



CELLULAR AND MOLECULAR BIOLOGY

Unraveling Polyphyly in *Flourensia* (Asteraceae, Heliantheae, Enceliinae) and the Establishment of a New Genus *Austroflourensia*

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Abstract: The monophyly of *Flourensia* was examined for the first time by sequencing the nuclear ITS and plastid *psbA-trnH* regions in 18 species of the genus, analyzing them along with representatives of the remaining genera of subtribe Enceliinae. Results showed strong evidence for the polyphyly of *Flourensia* identifying two well-supported groups: *Flourensia*, a clade from North America including the type *F. laurifolia*, and another clade, here designed as the new genus *Austroflourensia*, containing the South American species. *Austroflourensia* is related to the other four genera composing the subtribe Enceliinae, whereas *Flourensia* s.s. is sister to all of them. *Austroflourensia* can be mainly distinguished by having a shrubby or subshrubby habit, capitula always radiate usually arranged in weakly cymose-corymbose capitulescences, phyllaries 2-3-seriate, and disc corollas shortly dentate. This paper proposes twelve new combinations to accommodate species previously described in the genus *Flourensia* and provides emended descriptions of *Flourensia* and the new genus *Austroflourensia*. The illustration of the type of the new genus, a distribution map, and a key to the genera of Enceliinae are also provided.

Key words: Compositae, ITS, South America, taxonomy, phylogeny, *psbA-trnH*.

INTRODUCTION

The subtribe Enceliinae (Asteraceae, Heliantheae) is composed of five genera of shrubs and herbs i.e. *Encelia* Adans. 1763, *Enceliopsis* A. Nelson 1909, *Flourensia* DC. 1836, *Geraea* Torr. & A. Gray 1846, and *Helianthella* Torr. & A. Gray 1842, distributed in the arid to semi-arid lands of western North and South America (Panero 2007).

Flourensia is the largest genus of subtribe Enceliinae (Panero 2005, 2007) with an amphitropical disjunct distribution in arid to semi-arid regions of North and South America. Dillon (1984) published a complete monograph of *Flourensia* in which 31 species of resinous shrubs or small trees were recognized; subsequently

one additional species from Peru was described (Dillon 1986). Our recent taxonomic work on South American species of the genus reduced the number to 25 (Ospina et al. 2018). Dillon (1984) divided *Flourensia* into North and South American species, with the North American group including the type species *F. laurifolia* DC. Although these species were not formally grouped into infrageneric categories and no diagnostic characters were noted to separate these two groups, he suggested that *Flourensia*, as many genera of the Heliantheae of the New World, had its origin in North America with early incursions into South America.

The genus is considered as a probably monophyletic group supported by the

morphological characters: shrubs or small trees with resinous or glutinose leaves, disc corollas yellow, and cypselae biconvex with sparsely to densely pubescent faces (Panero 2007). Despite progress in understanding the phylogeny of the subtribe Enceliinae (e.g. Clark 1998, Fehlberg & Ranker 2007, Schilling & Panero 2011), the use of molecular data to test hypotheses of generic boundaries of *Flourensia* remains totally unexplored.

The main objective of this paper is to perform a molecular phylogenetic study to test the monophyly of the genus *Flourensia*. Additionally, we will analyze the morphological features of the group and related genera to determine diagnostic characters for the natural groups obtained in the molecular phylogeny.

MATERIALS AND METHODS

Molecular phylogenetic analysis

Taxon sampling

The plastid *psbA-trnH* and nuclear ITS markers were sequenced for 18 species of *Flourensia*, eight from South America and ten from North America, for a total of 17 ITS and 12 *psbA-trnH* new sequences for the genus. We also sequenced the ITS and the *psbA-trnH* of *Geraea canescens* Torr. & A. Gray and *Enceliopsis argophylla* (D.C. Eaton) A. Nelson. We produced 33 new sequences for this study. We also included in the data matrix representatives of the Enceliinae available in GenBank including 17 sequences of *Encelia*, four of *Enceliopsis*, one of *Geraea*, and two sequences of *Helianthella*. To serve as outgroups in the analyses, we included in the data matrix several representatives of other subtribes of the Heliantheae related to Enceliinae (Panero 2007, Schilling & Panero 2011) including one species each of *Ambrosia* L. (Ambrosiinae), *Chromolepis* Benth. (Chromolepidinae), *Calanticaria* (B.L.

Rob. & Greenm.) E.E. Schill. & Panero and *Simsia* Pers. (Helianthinae), *Acmella* Rich. ex Pers. and *Spilanthes* Jacq. (Spilanthinae) and *Zaluzania* Pers. (Zaluzaniinae). After adding the outgroup species, the data matrix contained 51 taxa. *Chromolepis heterophylla* Benth. was chosen to root the trees. The detail of all species included in our analyses and their GenBank numbers are listed in the Appendix; the GenBank Accessions of the new sequences (MK417525 - MK417557) and their voucher information are highlighted in bold.

DNA extraction and sequencing

Samples were either collected in the field and leaves dried in silica gel or leaf fragments were removed from herbarium specimens. Total DNA was extracted using the modified CTAB protocol of Doyle & Doyle (1987). The DNeasy plant mini kit (Qiagen, Hilden, Germany) was used to extract DNA from herbarium specimens. The plastid *psbA-trnH* and the nuclear ITS marker were amplified using PCR. For *psbA-trnH*, the primers designed by Hamilton (1999) were used; the ITS region was amplified using the ITS4 and ITS5 universal primers. The PCR reactions were performed in 25 µl of final volume with 50–100 ng of template DNA, 0.2 µM of each primer, 25 µM of dNTPs, 5 µM MgCl₂, buffer 10x, and 1.5 units of Taq polymerase (Invitrogen, Brazil). The reaction conditions were: an initial period of denaturation at 94 °C for 5 min, followed by 35 cycles of denaturation at 94°C for 30 s, annealing at 48°C for *psbA-trnH* and 52°C for ITS for 1 min, extension at 72°C for 1 min, 30 s, and a final extension at 72°C for 6 min. Products were run on 1% TBE agarose gel and stained with SybrSafe (Invitrogen). Sequencing reactions were performed by Macrogen, Inc. (Seoul, Korea). Editing and manual alignment of the sequences were performed by BioEdit 5.0.9 (Hall 1999).

Data analysis

The nuclear and plastid matrix were initially analyzed separately using parsimony. The two consensus trees obtained in the separate analyses were assessed for congruence. Because the plastid tree was mainly unresolved and did not contradict the nuclear topology, both matrices were assembled in a combined matrix (Supplementary Material Appendix SI) and a simultaneous analysis (Nixon & Carpenter 1996) was carried out. The matrices and the analyses can be found in TreeBase: S26566 (nuclear matrix, separated analysis), S26567 (plastid matrix, separated analysis), and S26568 (combined matrix, simultaneous analysis). Additionally, the nuclear matrix was analyzed under Bayesian Inference (TreeBase: S26572) to assess congruence between the results of both methods.

Parsimony analyses were carried out using TNT version 1.1 (Goloboff et al. 2008). Uninformative characters were not used in parsimony searches. Informative indels for the ingroup were coded as Present/Absent (see Table I and matrices in Appendix SI). The search strategy involved 1000 replicates, each of which generated a Wagner tree using a random addition sequence of taxa from the data matrix, swapping the initial tree with TBR (tree bisection and reconnection) and retaining a maximum of 10 trees in each replicate. Subsequently, all

Table I. Positions in the alignment of the informative indels coded for each marker.

