

Transfers to *Simsia* and description of *Davilanthus*, a new genus of Asteraceae (Heliantheae)

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Abstract. Taxonomic changes are made to reflect a reassessment of morphology based on the results of molecular phylogenetic studies. A new genus, *Davilanthus*, is described to include six species that collectively form the sister group to *Simsia*, and includes the following species transferred from *Viguiera*: *Davilanthus davilae*, *Davilanthus hidalgoanus*, *Davilanthus hypargyreus*, *Davilanthus huajuapanus*, *Davilanthus purpusii*, and *Davilanthus sericeus*. Three species formerly placed in *Viguiera* ser. *Grammatoglossae* are transferred to *Simsia*: *Simsia benziorium*, *Simsia ovata*, and *Simsia rhombifolia*.

Key Words: *Davilanthus*, *Simsia*, *Viguiera*, Helianthinae, Asteraceae.

The delimitation of *Simsia* is one of several remaining problems for the generic level taxonomy of subtribe Helianthinae (Schilling & Panero, 2002). Although there is a core of species of *Simsia* that exhibit a highly distinctive cypselae, characterized by lateral flattening as well as a pappus of narrow awns and lack of intermediate scales, there is an additional suite of a relatively small number of intergrading characters whose plasticity and inconsistency of correlation make it difficult to erect an exact boundary for the genus. Even though it was clearly recognized, the thorough field studies and quantitative morphological analyses of Spooner (1990) have not provided a decisive resolution to this problem. The larger suite of morphological features includes nodal disks, herbaceous phyllaries, long and narrow ray ovaries, long and tapering style branches, and setose anther connectives that collectively characterize the genus, but are not all found in every species (Spooner, 1990; Panero & Schilling, 1992). Two novel species that had biconvex rather than flattened cypselae but most of the other distinctive morphological features of the genus were placed by Panero and Schilling

(1992) in *Simsia*. There are also three species of *Viguiera* ser. *Grammatoglossae*, a group defined in part by herbaceous phyllaries (Blake, 1918), that closely resemble *Simsia* and exhibit most of these traits, but that have biconvex cypselae. These species are placed by plastid DNA analyses in a clade together with members of *Simsia* (Schilling & Panero, 1996a). The plastid DNA based phylogeny does not provide a definitive test, because some other distinctive elements, including some but not all species of *Tithonia*, were also placed in the same clade; later study using the nuclear ITS region suggested that this may have been based on plastid DNA transfer through past hybridization (Schilling & Panero, 1996b). Hence, there is the need for additional data to clarify the limits of *Simsia*.

The current study expanded the nuclear ITS data set to include a comprehensive sampling of species that were part of the plastid DNA-based clade that included *Simsia* to evaluate the delimitation of the genus. Sampling included all of the species of *Viguiera* ser. *Grammatoglossae*, all currently recognized species of *Simsia*, as well as

representative samples of *Alvordia*, *Lagascea*, *Tithonia*, and *Viguiera* subgen. *Amphilepis*. The results helped to clarify the limits of *Simsia* and to identify its closest outgroup, which is here described as the new genus *Davilanthus*.

Materials and methods

Plant Material. Samples for analysis included some collected fresh in the field and others from herbarium specimens at TENN (Table 1). Previously published sequences from a species of *Helianthus* (AF047970), and one of *Phoebanthus* (AF047971), were utilized as outgroups for phylogenetic analysis; both genera have been comprehensively analyzed for ITS sequence data and are suggested by both plastid DNA and ITS analyses (Schilling & Panero, 1996b) to be a near outgroup to the species being analyzed in the current study.

Molecular Methods. Preparations of total DNA were performed with the Dneasy Plant Minikit (Qiagen, Valencia CA) and typically utilized a portion (ca 0.1 g) of a single leaf. The crude DNA extracts of some samples required further purification using the Wizard Kit protocol (Promega, Madison WI). ITS amplifications were performed in 20 μ l reactions using 10–20 ng of genomic DNA, 10X PCR buffer (Promega), 1.8–2.25 mM MgCl₂, 0.2 mM each dNTP, 1.25 units of *Taq* polymerase, and 0.2 μ M each primer. Primers used were “ITS-4” (5'-TCCTCCGCTTATT GATATGC-3') and “ITS-5” (5'-GGAAG TAAAAGTCG-TAACAAGG-3'; White et al., 1990). PCR was performed with the “ETS” protocol: 95°C for 2 min; 10 cycles of 95°C for 1 min, 55°C for 1 min, and 72°C initially for 1 min, with 4 sec added per cycle; 20 cycles of 95°C for 1 min, 50°C for 1 min, and 72°C initially for 1:40, with 4 sec added per cycle; and a final extension of 72°C for 7 min. All PCR products were checked by agarose gel electrophoresis. Sequences were prepared utilizing the ABI Prism Dye Terminator Cycle Sequencing reaction kit and run at the University of Tennessee Automated Sequencing Facility on an ABI 3100 DNA sequencer (Perkin-Elmer Inc., Foster City, CA). The initial sequence data text files were edited following comparison with the same data dis-

played in four-color electropherograms before they were analyzed further. Sequence alignment was performed manually. GenBank accession numbers are provided in Table 1.

