated under the synonymy of *Psorothamnus* spp. by Barneby (1977).

Psorodendron arborescens (Torr.) Rydb. = *Dalea amoena* S. Watson = *Dalea arborescens* Torr. ex A.Gray = *Dalea californica* (S.Watson) Vail = *Dalea fremontii* var. *minutifolia* (Parish) L.Benson = *Dalea fremontii* var. *pubescens* (Parish) L.Benson = *Dalea fremontii* var. *saundersii* (Parish) Munz = *Dalea fremontii* var. *simplifolia* (Parish) L.Benson = *Dalea saundersii* Parish = *Parosela amoena* (S. Watson) Vail = *Parosela arborescens* (Torr.) A.Hell. = *Parosela californica* (S.Watson) Vail= *Parosela fremontii* var. *wheleri* (Vail) B.L. Robins. ex MacBr. = *Parosela fremontii* var. *saundersii* (Parish) MacBride = *Parosela johnsoni* var. *minutifolia* Parish = *Parosela johnsoni* var. *saundersii* (Parish) Parish = *Parosela neglecta* Parish = *Parosela saundersii* (Parish) Abrams = *Parosela wheeleri* Vail = *Psorodendron amoenum* (S.Watson) Rydb.*; *Psorodendron californicum* (S.Watson) Rydb.* = *Psorodendron pubescens* (Parish) Rydb.* = *Psorodendron saundersii* (Parish) Rydb.* = *Psorodendron wheeleri* (Vail) Rydb.* = *Psorothamnus arborescens* (A.Gray) Barneby = *Psorothamnus arborescens* (A.Gray) Barneby var. *minutifolius* (Parish) Barneby = *Psorothamnus arborescens* (A.Gray) Barneby var. *pubescens* (Parish) Barneby.

Psorodendron fremontii (Torr.) Rydb. = *Dalea fremontii* Torr. ex A.Gray = *Dalea johnsonii* S.Watson = *Parosela fremontii* (Torr.) Vail = *Parosela johnsonii* (S.Watson) Vail = *Psorodendron johnsonii* (S.Watson) Rydb. = *Psorothamnus fremontii* (Torr.) Barneby.

Psorodendron kingii (S. Watson) Rydb. = *Dalea kingii* S.Wats. = *Parosella kingii* A. Heller = *Psorothamnus kingii* (S.Watson) Barneby.

Psorodendron schottii (Torr.) Rydb. = *Dalea schottii* Torr. = *Parosela schottii* (Torr.) A.Hell. = *Parosela schottii* var. *puberula* Parish = *Psorodendron puberulum* (Parish) Rydb.* = *Psorothamnus schottii* (Torr.) Barneby.

Psorodendron spinosum (A.Gray) Rydb. = *Dalea spinosa* A.Gray = *Asagraea spinosa* (A.Gray) Baillon = *Parosella spinosa* (A.Gray) A. Hell. = *Psorothamnus spinosus* (A.Gray) Barneby.

4. *Dalea* is paraphyletic with respect to *Marina,* as *D. filiciformis* results sister to *Marina*. This result was obtained in all the partitioned and the combined analyses, including that based on the ITS-*trnK/matK* dataset with a significantly increased sampling within the species-rich *Dalea*. The bootstrap values that support this particular result ranged from 95 % in the ITS-based analysis (Suppl. Fig. 1) to 100 % in the combined ITS + *matK/trnK* analysis (Fig. 2). Barneby (1977: 149) already stated that *D. filiciformis* "has no really close relative in *Dalea* and its affinities are difficult to estimate," and pointed out its pod morphology resembles that found in *Marina* species. Thus, the following formal transfer is required:

Marina filiciformis (B.L. Rob. & Greenm.) Piñeros-U. & F. González, **comb. nov.**

Basionym: *Dalea filiciformis* B.L.Rob. & Greenm., Proc. Amer. Acad. 29: 382. 1894 = *Parosela filiciformis* (B.L.Rob. & Greenm.) Rose, Contrib. U.S. Nat. Herb. 8: 303. 1905.

The transfer of *Dalea filiciformis* to the genus *Marina* (suggested but not formally validated by McMahon and Hufford, 2004) is consistent with the presence of pedicellate flowers and harp-shaped pods with two distinct crescents of blister glands, two traits that are distinctive of *Marina* (Barneby 1977). However, other morphological traits commonly found in *Dalea* and likely present in *M. filiciformis*, such as leaflets with minute blister glands, two collateral ovules per ovary, spiral trichomes on the calyx, and a preliminary chromosome counting of 8 (*versus* leaflets with lineariform glands, one ovule per ovary, calyx trichomes not spirally twisted, and x = 10 in most *Marina* spp.) remain to be studied in detail.