ITS	<i>psbA-trnH</i>
94	108
147-148	205-220
468	232-238
479-480	408-429
	410-411
	452
	468

optimal trees were swapped using TBR, holding a maximum of 10,000 trees. A strict consensus tree was generated from the most parsimonious trees. Branch support were estimated with Bootstrap (Felsenstein 1985) using a total of 10,000 replicates. Each replicate was analyzed using 10 Wagner trees as a starting point followed by TBR branch swapping, saving only one tree per replicate. Bootstrap values (BS) over 50 % are reported.

The Bayesian analysis was conducted with BEAST v1.10.4 package (Drummond et al. 2012). Parameters in BEAUti were set as follows: GTR+I+ Γ as the nucleotide substitution model, site-rate heterogeneity modeled with four gamma categories, estimated base frequencies, a lognormal uncorrelated relaxed clock, a Yule process as tree prior, and default values for all other operators. Two independent runs, each using four Markov chains (one cold and three hot) of 10 million generations, were sampled every 1000 generations. To identify when the analyses had reached stationarity, we checked the output files for convergence and effective sample size (ESS) > 200 with Tracer v1.6 (Rambaut et al. 2014). Based on this convergence diagnostic, the first 2500 sampled trees were discarded as burn-in from each analysis using TreeAnnotator 1.7.1 (Drummond et al. 2012). Trees of the two runs were combined using LogCombiner 1.8.4 and the Maximum Credibility Tree was displayed in FigTree 1.3.1 (Rambaut 2009). Statistical support was determined by assessing the Bayesian posterior probabilities (PP).

Morphological analysis

This study is based on herbarium collections from the following herbaria: BAA, CORD, LIL, LP, MERL, SI, TEX, and fieldwork across the Argentinean mountain ranges in February 2012 and March 2016. Characters were taken from direct examination of herbarium specimens, and

information for the related genera was obtained from the literature (Stuessy 1977, Cabrera 1978, Robinson 1981, Dillon 1984, Ariza Espinar 2000, Panero 2007, Ospina et al. 2018).

RESULTS

The nuclear matrix had 50 taxa and 548 base positions, 165 of which were informative, also four informative indels were coded for the parsimony analysis (Table I). Parsimony analysis of ITS sequences yielded 576 most parsimonious trees of 465 steps. The strict consensus tree is shown as Supplementary Material - Figure S1. The Bayesian analysis of the ITS sequences yielded a Maximum Credibility Tree displaying a topology congruent with that obtained in the parsimony analysis; the Maximum Credibility Tree is shown in Figure S2.

The plastid matrix was composed of 36 taxa and 511 characters, 63 of these being informative; also, seven informative indels were coded (Table I). Parsimony analysis of *psbA-trnH* sequences resulted in four trees 87 steps long. The strict consensus tree (data not shown) was poorly resolved (due to the low variability among the sequences). However, the topology obtained did not contradict the ITS consensus tree, so both matrices were combined and analyzed in a simultaneous analysis.

The combined matrix (ITS + *psbA-trnH*) had 1070 characters and 51 taxa. The simultaneous analysis yielded 832 most parsimonious trees 559 steps long. The strict consensus tree obtained from the combined sequences is shown in Figure 1. The topology obtained in the simultaneous analysis (Fig. 1) was mostly congruent with those obtained from the analyses of the ITS matrix (Figure S1, S2).

All the analyses displayed, ITS (under Parsimony and Bayesian) and the simultaneous analysis, strongly rejected the monophyly of

Flourensia (Fig. 1). The two well-supported and independent lineages of *Flourensia* s.l. were *Flourensia* s.s., grouping the North American *Flourensia* species, including the type *F. laurifolia*, (BS = 89%, PP = 1, and BS = 87%), and another clade containing all the South American species of *Flourensia* (BS = 100%, PP = 1, and BS = 99%). In addition, two indels (at positions 147-148 and 479-480 of the ITS alignment) support the differentiation of these two lineages.

The South American *Flourensia* clade is in a strongly supported group (BS = 99%, PP = 1, and BS = 99%) sister to the remaining North American genera of Enceliinae, i.e. *Helianthella*, *Geraea*, *Enceliopsis*, and *Encelia*. Within this clade the relationships between the genera remain unresolved or with low support. *Flourensia* s.s. is the sister group of the entire clade including the South American *Flourensia* and the remaining genera of Enceliinae. These two sister clades constitute the subtribe Enceliinae and is recovered as monophyletic with high support (BS = 100, PP = 1, and BS = 99%).

Within *Flourensia* s.s. two groups of species can be identified, but both of them with low support: the 'microphylla subclade' (BS = 58%, PP = 0.71, and BS = 59%) including *F. microphylla* (A. Gray) S.F. Blake, *F. pulcherrima* M.O. Dillon, and *F. monticola* M.O. Dillon, and the 'cernua subclade' (BS = 65) including *F. cernua* DC., *F. solitaria* S.F. Blake, *F. resinosa* (Brandege) S.F. Blake, and *F. dentata* S.F. Blake (BS = 72%, PP = 0.54, and BS 65%).

Within the South American *Flourensia* clade, interspecific relationships are mostly unresolved or resolved with low support. Our analyses showed some discrepancies: species whose relationships were unresolved in the ITS analyses, were resolved in the combined analysis (but with low support), whereas other species whose relationships were resolved in the