Data Analysis. Phylogenetic relationships were analyzed using both maximum parsimony and Bayesian approaches, implemented with the computer programs PAUP* 4.0b10 (Swofford, 2003) and MrBayes 3.1.2 (Huelsenbeck & Ronquist, 2001). For maximum parsimony, a heuristic search with 1,000 random addition replicates and with TBR branch swapping was used, with gaps treated as missing data. Bootstrap analysis (Felsenstein, 1985) was performed with 1000 replicates using the “Faststep” search strategy. Bayesian analysis was run for a million generations with four separate chains and trees saved every 1000 generations. The number of trees to discard as “burn-in” was assessed by plotting likelihoods of trees sampled throughout the run and discarding all trees prior to the stable likelihood plateau (in this case the first 15% were discarded). An appropriate maximum likelihood model of sequence evolution (GTR+I+G; General Time Reversible model with a proportion of invariant sites and gamma distributed rates) for the Bayesian analysis was chosen using Modeltest (Posada and Crandall, 1998). Plastid DNA restriction site data from Schilling and Panero (1996a) were available for 39 of the 58 samples as well as the two outgroup taxa and were analyzed separately using maximum parsimony and bootstrap approaches. A partition homogeneity analysis of the ITS and plastid data sets was run using PAUP.

Results

The ITS region in the majority of samples of *Simsia* and other Helianthinae that were sequenced was of length 651 bp, although some length variability from 647 to 653 bp was observed. Alignment did not present any issues, with a total of 13 gaps required, all of which were short (1–4 bp) insertions or deletions and most present either in a single sample or in a group of related samples. Most of the samples gave clean sequence, with at most three polymorphic positions, although a few, notably in *Viguiera* subgen. *Amphilepis*,

TABLE I

SPECIES OF *SIMSIA* AND RELATED GENERA SAMPLED FOR DNA SEQUENCE DATA, VOUCHERS AT TENN UNLESS OTHERWISE NOTED; JP, JOSE L. PANERO; ES, EDWARD SCHILLING; DS, DAVID SPOONER; OS, OTMAR SPRING; JV, JOSE L. VILLASEÑOR.