Table 1. Accession numbers of the sequences used in this study. *LP* abbreviation stands for *Liseth Paola Piñeros-Urrego* as the first collector). NS= New sequences obtained during this research, to be submitted to GenBank.

	CNGC4	ITS	*matK/trnK*
Outgroup taxa			
Astragalus falcatus	DQ107241.1	KX954943.1	KX955106.1
Lupinus angustifolius	DU723428.1	AF007477.1	KM487292.1
Medicago truncatula	BV164997.1	AF233339.1	AF522109.1
Pisum sativum	BV165001.1	KM189821.1	JK677856.1
Ingroup taxa			
Amorpha apiculata	DQ023320.1	AY426771.1	AY391784.1
A. californica Torr. & A. Gray	DQ023322.1	AY426772.1	
A. canescens	DQ023323.1	AY426773.1	
A. fruticosa		AY426774.1	AY391785.1
A. georgiana Wilbur		AY426775.1	
Apoplanesia paniculata C.Presl	DQ023327.1	AY426776.1	AF270860.1
Dalea bicolor		AY426777.1	AY391786.1
D. candida Willd.		AY426778.1	
D. carthagenensis		AY426779.1	
D. cliffortiana Willd.		AY426780.1	AY391787.1
D. coerulea (LP101)	*NS*	*NS*	*NS*
D. coerulea (LP103)	*NS*	*NS*	*NS*
D. coerulea (LP107)	*NS*	*NS*	*NS*
D. cuatrecasasii (LP79)	*NS*	*NS*	*NS*
D. cuatrecasasii (LP80)	*NS*	*NS*	*NS*
D. cuatrecasasii (LP83)	*NS*	*NS*	*NS*
D. cuatrecasasii (LP86)	*NS*	*NS*	*NS*
D. filiciformis		AY426781.1	AY391788.1
D. foliolosa (LP93)	*NS*	*NS*	*NS*
D. foliolosa (LP94)	*NS*	*NS*	*NS*
D. gypsophila Barneby		AY426782.1	
D. hospes (Rose) Bullock		AY426783.1	AY391789.1
D. lanata Spreng.		AY426784.1	AY391790.1

(Continúa)

	CNGC4	ITS	*matK/trnK*
D. lumholtzii Robinson & Fernald		AY426785.1	AY391791.1
D. melantha		AY426786.1	AY391792.1
D. mollis Benth.		AY426787.1	AY391793.1
D. mollissima (Rydb.) Munz		AY426788.1	AY391794.1
D. myriadenia Ulbr.		AY426789.1	
D. neomexicana (A.Gray) Cory		AY426790.1	AY391795.1
D. pinetorum Gentry		AY426791.1	
D. pogonathera A.Gray		AY426792.1	AY391796.1
D. pulchra		AY426793.1	AY391797.1
D. purpurea Vent.		AY426794.1	AY391798.1
D. purpusi		AY426795.1	AY391799.1
D. saffordii (Rose) Bullock		AY426796.1	
D. scandens (Mill.) R.T.Clausen		AY426797.1	AY391800.1
D. versicolor		AY426798.1	AY391801.1
D. weberbaueri		AY426799.1	
D. wilsonii (LP99)	*NS*	*NS*	*NS*
D. wilsonii (LP100)	*NS*	*NS*	*NS*
D. wilsonii (LP105)	*NS*	*NS*	*NS*
D. wrightii A.Gray		AY426800.1	AY391802.1
Errazurizia benthamii	DQ023324.1	AY426801.1	AY391803.1
E. megacarpa	DQ023321.1	AY426802.1	AY391804.1
E. rotundata	DQ023325.1	AY426803.1	AY391805.1
Eysenhardtia orthocarpa	DQ023328.1	AY426804.1	AY391806.1
E. platycarpa Pennell & Saff.		AY426805.1	
E. texana	DQ023326.1	AY426806.1	AY391807.1
***Marina alamosana* (Rose ex. Rydb.)** Barneby		AY426807.1	
M. calycosa (A.Gray) Barneby		AY426808.1	AY391808.1
M. crenulata (Hook. & Arn.) Barneby		AY426809.1	
M. maritima (Brandegee) Barneby		AY426810.1	AY391809.1
M. parryi (Torr. & A.Gray) Barneby		AY426811.1	AY391810.1
M. scopa Barneby		AY426812.1	AY391811.1
Parryella filifolia	DQ023329.1	AY426813.1	AY391812.1