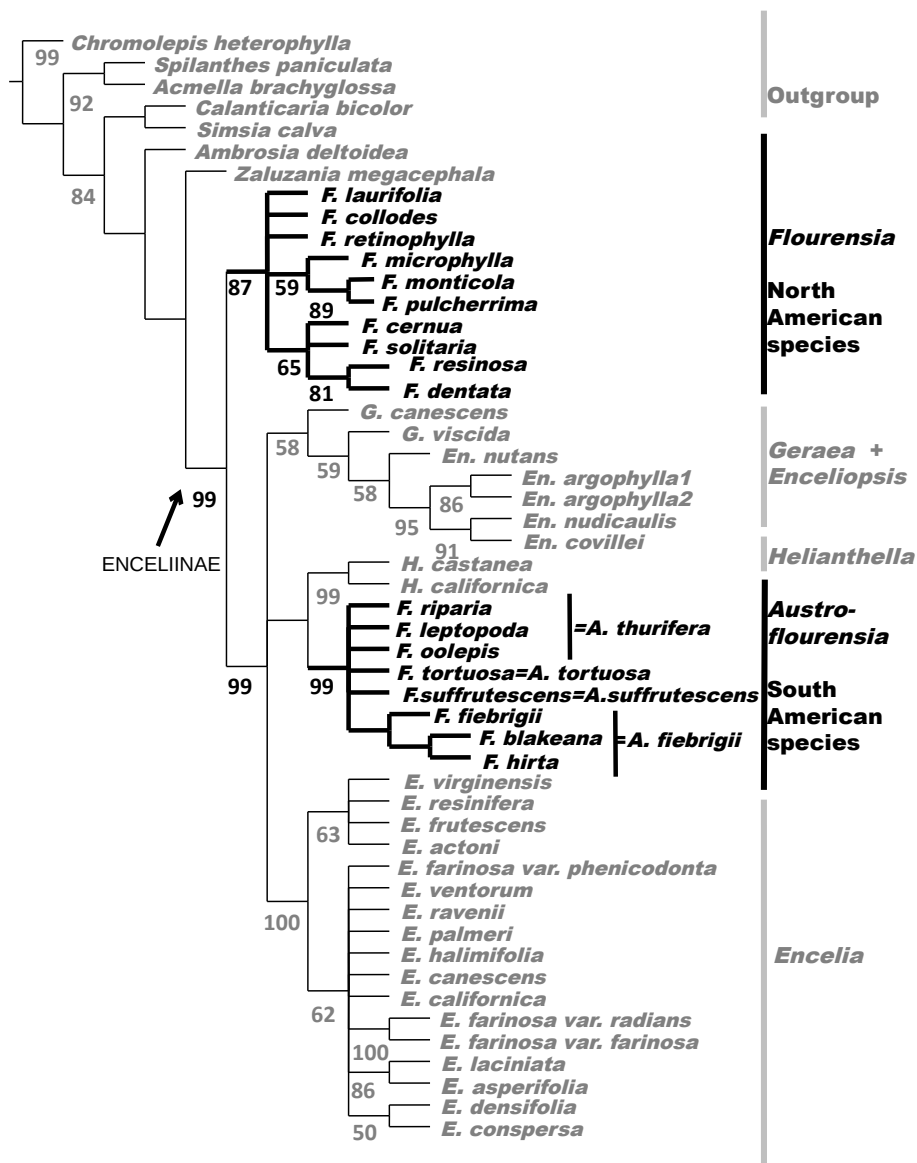


Figure 1. Parsimony strict consensus tree obtained from the simultaneous analysis on the combined matrix (ITS + *psbA-trnH*). The two independent lineages of *Flourensia* s.l.: *Flourensia* s.s. from North America and *Austroflourensia* from South America are indicated. Numbers above branches indicate BS \geq 50%. At left species names *sensu* Dillon (1984), at right *sensu* Ospina et al. 2018 (the last used in the Taxonomic treatment).

ITS analyses, were unresolved in the combined analysis.

The morphological features recorded and observed for *Flourensia* s.s., the South American clade, and the remaining genera of the subtribe Enceliinae are summarized in Table II.

DISCUSSION

Molecular phylogenetic analysis

The molecular phylogenetic analyses performed here included 60% of the species of *Flourensia*,

most of them sampled for the first time. The results obtained confirm *Flourensia* as polyphyletic with respect to the remaining genera of Enceliinae. Our results showing two lineages of *Flourensia* s.l., i.e. *Flourensia* s.s. and the South American clade, agree with those of Dillon (1984) in supporting the subdivision of *Flourensia* into two main geographical groups.

North American clade: *Flourensia*

From a total of thirteen North American *Flourensia* species, ten were analyzed in this study,

Table II. Diagnostic characters of the two lineages of *Flourensia* s.l. and the remaining genera of the subtribe Enceliinae.

Characters	<i>Flourensia</i> s.s.	<i>Austroflourensia</i>	<i>Enceliopsis</i>	<i>Geraea</i>	<i>Encelia</i>	<i>Helianthella</i>
Habit	shrubs to small trees, resinous	shrubs or subshrubs, resinous	perennial herbs or shrubs scapiform	annual or perennial herbs	perennial herbs or shrubs	perennial herbs
Leaves	commonly strigillose to glabrous		canescent or silver velutinous	glandular	canescent	glabrous or hairy
Capitula and capitulescence	discoid or radiate usually solitary or 2-5-headed	radiate usually 2-8-headed	discoid or radiate solitary (2-3)	discoid or radiate solitary to paniculate	discoid or radiate solitary to paniculate	discoid or radiate solitary to corymbose
Phyllaries	2-4(5) seriate, imbricate or subequal, equaling or overtopping the disc, herbaceous to indurate	2-3 seriate, usually equal or subequal, and equaling the disc, herbaceous to subherbaceous	2-3 seriate	2-3 seriate	2-3 seriate	2-4 seriate
Ray florets	neuter or female (sterile) subtentire or 2-lobed		neuter entire or 2-3-lobed	neuter entire or 3-lobed	neuter 3-lobed	neuter 2-3-lobed
Disc corollas	yellow		yellow	golden yellow	yellow or deep purple	yellow or purple
Achenes	laterally compressed to thickened		strongly compressed	strongly compressed	strongly compressed	compressed slightly winged
Pappus	2(3-4) awns (absent), true squamellae absent	2(3-4) awns, sometimes with few squamellae	2 awns with few squamellae	2 awns fused to squamellae	2 (1) awns or absent	2 awns with squamellae or absent
Distribution	Mexico, SW USA	Peru, Bolivia, Chile, Argentina	SW USA	S USA, Mexico	SW USA, Mexico, Chile, Galápagos	W USA, Mexico, SW Canada

including the type *F. laurifolia*. All these species form a strongly supported clade, redefined here as the genus *Flourensia*, which is sister to all the remaining genera of the Enceliinae. They are diagnosed by the combination of the following morphological characters: shrubs or small trees with discoid or radiate capitula, phyllaries

in 2-4(-5) series, usually solitary capitula or weakly cymose 2-5-headed, and disc corollas shallowly to deeply dentate. Within *Flourensia*, the two internal clades identified show low support and scarcely contrasting morphologies. The “microphylla subclade” comprises three shrubby species, *F. microphylla*, *F. pulcherrima*,

and *F. monticola* characterized by having solitary radiate capitula with 10-13(15) ray florets. The close relationship between *Flourensia pulcherrima* and *F. monticola* has been previously recognized by Dillon (1984), as they share lanceolate leaves, capitula with ligules 20-30 mm long, and achenes with sericeous margins and faces sparsely sericeous to glabrescent. The “cernua subclade” comprises also four shrubby species, *F. cernua*, *F. solitaria*, *F. resinosa*, and *F. dentata* characterized by having usually discoid capitula which are solitary or arranged in weakly cymose 2-4(5) headed capitulescences.

South American clade: *Austroflourensia*

This monophyletic group comprises all analyzed South American species of *Flourensia* s.l. i.e. *F. riparia* Griseb., *F. leptopoda* S. F. Blake, *F. oolepis* S. F. Blake, *F. tortuosa* Griseb., *F. suffrutescens* (R.E. Fr.) S.F. Blake, *F. fiebrigii* S.F. Blake, *F. blakeana* M. O. Dillon, and *F. hirta* S. F. Blake. Here, we define the South American clade as the new genus *Austroflourensia*. *Austroflourensia* is diagnosed by the combination of the following morphological characters: shrubs or subshrubs with radiate capitula, phyllaries in 2-3 series, solitary capitula or weakly cymose capitulescences, and disc corollas shortly dentate. Within this clade, the combined analysis shows five species in a basal polytomy and the remaining three species in an unsupported subclade (Fig. 1). The members of this subclade, i.e. *F. hirta*, *F. fiebrigii* and *F. blakeana* were recognized as three species *sensu* Dillon (1984) or a single polymorphic species *sensu* Ospina et al. (2018), the last emphasizing the lack of differentiation in foliar, floral and capitulescence morphology. In the Taxonomic Treatment section, we follow Ospina et al. 2018.

The molecular markers used in this study were not sufficient to clarify the relationships within *Austroflourensia* or within *Flourensia*,

because of the low variability displayed. Future studies using more variable markers would be useful to identify the interspecific relationships within the two groups.

Austroflourensia is sister to *Helianthella* (Fig. 1), although with low support (less than 50%). Both share their glabrous leaves and solitary to corymbose capitula. However, *Austroflourensia* mainly differs from *Helianthella* by its shrub or subshrubby habit, foliage with resin, yellow florets and pappose achenes not winged (Table II). Regarding intergeneric relationships of *Austroflourensia* with the remaining genera of Enceliinae, this genus shares with *Encelia*, *Enceliopsis*, and *Geraea* many morphological characters, e.g. radiate capitula, neuter ray florets, phyllaries 2-3-seriate (Table II). However, *Austroflourensia* species differ mainly from the mentioned genera by their shrub or subshrubby habit, foliage with resin, achenes slightly compressed, and the absence of ray florets with 3-lobed corollas (Table II).

Unfortunately, the phylogenetic relationships between *Austroflourensia* and the remaining North American genera of Enceliinae were not resolved by the molecular markers used here.