Species	Voucher	Genbank
<i>Alvordia</i> Brandegee		
<i>A. fruticosa</i> Brandegee	JP 2846	GQ864155
<i>A. glomerata</i> Brandegee	JP 2833	GQ864156
<i>Davilanthus</i> E. E. Schill. & Panero		
<i>D. davilae</i> (Panero & Villaseñor) E. E. Schill. & Panero	JP 2581	GQ864149
<i>D. hidalgoanus</i> (E. E. Schill. & Panero) E. E. Schill. & Panero	ES & JP 88-28	GQ864151
<i>D. huajuapanus</i> (Panero & Villaseñor) E. E. Schill. & Panero	JP et al. 6141	GU053571
<i>D. hypargyreus</i> (B. L. Rob. & Greenm.) E. E. Schill. & Panero	JP 2832	GQ864150
<i>D. purpusii</i> (Brandegee) E. E. Schill. & Panero	JP 2313	GQ864152
<i>D. sericeus</i> (S. F. Blake) E. E. Schill. & Panero	JP 2595	GQ864148
<i>Lagascea</i> Cav.		
<i>L. helianthifolia</i> HBK.	JP 3061	GQ864099
<i>L. decipiens</i> Hemsl.	ES & OS 297	GQ864100
<i>Simsia</i> Pers.		
<i>S. amplexicaulis</i> (Cav.) Pers.	ES & JP 88-27	GQ864104
<i>S. annectens</i> S. F. Blake var. <i>annectens</i>	JP 1732	GQ864105
<i>S. annectens</i> var. <i>grayi</i> (Sch.-Bip.) D. M. Spooner	JP & ES 443	GQ864106
<i>S. benziorum</i> (B. L. Turner) E. E. Schill. & Panero	JP 1814	GQ864101
<i>S. calva</i> (A. Gray & Engelm.) A. Gray	ES & DS 84-1	GQ864107
<i>S. chaseae</i> (Millsbaugh) S. F. Blake	DS 2880	GQ864108
<i>S. dombeyana</i> DC.	JP 1336	GQ864109
<i>S. eurylepis</i> S. F. Blake	DS 2885	GQ864110
<i>S. foetida</i> (Cav.) S. F. Blake	DS 2699	GQ864111
<i>S. fruticulosa</i> (Spreng.) S. F. Blake	DS 2918	GQ864112
<i>S. ghiesbreghtii</i> (A. Gray) S. F. Blake	JP 1803	GQ864113
<i>S. holwayi</i> S. F. Blake	DS 2692	GQ864114
<i>S. lagascaeformis</i> DC.	ES & OS 313	GQ864115
<i>S. molinae</i> H. Rob. & R. D. Brettell	DS 2701	GQ864116
<i>S. ovata</i> (A. Gray) E. E. Schill. & Panero	ES & JP 88-36	GQ864102
<i>S. rhombifolia</i> (Rob. & Greenm.) E.E.Schill. & Panero	ES & JP 88-31	GQ864103
<i>S. sanguinea</i> A. Gray	JP 2406	GQ864117
<i>S. santarosensis</i> D. M. Spooner	DS 2900	GQ864118
<i>S. setosa</i> S. F. Blake	DS & JV 2528	GQ864119
<i>S. spooneri</i> Panero & E. E. Schill.	JP 2032	GQ864120
<i>S. steyermarkii</i> H. Rob. & R. D. Brettell	DS 2748	GQ864121
<i>S. sylvicola</i> Panero & E. E. Schill.	ES & JP 88-35	GQ864122
<i>S. tenuis</i> (Fern.) S. F. Blake	DS & JV 2550	GQ864123
<i>S. villasenorii</i> D. M. Spooner	DS 4204	GQ864124
<i>Tithonia</i> Desf.		
<i>T. calva</i> Sch.-Bip.	JP 2213	GQ864125
<i>T. diversifolia</i> (Hemsl.) A. Gray	JP & ES 620	GQ864126
<i>T. koelzii</i> McVaugh	LaDuke 477 (OS)	GQ864127
<i>T. longiradiata</i> (Bertol.) S. F. Blake	JP 1795	GQ864128
<i>T. pedunculata</i> A. Cronquist	JP 2505	GQ864129
<i>T. rotundifolia</i> (Miller) S. F. Blake	JP 2395	GQ864130
<i>T. thurberi</i> A. Gray	ES & OS 296	GQ864131
<i>T. tubaeformis</i> (Jacq.) Cass.	ES & JP 88-8	GQ864132
<i>Viguiera</i> Cav. subg. <i>Amphilepis</i> S. F. Blake		
<i>V. angustifolia</i> (Hook. & Arn.) S. F. Blake	JP 2447	GQ864133
<i>V. buddleiformis</i> (DC.) Benth. & Hook.	JP 2383	GQ864134
<i>V. ensifolia</i> (Sch.-Bip.) S. F. Blake	JP 2781	GQ864135
<i>V. excelsa</i> (Willd.) Benth. & Hook.	JP 2461	GQ864136
<i>V. grahamii</i> McVaugh	JP 3155	GQ864138
<i>V. hemsleyana</i> S. F. Blake	JP 2399	GQ864139
<i>V. hypochlora</i> (S. F. Blake) S. F. Blake	JP 2560	GQ864140
<i>V. pachycephala</i> (DC.) Hemsl.	JP 2443	GQ864141
<i>V. schultzei</i> S. F. Blake	ES & JP 88-47	GQ864142

TABLE I (continued).

Species	Voucher	Genbank
<i>Viguiera</i> ser. <i>Grammatoglossae</i> S. F. Blake		
<i>V. cordifolia</i> A. Gray	ES & JP 88-11	GQ864143
<i>V. pringlei</i> B. Rob. & Greenm.	JP 2861	GQ864144
<i>V. seemannii</i> Sch.-Bip.	JP 2780	GQ864145
<i>V. parkinsonii</i> Hemsl.	ES & JP 88-45	GQ864146
<i>V. sessilifolia</i> DC.	ES & JP 85-25	GQ864147
<i>Viguiera</i> ser. <i>Pinnatilobatae</i> S. F. Blake		
<i>V. pinnatilobata</i> (Sch. Bip.) S. F. Blake	ES & JP 85-28	GQ864153
<i>V. stenoloba</i> S. F. Blake	ES & OS 267	GQ864154

had multiple positions with more than a single peak. Within *Simsia*, there were high numbers of polymorphic positions in samples of *S. annectens* var. *annectens* (ten), *S. fruticulosa* (18), and *S. holwayi* (ten); but no other sample of the genus had more than five polymorphic positions, and the majority had fewer than two polymorphisms. Although the polymorphisms were clear and involved dual peaks of about equal intensity, there was no evidence of frame shifts to suggest sequences of different lengths that might be indicative of the possible presence of pseudogenes. Although such polymorphisms might be evidence of a history of hybridization, the patterns were not indicative of a simple additive combination of sequences from other species. Removal of these samples from the analyses did not affect the topology or relative support values in the trees, and the source of the polymorphisms was not investigated further.