(Continúa)

	CNGC4	ITS	*matK/trnK*
Psorothamnus arborescens var. *minutifolius* (Parish) Barneby			AY391813.1
P. arborescens var. *pubescens* (Parish) Barneby		AY426814.1	AY391814.1
P. emoryi var. *arenarius* (Brandegee) Barneby		AY426815.1	AY391815.1
P. emoryi var. *emoryi*		AY426816.1	AY391816.1
P. fremontii	DQ023330.1	AY426817.1	AY391817.1
P. kingii	DQ023331.1		AY391818.1
P. polydenius var. *jonesii* Barneby		AY426819.1	AY391819.1
P. polydenius (S. Watson) Rydb. var. *polydenius*		AY426820.1	AY391820.1
P. schottii	DQ023332.1	AY426821.1	KX857729.1
P. scoparius Rydb.		AY426822.1	AY391821.1
P. spinosus		AY426823.1	AY391822.1
P. thompsoniae (Vail) S.L.Welsh & N.D.Atwood		AY426824.1	AY391823.1

Finally, the phylogenetic relationships of the Colombian species of *Dalea* (*D. coerulea, D. cuatrecasasii, D. foliolosa* and *D. wilsonii*) remains uncertain. The analysis based on ITS does not recover them as monophyletic (Suppl. Fig. 1), as *D. coerulea* results closely related to the Peruvian *D. myriadenia* and *D. weberbaueri*, whereas *D. cuatrecasasii* clusters with *D. bicolor* and *D. versicolor,* from southern United States and Mexico. Conversely, in the analyses based on *matK/trnK* (Suppl. Fig. 3) and the combined ITS + *matK/trnK* (Fig. 2), they come out as monophyletic, clustered either with *D. pulchra*, from southern United States, or with *D. melantha*, from southern North America and Mexico, respectively. More data are required to arrive at a better understanding of the phylogenetic relationship between the North- and Mesoamerican species of *Dalea* and their South American congeners.

Table 2. Statistics of the parsimony analyses. CI = Consistency Index; L = Length, MPTs = Most Parsimonious Trees; RC = Rescaled Consistency Index; RI = Retention Index.

	CNGC4	ITS	*matK/trnK*	CNGC4 ITS +	CNGC4+ *matK/trnK*	ITS + *matK/trnK*	CNGC4+ITS + *matK/trnK*
Terminals	28	70	58	28	27	57	25
Total sites	929	931	3055	1456	3353	3986	4511
Non-informative sites	355	547	2394	916	2635	2958	3496
Informative sites	574	384	661	540	718	1028	1015
MPTs	3	88	788	4	2	2	1
L	611	1607	2387	1487	1787	3279	2572
CI	0.62	0.45	0.71	0.61	0.65	0.53	0.63
RI	0.76	0.79	0.89	0.79	0.78	0.77	0.78
RC	0.47	0.35	0.63	0.48	0.50	0.40	0.49
Collapsed nodes in the strict consensus tree	3	11	18	2	1	1	-

AUTHORS PARTICIPATION

LPPU, NPM and FG planned the research project and did fieldwork , all authors performed the experiments, analyzed the data, and wrote and revised the manuscript.

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CONFLICT OF INTEREST

The authors declare that they have no conflict of interest.