Although *Austroflourensia* is vegetatively and reproductively similar to *Flourensia* in their leaves (e.g. shape, size, pubescence), ray and disc florets (e.g. sex, number, disc corolla color), achenes, pappus, and all are resinous plants, they can be mainly differentiated by their shrubby or subshrubby habit (vs. shrubs or small trees), capitula always radiate (vs. radiate or discoid), usually arranged in weakly cymose-corymbose 2-8-headed capitulescences (vs. usually solitary or weakly cymose 2-5-headed capitulescences), phyllaries 2-3-seriate (vs. 2-4(-5)-seriate), and disc corollas shortly dentate (vs. shallowly to deeply dentate) (Table II).

We agree with Dillon (1984) that the North American species of *Flourensia* have greater morphological divergence compared to the South American *Flourensia* species. For example, phyllaries imbricate or subequal, equaling or overtopping the disc florets (vs. usually subequal to equal and equaling the disc florets), disc corollas shallowly to deeply 5-lobed (vs. shallowly 5-lobed), achenes from densely villous-sericeous to glabrous (vs. villous-sericeous to glabrescent) (Figure 2). Dillon (1984) suggested a North American origin for *Flourensia* s.l. based on the greater morphological divergence among North American taxa; this assumption agrees with our phylogenetic results in the sense that there is higher resolution of the North American species as compared to the South American taxa and the sister position of the former (Fig. 1).

We hypothesize that the low sequence divergence and the few morphological differences between *Flourensia* and

Austroflourensia are probably the result of a rapid and recent diversification of their species in the arid and semiarid regions of both hemispheres. The Enceliinae have diversified in many areas of North America since the ancestor of *Austroflourensia* dispersed to South America. For example, species of *Geraea*, *Enceliopsis* and *Helianthella* have adapted to a myriad of habitats including the interior deserts and the chaparral area of the Californian Mediterranean region and the deserts of the western United States. Some species of *Helianthella* are endemic to the Chihuahuan desert and the conifer and conifer-oak forests of northern Mexico, the western United States and western Canada.

In South America, the species of *Austroflourensia* have radiated in the inter-Andean valleys of the High Monte ecoregion (sensu Olson et al. 2001) that hold some of the most arid environments found in the Southern Cone of South America (Abraham

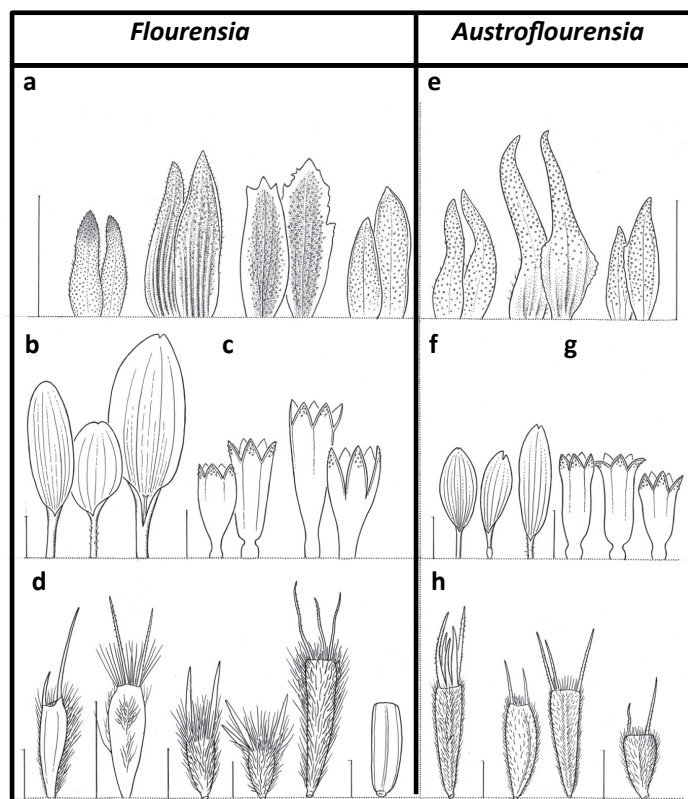


Figure 2. Floral characters showing greater morphological divergence among *Flourensia* s.s. (a-d) than among *Austroflourensia* (e-h): a. Phyllaries: *F. cernua*, *F. collodes*, *F. dentata*, *F. glutinosa*. b. Neuter ray florets: *F. collodes*, *F. glutinosa*, *F. monticola* (ray floret styloferous). c. Disc corollas florets: *F. cernua*, *F. collodes*, *F. glutinosa*, *F. ilicifolia*. d. Achenes: *F. collodes*, *F. cernua*, *F. ilicifolia* (central two), *F. laurifolia*, *F. solitaria*. e. Phyllaries: *A. fiebrigii*, *A. niederleinii*, *A. suffrutescens*. f. Neuter ray florets: *A. fiebrigii*, *A. niederleinii*, *A. suffrutescens*. g. Disc corollas florets: *A. fiebrigii*, *A. niederleinii*, *A. suffrutescens*. h. Achenes: *A. thurifera*, *A. niederleinii* (ray floret with ovary), *A. fiebrigii*, *A. suffrutescens*. Species are shown from left to right. Scale bars: a, b, e, f = 5 mm; c, d, g, h = 2 mm. *Flourensia cernua* (Reina 2003-1243 TEX), *F. collodes* (Cronquist & Souza 10453 TEX), *F. dentata* (García et al. 1190 TEX), *F. glutinosa* (Breedlove 35938 TEX), *F. ilicifolia* (Rodriguez & Carranza s.n. TEX), *F. laurifolia* (Henrickson 22462 TEX), *F. monticola* (Hinton 20738 TEX), *F. solitaria* (Henrickson 20523 TEX). *Austroflourensia fiebrigii* (Pozner & Belgrano 292 SI), *A. niederleinii* (Meyer 4084 SI), *A. suffrutescens* (Cabrera et al. 31606 SI), *A. thurifera* (Aagesen 2/2015 SI).

et al. 2009). However, this expansion has not resulted in differences in growth forms. Sorting out the phylogeny and divergence time of the *Austroflourensia* clade would provide valuable information on the assembling of the arid adapted flora of the Southern Cone.

We recognize that additional multilocus analyses will be necessary to confirm and expand the results obtained here. For now, this study represents the first molecular phylogeny of *Flourensia*, and it strongly supports the polyphyly of the genus and the transfer of the South American species to a new genus, *Austroflourensia*.

Taxonomic treatment

Flourensia DC., Prodr. 5: 592. 1836. –TYPE: *Flourensia laurifolia* DC.

Shrubs or small trees up to 5 m tall; trunks and stems (much-branched, rarely unbranched) with bark gray-brown or brown to black; branchlets resinous, aromatic, pilose to glabrescent. Leaves alternate, sessile to shortly petiolate (petioles 1–20 mm long); blade simple, lanceolate or oblanceolate to ovate, margins dentate or more commonly entire, pinnatinerved with upper and lower surfaces strigillose or puberulent to glabrous, coriaceous, resinous. Capitula discoid or radiate, usually solitary, terminal on branchlets or weakly cymose bracteate, 2–5-headed, sometimes arranged in leafy cymose-paniculiform capitulescences up to 20-headed; peduncles 1–20 cm long. Involucre hemispheric or cylindrical-campanulate; phyllaries 2–4(5) seriate, imbricate or subequal, equaling or overtopping the disc florets, herbaceous to indurate, glandulose to hispid-glandulose, usually ciliolate, resinous; paleae commonly oblanceolate (lanceolate), scarious, apically obtuse to rounded or acute to acuminate, usually glabrous, resinous; receptacle flat to convex. Ray florets 7–21 (or absent), usually

neuter (rarely styliiferous, sterile), corolla yellow, ligulate, ligule oblong to oval, 10–30 mm long, subentire or minutely 2-lobed, tube sericeous (rarely glabrous). Disc florets 10–100 (–150), corollas yellow, cylindrical-campanulate to cylindrical, (3–5) 6–7 (8) mm long, tube 1–1.5 (–2) mm long, shallowly to deeply 5-lobed, lobes 0.3–1.5 (–2.5) mm long, glandulose, resinous; anthers pale, apical appendages ovate, basally subacute; style branches broadly acute to attenuate, dorsally papillose. Achenes laterally compressed to thickened, oblong to obconical, 4–12 mm long, densely villous-sericeous or sometimes margins sericeous and faces sparsely sericeous to glabrescent (rarely glabrous), resinous, often striate. Pappus of 2 (rarely 3 or 4 or absent) awns, ciliolate, usually persistent; true squamellae absent (Figure 2).