The Bayesian analysis of the ITS sequence data produced a tree that had relatively well-resolved major clades with high posterior probability values (Fig. 1). Phylogenetic analysis of the ITS sequence data using parsimony analysis produced 37,138 minimally short trees, the strict consensus of which (not shown) was congruent with the tree generated by the Bayesian analysis, although with somewhat less resolution and slightly lower support values. The large number of trees from parsimony analysis was due in large part to the lack of resolution within the clades that included *Viguiera* subgen. *Amphilepis* and *Tithonia*. The initial branching of the tree above the outgroups split the two species of *V. ser. Pinnatilobatae* (*V. pinnatilobata* and *V. stenoloba*) from the remaining samples, although in the parsimony analysis the former was included in a polytomy at the next level, which had one branch

including samples of *Viguiera* subgen. *Amphilepis*, *Alvordia*, and four samples of *V. ser. Grammatoglossae*; a second with the sample of *V. cordifolia*; and a third including *Tithonia*, *Lagascea*, *Simsia*, and the remaining samples of *V. ser. Grammatoglossae*. Within the last branch, there was an initial split separating *Tithonia* + *Lagascea* from *Simsia* + a subset of *V. ser. Grammatoglossae*. The branch leading to *Tithonia* had a posterior probability of only 0.75 and lacked bootstrap support above 50%, but the remaining branches to *Lagascea*, to *Simsia*, and to the subset of *V. ser. Grammatoglossae* were each strongly supported with posterior probabilities of 1.0 and bootstrap values of at least 92%. Within *Simsia* there was some evident substructure, with a basal split into three clades. One poorly supported clade had *S. calva* and *S. fruticulosa*. A second clade contained the three samples of *V. ser. Grammatoglossae* that are morphologically most like *Simsia*, three species of *Simsia* that have biconvex cypselae, and *S. amplexicaulis*. The third clade included a large number of species, and was further subdivided. Two terminal branches had posterior probability values of 1.0, one which included *S. chaseae* and *S. dombeyana*, and the other included *S. foetida*, *S. lagascaeiformis*, and *S. eurylepis*.

The plastid DNA restriction site data set produced a tree with well supported nodes that differed significantly from the ITS-based tree (Fig. 2). The homogeneity partition test showed that the ITS and plastid data sets were strongly incongruent ($p \leq 0.01$), so the data sets were not combined. In the plastid data-based tree, there was a relatively basal split that separated samples into two groups, one of which included the two samples of *Davilanthus* for which data were available. The other