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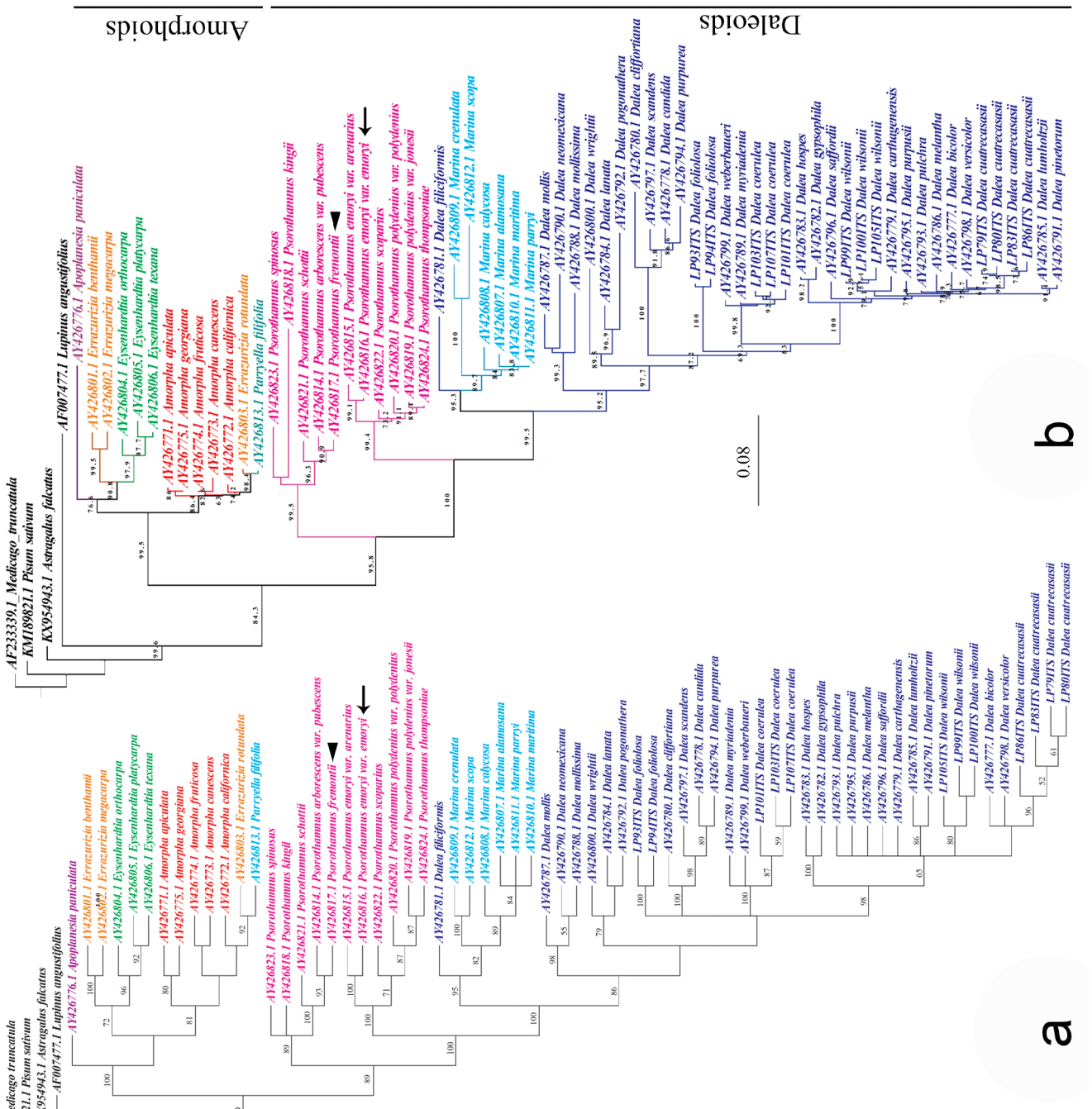