Distribution and habitat. The genus is found on dry, limestone slopes and rocky soils, mainly restricted to Mexico, only two species (*F. cernua* and *F. pringlei*) extend into the southwestern United States, inhabiting the Chihuahuan Desert region and the tropical deciduous forests of eastern and southern Mexico, between 400–2100 m. (Figure 3).

Thirteen North American species:

1. *Flourensia cernua* DC., Prodr. 5: 593, 1836.

Based on the same type *Helianthus cernuus* (DC.) Benth. & Hook. f. ex Hemsl., Biol. Cent.-Amer. Bot. 2: 179, 1881.

Type: Mexico. Nuevo León: Monterrey, Jan 1828, *J. L. Berlandier 1401* (lectotype: G-DC 00454733! IDC Microfiche 800. 952: l. 5, designated by Dillon 1984: 13; isolectotypes: BM 001009702!, F 0050233F!, G-DC 00454733!, GH 00008151!, HAL 0111375!, K 000497236!, MO 191011!).

2. *Flourensia collodes* (Greenm.) S.F. Blake, Proc. Amer. Acad. Arts 49: 373, 1913.

Basionym: *Encelia collodes* Greenm., Proc. Amer. Acad. Arts 39: 110, 1903.

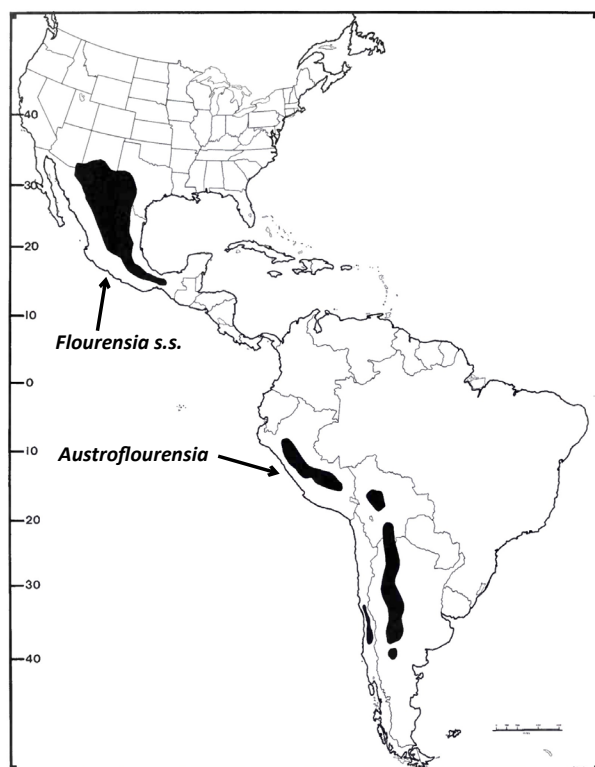


Figure 3. Distribution of *Flourensia* and *Austroflourensia* (modified from Dillon 1984).

Type: Mexico. Chiapas: along road from Ocuilapa to Tuxtla, 2100-3000 ft, 29 Aug 1895, *E. W. Nelson 3017* (lectotype: GH 00006548!, designated by Dillon (1984: 22); isolectotype: US 00125364!).

3. *Flourensia dentata* S.F. Blake, *J. Wash. Acad. Sci.* 25: 315, 1935.

Type: Mexico. Durango: Terreros near Pedriceño, campos guayuleros, ad viam, 11 Nov 1925, *S. Juzepczuk 609* (holotype: US 00125309!; isotype-fragment: TEX).

4. *Flourensia glutinosa* (B.L. Rob. & Greenm.) S.F. Blake, *Proc. Amer. Acad. Arts* 49: 374, 1913.

Basionym: *Encelia glutinosa* B.L. Rob. & Greenm., *Amer. J. Sci. ser 3*, 50: 155, 1895.

Type: Mexico. Oaxaca: Las Hoyas Canyon, 4500 ft, 2 Nov 1894, *C. G. Pringle 6024* (holotype: GH 00006552!; isotypes: AC 00319394!, BKL 00000257!, BM 001009700!, BR 0000005267439!, CM 2329!, E 00413813!, M 0029997!, G 00223811!,

G 00223812!, GH 00006553!, GOET 001556!, ISC v-0000089!, JE 00000736!, MSC 0091664!, MEXU 01215344!, MIN 1000915!, P 02140235!, NDG 66119!, NY 00168342!, P 02140236!, RSA 0001102!, S G-2255!, TEX 00000448!, UC 88692!, US 00125368!, UVMVT 027533!

5. *Flourensia ilicifolia* Brandegee, *Zoe* 5: 238, 1906.

Type: Mexico. Coahuila: Arroyo near Parras, Mar 1905, *C. A. Purpus 1150* (holotype: UC 88726!; isotypes: BM 001009701!, F 0050234F!, GH 00008153!, GH 00008154!, MO 191010!, NY 00169382!, RSA 0001199!, UC 88726!).

6. *Flourensia laurifolia* DC., *Prodr.* 5: 592, 1836.

Type: Mexico. Tamaulipas: between Vittoria [Victoria] and Tula, Nov 1830, *J. L. Berlandier 2205* (lectotype: G-DC 00454719! IDC Microfiche 800. 952: I. 3, designated by Dillon 1984: 10; isolectotypes: BM 001009706!, F 0050235F!, G-DC00454719! IDC Microfiche 800. 952: I. 4, GH 00008155!, K 000497238!, MO 191009!, NY 00169383!, P 00710145!, P 00710146!).

Nomenclatural synonym: *Helianthus laurifolius* (DC.) Benth. & Hook. f. ex Hemsl., *Biol. Cent.-Amer. Bot.* 2: 179, 1881.

7. *Flourensia microphylla* (A. Gray) S.F. Blake, *Proc. Amer. Acad. Arts* 49: 374, 1913.

Basionym: *Encelia microphylla* A. Gray, *Proc. Amer. Acad. Arts* 15: 37, 1879.

Type: Mexico. Coahuila: gravelly hills near Saltillo, Aug 1878, *C. C. Parry 462* (holotype: GH 00006557!; isotypes: K 000497235!, NY 00168344!).

8. *Flourensia monticola* M.O. Dillon, *Southw. Naturalist* 21: 147, 1976.

Type: Mexico. Coahuila: dry, limestone and shale slopes, 13.5 km E of Los Lirios, 24 km of La Jacinta (N.L.) very near Nuevo León state line, 2150 m, 7 Nov 1972, *F. Chiang, T. Wendt & M. C. Johnston 10130* (holotype: TEX 00373838!; isotype: MEXU 00563376!).

9. *Flourensia pringlei* (A. Gray) S.F. Blake, Proc. Amer. Acad. Arts, 49: 375, 1913.

Basionym: *Helianthella pringlei* A. Gray, Proc. Amer. Acad. Arts, 21: 389, 1886.