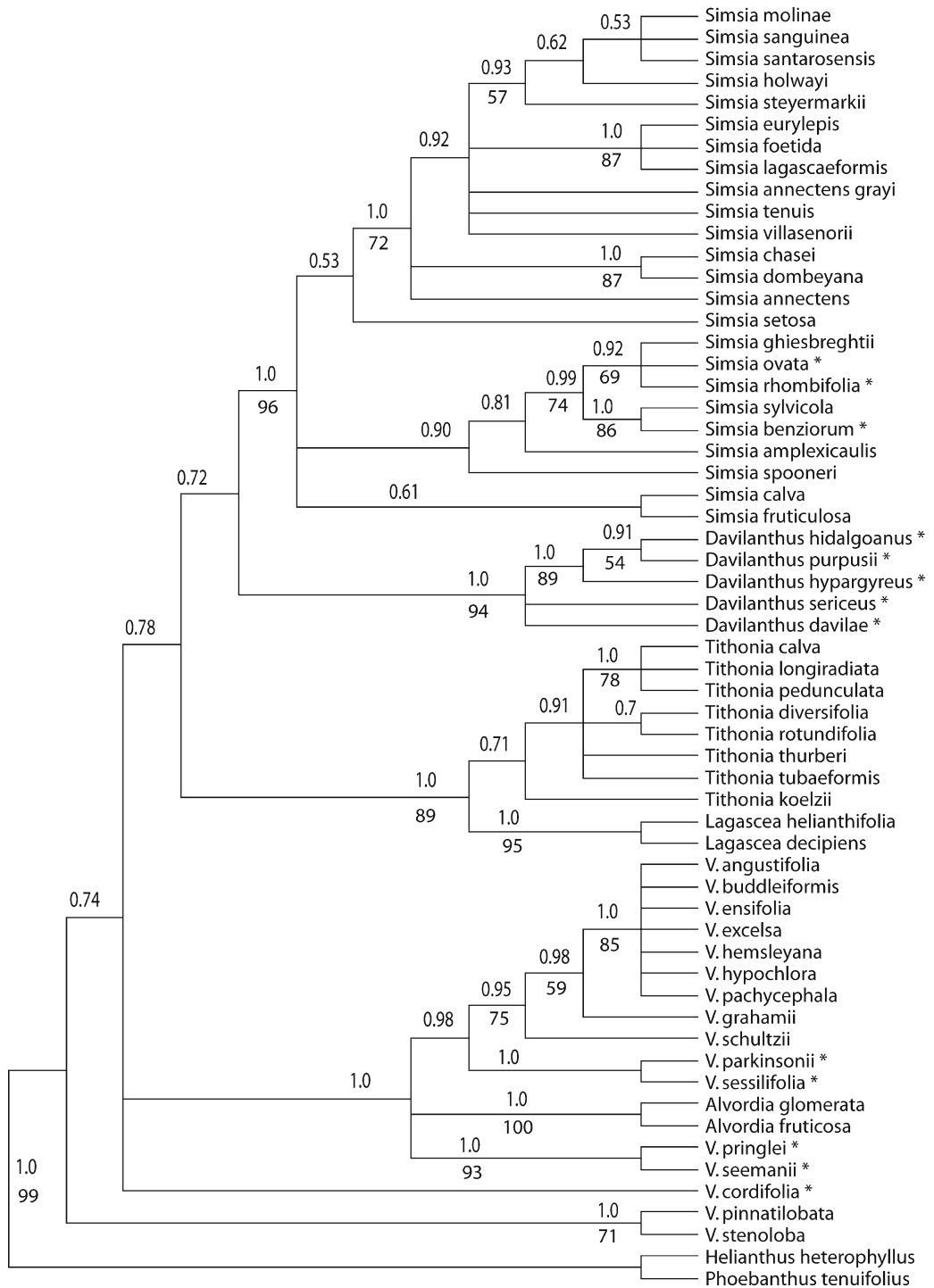
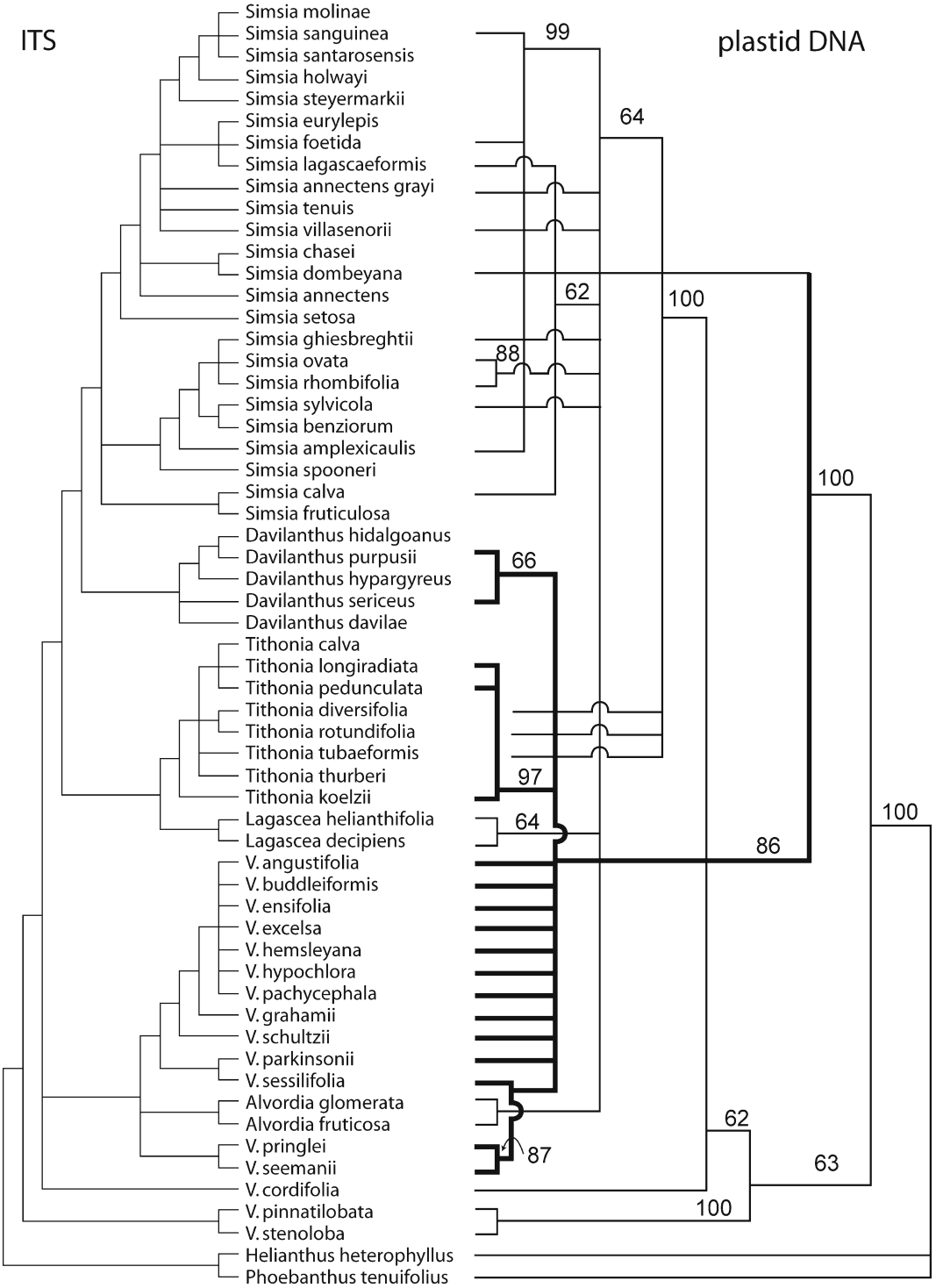