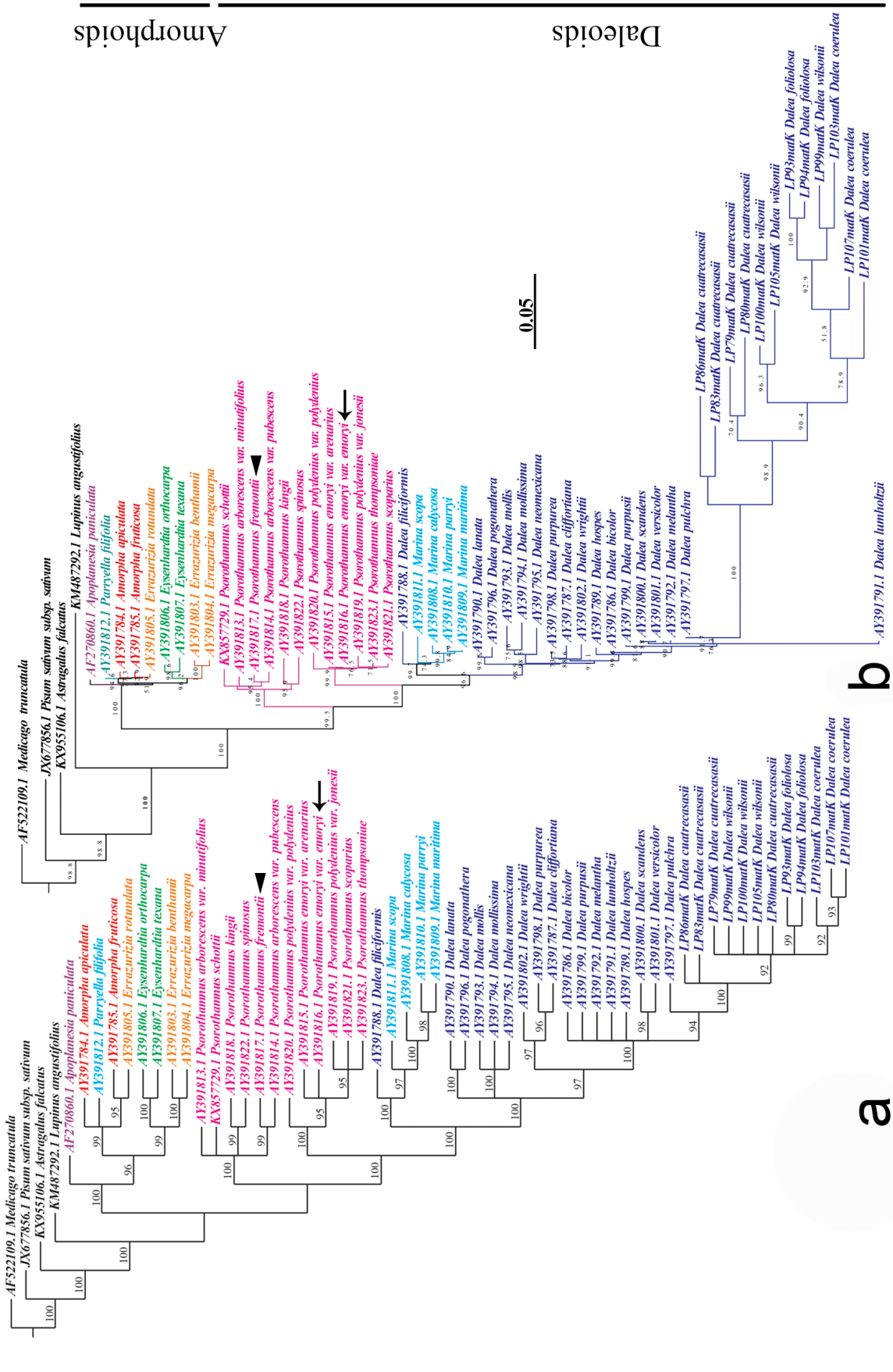
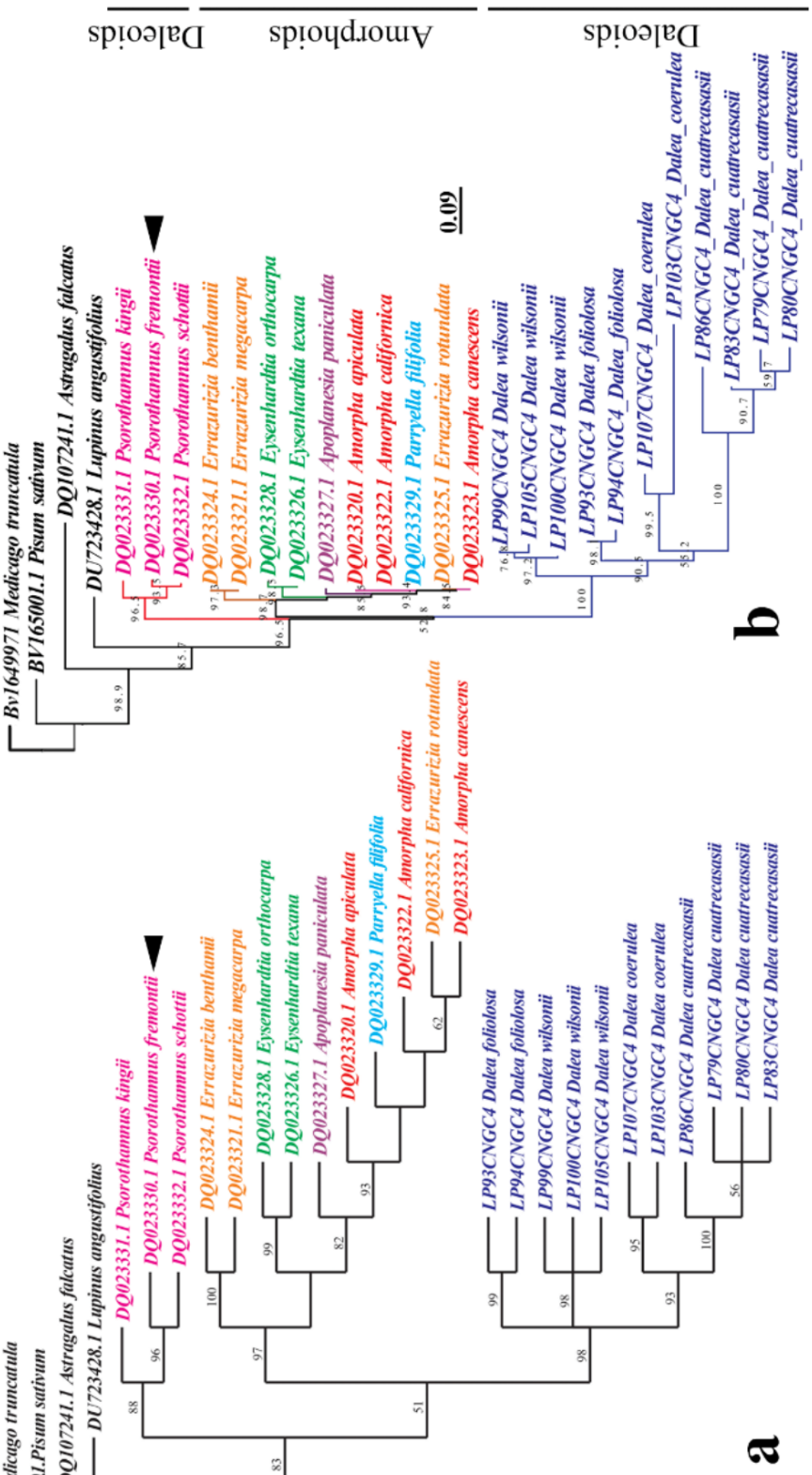