Type: Mexico. Chihuahua: rocky hills near Chihuahua City, 7 Sep 1885, C. G. Pringle 646 (holotype: GH 00008795!; isotypes: AC 00319448!, BR 0000005317875!, COLO 00369785!, CORD 00005416!, CORD 00005417!, GOET 001606!, JE 00004592!, K 000497232!, M 0029998!, MICH 1107439!, MO 191008!, MO 193873!, NY 00179066!, NY 00179067!, P 02140272!, P 02140273!, P 02140274!, PH 00014138!, PH 00014139!, RSA 0001270!, US 00931081!, US 00125393!, UVMVT 027535!).

Taxonomic synonym: *Encelia oblonga* B. L. Rob. & Fernald, Proc. Amer. Acad. Arts 30, 118, 1894. **Type:** Mexico. Chihuahua: plains near Casas Grandes, 10 Oct 1891, C. V. Hartman 812 (holotype: GH 00006559!; isotype: K 000497233!, US 00125375!).

10. *Flourensia pulcherrima* M.O. Dillon, Southw. Naturalist 21: 145, 1976.

Type: Mexico. Durango: steep limestone slopes, N end of Sierra de Rosario ca. 20 km SW of Mapimi and 3 km E of Santa Librada, 2000 m, 25 Jun 1973, M. C. Johnston, F. Chiang & T. Wendt 11469 (holotype: TEX 00373837!; isotype: MEXU).

11. *Flourensia resinosa* (Brandegee) S.F. Blake, Proc. Amer. Acad. Arts 49: 375, 1913.

Basionym: *Encelia resinosa* Brandegee, Zoe 5: 240, 1906.

Type: Mexico. Hidalgo: Ixmiquilpan, mountains, Aug 1905, C. A. Purpus 1458 (holotype: UC 125663!; isotypes: F 0050236F!, GH 00006563!, MO 191006!, NY 00168348!).

12. *Flourensia retinophylla* S.F. Blake, Proc. Amer. Acad. Arts, 49: 505, 1913.

Type: Mexico. Coahuila: Sierra de la Paila, Nov 1910, C. A. Purpus 4728 (holotype: GH 00008156!; isotypes: BM 001009705!, F 0050237F!, MO 191007!, NY 00169384!, UC 148360!, US 00125314!).

13. *F. solitaria* S.F. Blake, J. Wash. Acad. Sci. 40: 49, 1950.

Type: Mexico. Coahuila: rocky flats and slopes, top of grade at Cuesta de Zozaya, road from Ocampo W over mountains to Puertecito via Cuesta de Zozaya, 20 Sep 1941, I. M. Johnston 9289 (holotype: GH 00008157!; isotypes: LL 00373841!, US 00125316!).

Austroflourensia J.C. Ospina & S.E. Freire, **gen. nov.** –TYPE: *Austroflourensia thurifera* (Molina) J.C. Ospina & S.E. Freire. Figure 4.

Austroflourensia is distinguished from *Flourensia* by its shrubby or subshrubby habit, capitula always radiate, usually arranged in weakly cymose-corymbose capitulescences,

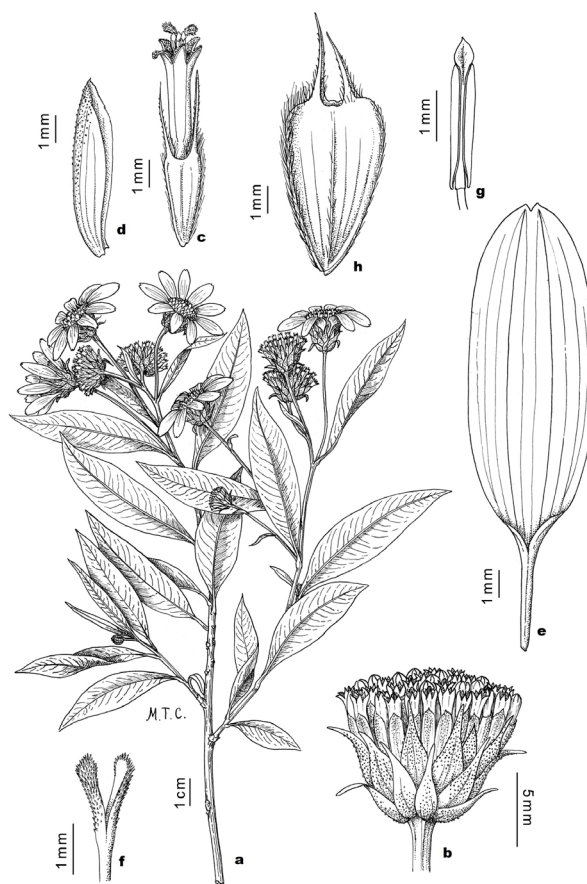


Figure 4. *Austroflourensia thurifera* [sub *F. riparia* from Ariza and Ospina in *Fl. Argentina* 7(2): 210. 2015]. a: Habit; b: Capitulum without ray florets; c: Disc floret; d: Palea; e: Ray floret (neuter); f: Style branches; g: Stamen; h: Disc achene.

phyllaries 2–3-seriate, and disc corollas shortly dentate.

Shrubs or subshrubs up to 2 (3) m tall; stems usually ascending, rarely erect or erect to ascending, much-branched, rarely unbranched with bark brown to gray; branchlets resinous, aromatic, pilose-hirsute or puberulous to glabrescent. Leaves alternate, sessile to shortly petiolate (petiole 1–17 mm long); blade simple, linear-lanceolate or oblanceolate to ovate, margins dentate or more commonly entire, pinnatinerved with upper and lower surfaces densely hirsute or sericeous or more commonly strigillose to glabrous, coriaceous, resinous. Capitula radiate, usually weakly cymose-corymbose bracteate 2–8-headed, more rarely solitary, terminal on branchlets or arranged in leafy cymose-paniculiform capitulescences up to 20-headed; peduncles 0.5–11 cm long. Involucre usually hemispheric, sometimes campanulate or cylindrical-campanulate; phyllaries 2–3-seriate, usually subequal to equal, more rarely imbricate, sometimes overtopping the disc florets, herbaceous to subherbaceous, usually ciliolate or hirsute-pilose, resinous; paleae oblanceolate, scarious, apically obtuse (acute) to rounded or truncate, usually glabrous, resinous; receptacle flat to convex. Ray florets 5–21, usually neuter (rarely with an ovary or style, sterile), corolla yellow, ligulate, ligule oblong to oval, 7–50 mm long, subentire or minutely 2-lobed, tube sericeous or villous (glabrous). Disc florets 10–75, corollas yellow, cylindrical-campanulate to cylindrical, (3–)4–7 mm long, tube (0.5–0.8) 1–1.5 mm long, shallowly 5-lobed, lobes 0.5–1 mm long, resinous; anthers pale, apical appendages ovate, basally subacute; style branches broadly acute to attenuate, dorsally papillose. Achenes laterally compressed to thickened, oblong to obconical, 4–11 mm long, densely villous-sericeous or sometimes margins sericeous and faces sparsely sericeous to

glabrescent, resinous. Pappus of 2 (rarely 3 or 4) awns, ciliolate, usually persistent; sometimes with highly developed squamellae between the pappus awns (Figure 2).

Etymology. The name *Austroflourensia* combines its southern distribution (from Latin *australis*=southern) with the genus name *Flourensia*.

Distribution and habitat. The genus is found on dry, rocky slopes in the Andes of Peru, Bolivia, Chile, and northern Argentina (500–4000 m) to southern Argentina in the Patagonian steppe (250–360 m). Figure 3.