FIG. 1. Tree from Bayesian analysis of ITS sequence data showing relationships of *Simsia* and related species. Numbers above branches are posterior probabilities; those below are bootstrap support values (1000 replicates, FastStep option of PAUP) from parsimony analysis. *Helianthus heterophyllus* and *Phoebanthus tenuifolius* were designated the outgroup. Asterisks designate members of *Viguiera* ser. *Grammatoglossae*.

ITS

plastid DNA



group included *S. ovata* and *S. rhombifolia* with all other samples of *Simsia*, except for the anomalous *S. dombeyana* (Schilling & Panero, 1996b).

Discussion

The consistency of results from ITS (Fig. 1) and plastid DNA data (Fig. 2; Schilling & Panero, 1996a) together with morphology, collectively suggested that *Simsia* be enlarged to include three species, *S. benziorium*, *S. ovata*, and *S. rhombifolia*, formerly placed in *Viguiera* ser. *Grammatoglossae*. The ITS data also suggested that the sister group to *Simsia* is formed by a subset of the species of *Viguiera* ser. *Grammatoglossae* that is both distinctive morphologically and also strongly supported as monophyletic by molecular data (Fig. 1). Based on these results, this group is recognized here as the novel genus *Davilanthus*.

The enlargement of *Simsia* to include additional species formerly of *Viguiera* ser. *Grammatoglossae* follows Panero and Schilling (1992), who noted the inconsistency in giving emphasis to the presence of a flattened cypselas to delimit *Simsia*, when one species, *S. ghiesbreghtii*, was variable for this feature. The results of ITS sequence analysis showed that three species, *V. benziorium*, *V. ovata*, and *V. rhombifolia*, were phylogenetically embedded in *Simsia* and placed in a strongly supported clade with *S. ghiesbreghtii* as well as *S. sylvicola*. These three species each exhibit most of the morphological synapomorphies that were suggested by Panero and Schilling (1992) to characterize *Simsia*, including herbaceous phyllaries, long and narrow ray ovaries, long and tapering style branches, and setose anther connectives, although they lack nodal disks or flattened cypselas. These species, together with the morphologically similar *S. spooneri*, all occur in southern Mexico in the states of Guerrero, Oaxaca, Puebla, and Chiapas, where they are found in the open pine-oak woodlands and often in the eroded hillsides that occur frequently in the region.

Other members of *Viguiera* ser. *Grammatoglossae*, though also exhibiting the herbaceous phyllaries that Blake used to characterize the series, did not exhibit the other morphological features of *Simsia*, and the molecular data placed them in other clades. *Viguiera sessilifolia* and *V. parkinsonii* were grouped together and placed at the base of a clade with members of *Viguiera* subgen. *Amphilepis*, and *V. pringlei* and *V. seemannii*, which are morphologically very similar to one another. Another species, *V. cordifolia*, formed its own clade. The remaining members of *V. ser. Grammatoglossae* formed a single strongly supported clade that was placed as the sister group to *Simsia*. Based on this placement, it might be considered that *Simsia* be further enlarged to include these species, but there are several factors that suggest that this would be inadvisable. One is that, although this group was also supported as monophyletic based on plastid DNA data, it was placed near *Viguiera* subgen. *Amphilepis* rather than as sister to *Simsia* (Fig. 2; Schilling & Panero, 1996a), indicating that it has followed a different evolutionary path than *Simsia*. Another is that it is also well-characterized morphologically (Schilling & Panero, 1990), based on their shrubby habit, cordate leaf bases which tend to have naked basal veins, and leaves which are sericeous or hispid-pilose abaxially but lack sessile glandular trichomes. Finally, it has a discrete geographic distribution centered in the Tehuacán Valley area. Based on its combination of morphological, molecular, and biogeographic distinctiveness, this group is described here as a new genus.