Supplementary Figure 1. Phylogenetic trees calculated from the ITS dataset. **a.** Strict consensus tree of 88 MPTs (L = 1607, CI = 0.45 and RI = 0.79); **b.** Maximum Likelihood tree. Note the monophyly of the Amorphoids (*Amorpha*, *Apoplanesia*, *Errazurizia*, *Eysenhardtia*, and *Parryella*), and the Daleoids (*Dalea*, *Marina*, and *Psorothamnus*), the polyphyly of *Errazurizia*, the paraphyly of *Psorothamnus* with respect to *Dalea* + *Marina*, and the paraphyly of *Dalea* with respect to *Marina*. Arrow points to the type species of *Psorothamnus* (*P. emoryi*); arrowhead points to the type species of former genus *Psorodendron* (*P. fremontii*; see text). Details for terminal codes are given in Table 1. Numbers above branches are bootstrap percentages greater than 50 %.



Supplementary Figure 2. Phylogenetic trees calculated from the *matK/trnK* dataset. **a.** Strict consensus tree of 788 MPTs (L = 2387, CI = 0.71 and RI = 0.89); **b.** Maximum Likelihood tree. Note the monophyly of the Amorphoids (*Amorpha*, *Apoplanesia*, *Errazurizia*, *Eysenhardtia*, and *Parryella*), and the Daleoids (*Dalea*, *Marina*, and *Psorothamnus*), the polyphyly of *Errazurizia*, the paraphyly of *Psorothamnus* with respect to *Dalea* + *Marina*, and the paraphyly of *Dalea* with respect to *Marina*. Arrow points to the type species of *Psorothamnus* (*P. emoryi*); arrowhead points to the type species of former genus *Psorodendron* (*P. fremontii*; see text). Details for terminal codes are given in Table 1. Numbers above branches are bootstrap percentages greater than 50 %.



Supplementary Figure 3. Phylogenetic trees calculated from the CNGC4 dataset. **a.** Strict consensus tree of 3 MPTs (L = 611, CI = 0.62 and RI = 0.76); **b.** Maximum Likelihood tree. Note the paraphyly of the Daleoids (*Dalea* and *Psorothamnus*) with respect to the Amorphoids (*Amorpha*, *Apoplanesia*, *Errazurizia*, *Eysenhardtia*, and *Parryella*), and the polyphyly of *Errazurizia*. Arrowhead points to the type species of former genus *Psorodendron* (*P. fremontii*; see text). Details for terminal codes are given in Table 1. Numbers above branches are bootstrap percentages greater than 50%.