Comments. Ospina et al. (2018), based on a morphometric study, recognized twelve South American species of *Flourensia*, i.e. *F. angustifolia*, *F. cajabambensis*, *F. fiebrigii* (= *F. blakeana* and *F. hirta*), *F. heterolepis*, *F. hirtissima*, *F. macrophylla*, *F. niederleinii*; *F. peruviana*, *F. polycephala*, *F. thurifera* (= *F. campestris*, *F. leptopoda*, *F. oolepis* and *F. riparia*), *F. tortuosa* (= *F. macroligulata*) and *F. suffrutescens*. Until further studies employing more variable DNA regions with extensive sampling increase our knowledge on this genus, the following necessary combinations are proposed according to Ospina et al. (2018).

Twelve South American species:

1. *Austroflourensia angustifolia* (DC.) J.C. Ospina & S.E. Freire, **comb. nov.**

Basionym: *Flourensia thurifera* var. *angustifolia* DC., Prodr. 5: 592. 1836; based on the same type *Flourensia angustifolia* (DC.) S.F. Blake, Contr. U.S. Natl. Herb. 20: 407, 1921.

Type: Peru. Junin: Tarma, *J. Dombey* 24 pro parte (lectotype: G-DC 00454735!, designated by Dillon (1984 p. 35), specimen on the right).

2. *Austroflourensia cajabambensis* (M.O. Dillon) J.C. Ospina & S.E. Freire, **comb. nov.**
Basionym: *Flourensia cajabambensis* M.O. Dillon, Brittonia 38(1): 32 (no 32–34), f. 1, 1986.

Type: Peru. Cajamarca: ca. 8 km NW of Cajabamba, between Huamachuco and

Cajamarca; ca. 2550 m. 11 Jan. 1983, *M. Dillon et al.* 2855 (holotype: F 0043624F!; isotypes: NY 00169386!, TEX 00373839!, US 00005458!).

3. *Austroflourensia fiebrigii* (S.F. Blake) J.C. Ospina & S.E. Freire, **comb. nov.**

Basionym: *Flourensia fiebrigii* S.F. Blake, Bot. Jahrb. Syst. 54: 47, 1916.

Type: Bolivia. Tarija: W of Tarija, summit of pass near Paicho, 3200 m, 5 Feb 1904, *K. Fiebrig* 3050 (lectotype: F0050241F!, designated by Dillon 1984: 51; isolectotypes: BM 001009697!, G 00223813!, GH 00008161!, K 000497230!, LIL 001728!, LP 002053! fragment ex F, MO, S-R-2343!, SI 000864!, US 00125310!).

Taxonomic synonyms: *Flourensia hirta* S. F. Blake, Contr. U.S. Natl. Herb. 20: 402, 1921.

Type: Argentina. La Rioja: en las cercanías de Los Corrales, Sierra Famatina, 7 Feb 1897, *G. Hieronymus* & *G. Niederlein* 635 (lectotype: GH 00008162!, fragment ex Bt, designated by Dillon (1984 p. 54); isolectotype, CORD 00004562!). *Flourensia blakeana* M. O. Dillon (1981 p. 108).

Type: Argentina. Tucumán: [Tafí del Valle], along Ruta 307 at Km 95-105, between Amaicha del Valle and Tafí del Valle, 2900-3000 m s.m., 22 Feb 1973, *M. O. Dillon* & *E. Rodríguez* 560 (holotype: LL; isotypes: BM 001009695!, F 0050239F!, HUT, LP, MO, NY 00169385!, USM).

4. *Austroflourensia glutinosa* (Rusby) J.C. Ospina & S.E. Freire, **comb. nov.**

Basionym: *Viguiera glutinosa* Rusby, Mem. Torrey Bot. Club 4(3): 211, 1895; based on the same type *Flourensia heterolepis* S.F. Blake, Contr. Gray Herb. 54: 186, 1918, nov. nom. pro *V. glutinosa* Rusby, non *F. glutinosa* (B.L. Rob. & Greenm.) S.F. Blake, Proc. Amer. Acad. Arts 49: 374, 1913.

Type: Bolivia. Cochabamba: Cochabamba, 1891, *M. Bang* 977 (lectotype: NY 00277958!, designated here; isolectotypes: A 00013998!, BM 001009698!, E 00413812!, GH 00013997!, K 000497231!, M 0029967!, MICH 1107892!, MO-1183131!, NDG 60006!, NY 00277956!, NY 00277957!

(on the same sheet of NY 00277956!); NY 277959! (on the same sheet of NY 00277958!), PH 00028996!, US 00125085!).

5. *Austroflourensia hirtissima* (S.F. Blake) J.C. Ospina & S.E. Freire, **comb. nov.**

Basionym: *Flourensia hirtissima* S.F. Blake, Contr. U.S. Natl. Herb. 22(8): 629, 1924.

Type: Argentina. Río Negro: General Roca, 250-360 m, 31 Dec 1914, *W. Fisher* 194 (holotype, US 00125312!; isotypes, BM 001009694!, F 0050242F!, CORD 00004564!, GH 00008163!, LP 002057!, MO, NY 00169388!, SI 000865!).

6. *Austroflourensia macrophylla* (S.F. Blake) J.C. Ospina & S.E. Freire, **comb. nov.**

Basionym: *Flourensia macrophylla* S.F. Blake, Bot. Jahrb. Syst. 54: 47, 1916.

Type: Peru. Lima: Huarochiri, stony places, 1650-2370 m, along Lima-Oroya Railroad, between Matucana and Tambo de Viso, 26 Dec 1901, *A. Weberbauer* 119 (lectotype-fragment: GH 00008165!, designated by Dillon 1984: 35).

7. *Austroflourensia niederleinii* (S.F. Blake) J.C. Ospina & S.E. Freire, **comb. nov.**

Basionym: *Flourensia niederleinii* S.F. Blake, Contr. U.S. Natl. Herb. 20: 404, 1921.

Type: Argentina. La Rioja: Cuesta de Miranda, Sierra Famatina, 10 Mar 1879, *G. Hieronymus* and *G. Niederlein* 876 (lectotype GH 00008166!, fragment ex Bt, designated by Dillon 1984: 54; isolectotypes CORD 00004565!, G 00223810!).

8. *Austroflourensia peruviana* (M.O. Dillon) J.C. Ospina & S.E. Freire, **comb. nov.**

Basionym: *Flourensia peruviana* M.O. Dillon, Ann. Missouri Bot. Gard. 68(1): 108, 1981.

Type: Peru. Huancavelica: Huancavelica, Checcyancu, 4 km E de Conaica, 3000-3500 m, 14 Mar 1971, *O. Tovar* 193 (holotype: US 00125313!; isotypes: F 0043625F!, LP 002056!, MOL 00006509!).

9. *Austroflourensia polycephala* (M.O. Dillon) J.C. Ospina & S.E. Freire, **comb. nov.**

Basionym: *Flourensia polycephala* M.O. Dillon, Ann. Missouri Bot. Gard. 68(1): 106, 1981.

Type: Peru. Cuzco: Calca, Pisac, 3000 m, Apr 1943, *F. Marin* 231 (holotype: LIL; isotype: F 0043780F!).

10. *Austroflourensia suffrutescens* (R.E. Fr.) J.C. Ospina & S.E. Freire, **comb. nov.**

Basionym: *Encelia suffrutescens* R.E. Fr., *Nova Acta Regiae Soc. Sci. Upsal.*, ser. 4, 1(1): 83., 1905; based on the same type *Flourensia suffrutescens* (R.E. Fr.) S.F. Blake, *Proc. Amer. Acad. Arts* 49: 376, 1913.

Type: Argentina. Jujuy: El Moreno, in declivibus montis saxosis, 3600 m, 16 Dec 1901, *R. E. Fries* 926 (holotype: UPS; isotypes: CORD 00004556!, S-R-1912!, US 00125382!).