Although making a detailed analysis of relationships within *Simsia* was not a goal of this study, some groupings suggested by the results are notable. Two moderately supported clades were present: one that included all of the species with biconvex cypselas and a second formed by a large number of species, including *S. foetida* and *S. lagascaeformis*, and *S. dombeyana* (Fig. 1). Also placed within the "biconvex cypselas clade," was *S. amplexicaulis*. In contrast, this species

◀ **FIG. 2.** Comparison of minimum length tree based on plastid DNA restriction site data (right) with that from ITS data (left) for *Simsia* and related species; plastid data not available for all samples. Because the plastid tree is incongruent with the ITS tree, portions of it must be depicted in a distorted manner, and arcs indicate where lines cross but do not join; bold line highlights clade that includes species of *Davilanthus*. Numbers above branches are bootstrap support values (1000 replicates, heuristic search option in PAUP).

was placed with strong statistical support by plastid DNA data as sister to *S. foetida* and *S. sanguinea* (Fig. 2; Schilling and Panero, 1996b). One of the two South American species of the genus, *S. dombeyana*, was placed with good support as sister to *S. chaseae*, and the two were noted by Spooner (1990) to have a high degree of morphological similarity. There is, however, no indication from the data for a hybrid origin of *S. chaseae*, as was suggested by Spooner (1990). The other South American species, *S. fruticulosa*, as well as *S. calva* and *S.*

setosa, were not placed with statistical support in any major clade. Of course, considerable caution must be taken in interpreting these results, because no attempt was made to survey infraspecific variability in ITS sequences, and the demonstration by Spooner (1990) of lack of barriers to interspecific hybridization suggests a high probability that at least some species may exhibit infraspecific variation for this marker. The high level of variability within *Simsia* for ITS sequences suggests that further study of the genus using this marker may be worth pursuing.

Key to genera of Helianthinae of Mexico

1. Mature marginal paleae completely and closely enclosing the disk cypselae, the margins overlapping adaxially.
 2. Mature marginal paleae thickened and sclerified *Sclerocarpus*
 2. Mature marginal paleae membranaceous or chartaceous *Aldama*
1. Paleae not enlarged, typically conduplicate and at most loosely enclosing the disk cypselae.
 3. Capitula in dense clusters, with 1–8 florets per head.
 4. Cypselae epappose, glabrous *Calanticularia*
 4. Cypselae usually with a pappus of awns or bristles, usually pubescent at least at the apices.
 5. Pappus of 15–20 unequal, lanceolate, barbellate awns (or absent); shrubs *Alvordia*
 5. Pappus of 2–several short, unequal scales or of a ring of bristles; shrubs or herbs *Lagascea*
 3. Capitula not in dense clusters, usually with more than 8 florets per head.
 6. Plants with a rosette of leaves from a stout, woody caudex; cypselae strongly quadrate *Iostephane*
 6. Plants not rosulate, caudex various; cypselae biconvex or flattened.
 7. Peduncles fistulose; paleae usually rigid, acuminate to aristate *Tithonia*
 7. Peduncles not fistulose; paleae various.
 8. Style branches long and tapering, with a conspicuous terminal appendage; paleae 3-lobed; pappus deciduous and usually of 2 awns *Helianthus*
 8. Style branches long and tapering or short and deltate, but terminal appendage small or lacking; paleae unlobed; pappus various, of 2 persistent awns, of 2 awns and intermediate scales either persistent or deciduous, or lacking.
 9. Ray ovaries long and narrow (more than 4 mm long and 4–20 times as long as wide); style branches long and tapering; anther connectives often setose; cypselae often conspicuously flattened and with a broad marginal rim; disk corolla lobes with sclerified cells *Simsia*
 9. Ray ovaries short and broader (less than 4 mm long and 2–3.8 times as long as wide); style branches shortly deltate; anther connectives glabrous; cypselae biconvex; disk corolla lobes lacking sclerified cells.
 10. Involucre 1–2 seriate; herbs or weak shrubs.
 11. Subsessile glandular trichomes present on leaf abaxial surfaces; cypselae less than 2.5 mm long, glabrous and epappose; herbs *Heliomeris*
 11. Subsessile glandular trichomes absent on leaf abaxial surfaces; cypselae usually more than 2.5 mm long, either pubescent or pappus present; herbs or shrubs *Hymenostephium*
 10. Involucre 2–7 seriate; herbs, shrubs, or small trees.
 12. Outer phyllaries herbaceous throughout.
 13. Leaves petiolate, the petioles more than 4 mm long; lowermost leaves often with cordate bases and naked basal veins; leaves sericeous or hispidulous abaxially *Davilanthus*
 13. Leaves sessile or subsessile, the petioles less than 1.5 mm long; lowermost leaves with rounded bases and major pair of veins diverging above base, not naked; leaves hispid, hispidulous, or tuberculate-hispid abaxially *Viguiera*
 12. Outer phyllaries with an oval, usually indurate base that is narrower or broader than the herbaceous apex.
 14. Heads solitary at the ends of branches; leaf margins entire *Calanticularia*
 14. Inflorescence usually branched; leaf margins serrate, laciniate, or entire.