Taxonomic synonyms: *Flourensia polyclada* S. F. Blake, *Contr. U.S. Natl. Herb.* 20: 403, 1921. **Type:** Argentina. La Rioja: entre la Cueva de la Mesada y La Encrucijada, Sierra Famatina, 31 Jan 1879, *G. Hieronymus* & *G. Niederlein* 541 (lectotype: GH 00008168! fragment ex B†, designated by Ariza Espinar & Ospina 2015: 210; isolectotypes: CORD 00004567!, CORD 00004568!, G 00223809!)

11. *Austroflourensia thurifera* (Molina) J.C. Ospina & S.E. Freire, **comb. nov.**

Basionym: *Helianthus thurifera* Molina, *Sag. Stor. Nat. Chili* 160, 1782; based on the same type *Diomedea thurifera* (Molina) Bertero ex Colla, *Mém. Acad. Imp. Sci. Turin, Sci. Phys.* 38: 37. t. 31, 1835, *F. thurifera* (Molina) DC., *Prodr.* 5: 592, 1836.

Type: Chile. Valparaiso: sonnige Abhänge, 7 Oct 1895, *O. Buchtien* s.n. (neotype: US!, designated by Dillon 1984: 30; isoneotype: GH!).

Taxonomic synonyms: *Helianthus glutinosus* Hook. & Arn., *Bot. Beechey Voy.* 33, 1830. **Type:** Chile: Valparaiso, *T. Bridges* s.n. (holotype: GL). *Flourensia besseriana* Meyen & Walpers 1843: 270; based on the same type: *Helianthus besseriana* Benth. & Hook. f., *Gen. Pl.* 2: 376, 1873, nom. inval. **Type:** Chile. No exact locality: *B. Besser* s.n. (holotype B†; lectotype-fragment: GH, designated by Dillon 1984: 30; photo of B† specimen: F!). *Flourensia thurifera*

var. *lanceolata* J. Rémy in Gay, *Fl. Chil.* 4: 288, 1849.

Type: Chile (probably P, not located). *Flourensia campestris* Griseb., *Abh. Königl. Ges. Wiss. Göttingen* 19: 184, 1874; based on the same type: *Helianthus campestris* (Griseb.) Kuntze, *Revis. Gen. Pl.* 3: 157, 1898. **Type:** Argentina. Córdoba: Sudostlich von Córdoba, 1871, *P. G. Lorentz* 245 (lectotype: GOET 001555!, designated by Dillon 1984: 56; isolectotypes: CORD 00006330!, GH-fragment 00008159!). *Flourensia riparia* Griseb., *Abh. Königl. Ges. Wiss. Göttingen* 24: 196, 1879; based on the same type: *Helianthus riparius* (Griseb.) Kuntze, *Revis. Gen. Pl.* 3: 157, 1898. **Type:** Argentina. Salta: pasaje del Río Juramento, Feb 1873, *P. G. Lorentz* & *G. Hieronymus* 268 (lectotype: GOET 001557!, designated by Dillon 1984: 56; isolectotypes: CORD 00006484!, CORD 00006485!, CORD 00006486!, G 00223808!, GH 00008169!, GH 00008170!, GOET 001558!, SI 000866!, US; probable isolectotypes: NY 00169389!, S, s.n.). *Flourensia oolepis* S. F. Blake, *Contr. U.S. Natl. Herb.* 20: 406, 1921. **Type:** Argentina. Córdoba: Cuesta de la Oyada, Sierra Achala, 22 Mar 1876, *G. Hieronymus* s.n. (lectotype-fragment: GH 00008167!, designated by Dillon 1984: 48). *Flourensia grindelioides* S. Moore, *J. Bot.* 64: 192, 1926. **Type:** Argentina. [San Luis in the protologue]: no exact locality, Feb 1926, *D. Wright* s.n. (holotype: BM 001009696!; isotypes: GH, MO, US). *Flourensia leptopoda* S. F. Blake, *Contr. U.S. Natl. Herb.* 20: 406, 1921. **Type:** Argentina. La Rioja: Farrecillas, 5 Mar 1906, *J. S. Urriche* s.n. (lectotype-fragment: GH 00008164!, designated by Dillon 1984: 62).

12. *Austroflourensia tortuosa* (Griseb.) J.C. Ospina & S.E. Freire, **comb. nov.**

Basionym: *Flourensia tortuosa* Griseb. *Abh. Königl. Ges. Wiss. Göttingen* 19: 184, 1874. **Type:** Argentina. Catamarca: in Camp von Belén bis Yakutula, 24 Jan 1872, *P. G. Lorentz* 659 (lectotype: GOET 001559!, designated by Dillon 1984: 47; isolectotypes: CORD 00006331!, CORD 00006332!).

Taxonomic synonym: *Flourensia macroligulata* Seeligm., Lilloa 30: 113, 1960. **Type:** Argentina. Jujuy: Volcán, Loma de la Laguna, 15 Feb 1924, R. Schreiter 2663 (holotype: LIL 001729!).

Key to the Genera of Enceliinae subtribe (modified from Panero 2007)

1. Plants scapiform with leaves all or mostly basal and capitula on long leafless peduncles *Enceliopsis*
- 1'. Plants not scapiform.....2
2. Shrubs or small trees.....3
- 2'. Annual or perennial herbs 5
3. Achenes strongly compressed; leaves never resinous or glutinous; disc corollas yellow or deep purple *Encelia*
- 3'. Achenes laterally compressed to thickened; leaves resinous or glutinous; disc corollas yellow4
4. Shrubby or subshrubby; capitula radiate, usually corymbose 2-8-headed, rarely solitary or paniculiform cymes up to 20-headed, phyllaries 2-3-seriate, usually subequal to equal, rarely imbricate, sometimes overtopping the disc florets, herbaceous to subherbaceous; disc corollas shortly dentate.....*Austroflourensia*
- 4'. Shrubby or small trees; capitula discoid or radiate, usually solitary or weakly cymose 2-5-headed, sometimes paniculiform up to 20, phyllaries 2-4(5) seriate, imbricate or subequal, equaling or overtopping the disc florets, herbaceous to indurate; disc corollas shallowly to deeply 5-lobed *Flourensia*
5. Phyllaries conspicuously ciliate; cypselae apices with a conspicuous crown surrounding neck of cypselae and fused to awn..... *Geraea*
- 5'. Phyllaries glabrescent to pubescent, rarely ciliate; cypselae apices without a crown surrounding neck 6
6. Achenes epappose or with a pappus of two awns and short squamellae*Helianthella*

6'. Achenes with pappus of two (rarely absent or one) awns, without squamellae*Encelia*

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SUPPLEMENTARY MATERIAL

Appendix S1. Combined data matrix (ITS + *psbA-trnH*) used in the simultaneous analysis. The codification as Presence/Absence of informative indels for the ingroup are also shown.

Figure S1. Parsimony strict consensus tree obtained from the separate analysis of the nuclear matrix. The two clades of *Flourensia* are indicated: North American species clade and the South American species clade. Numbers above branches indicate Bootstrap values (BS) and below branches Posterior probabilities (PP) obtained in the Bayesian analysis of the same matrix. Only values of BS \geq 50% and PP \geq 0.95 are reported.

Figure S2. Maximum Credibility Tree obtained from the Bayesian analysis of the nuclear matrix. The tree is visualized with FigTree and Posterior probabilities are shown. The two clades of *Flourensia* and the Enceliinae subtribe are indicated.

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Author Contributions

LLA planned the research. SEF led the writing of the paper. MAS and JCO obtained the molecular evidence. MAS conducted the phylogenetic analysis and produced figures 1a, b. SEF produced figure 2 and table 2. SEF, JLP, LAE, and JCO, examined morphological characters of taxonomic relevance. All authors contributed to literature review, interpretation of the analysis, participated in taxonomy decisions, and approved the final draft.