15. Phyllaries usually with narrowed, elongate apices; abaxial surface of leaves usually either densely pubescent or resinous. *Bahiopsis*
15. Phyllaries usually with apices that are either short and triangular or broadly amplified, if apices narrowed and elongate, anther filaments pubescent; abaxial surface of leaves usually not densely pubescent or resinous. *Viguiera*

Taxonomic treatment and novelties

Simsia benziorium (B. L. Turner) E. E. Schill. & Panero, **comb. nov.** *Viguiera benziorium* B. L. Turner, *Phytologia* 63: 436. 1987. Type: Mexico. Oaxaca: Mpio. Yosondua, 26 Nov 1982, B. & K. Benz, B. Hallberg & M. Burd 677 (holotype: WIS).

Simsia ovata (A. Gray) E. E. Schill. & Panero, **comb. nov.** *Gymnolomia ovata* A. Gray, *Proc. Amer. Acad. Arts* 19: 4. 1883. Type: Mexico. Chiapas: Nov 1864–1870, A. B. Ghiesbreght 544 (holotype: GH).

Simsia rhombifolia (Rob. & Greenm.) E. E. Schill. & Panero, **comb. nov.** *Encelia rhombifolia* Rob. & Greenm., *Amer. Jour. Sci. Ser.* 3, 50: 155. 1895. Type: Mexico. Oaxaca: Las Sedas, Aug 1884, C. G. Pringle 4813 (lectotype, **here designated**: GH; isolectotypes: BM-n.v., K, NY, S-n.v., US, Z).

Davilanthus E. E. Schill. & Panero, **gen. nov.** Type: *Davilanthus purpusii* (Brandege) E. E. Schill. & Panero; *Viguiera purpusii* Brandege, *Univ. Calif. Publ. Bot.* 3: 393. 1909.

Genus ad *Helianthinas pertinens*. Frutices vel suffrutices foliis saepe cordatis infra sericeis et eglandulatis, phyllariis herbaceis, ovariis radii curtis et triquetris.

Shrubs, subshrubs, or rhizomatous herbs 0.5–2.0 m tall, stems strigose to densely pubescent when young, often becoming glabrous, brown or gray with age. *Leaves* opposite or the upper alternate, blades 25–110 mm long, 8–50 mm wide, triplinerved, often the larger with naked basal veins, deltate to ovate, lance-ovate or lanceolate, pubescent adaxially with appressed, septate trichomes from a multicellular base, densely pubescent abaxially with numerous, white, appressed-septate trichomes giving leaf a velvety white appearance or hispid-pilose, subsessile glandular trichomes (“resin dots”)

absent, apex acute, base cordate to rounded or in uppermost cuneate, margin entire to shallowly serrate or dentate; petiole 4–30 mm long, hispid-pilose. *Capitula* terminal, 2–12 per paracladium, on sericeous peduncles 1.5–21 cm long. *Involucre* hemispheric, phyllaries 12–35, in 2–3(–4) subequal to graduated series, oblong or lanceolate to ovate, obtuse to subacute, puberulent to pilose. *Ray florets* 6–16, corolla golden-yellow, limb oval-oblong, 10–25 mm long, 3–10 mm wide, often with prominent abaxial veins that darken in color when dried. *Disk florets* 30–70, corollas yellow to orange-yellow, narrowly campanulate; anthers dark brown, appendage lanceolate, light yellow; styles 5.8–7.0 mm long, tapered with a short appendage; paleae lance-ovate to lanceolate, 6–10 mm long, with an obtuse, acute or acuminate, often dark apex. *Disk cypselae* black or mottled black and brown, obovate, 3.0–4.8 mm long, sparsely pubescent or glabrous, epappose, or with a pappus of 2 awns and 3–12 deeply lacerated squamellae; awns slender, whitish, 2.5–4.2 mm long, squamellae 0.4–1.2 mm long. *Ray ovaries* trigonal, 2.5–3.7 mm long, glabrous or sparsely pubescent, pappus of 3 squamellae or absent. *Chromosome number* $x=17$ (Turner et al., 1962; Schilling & Panero, 1990; Strother & Panero, 2001).

Etymology.—The genus name honors Dr. Patricia Dávila Aranda who has contributed greatly to the conservation and knowledge of the fascinating flora of the Tehuacán Valley area and who has helped to facilitate the studies of other botanists working throughout Mexico.

The species of *Davilanthus* are characterized by the herbaceous phyllaries which are not strongly differentiated between the base and the apex, the basically opposite and trinervate leaves, often in the larger leaves with the base cordate and the basal veins naked, the lack of the typical (for *Helianthi-*

nae) sessile glandular trichomes on the leaf undersurfaces, and the ray ovaries which are relatively short and broad, especially compared to those of *Simsia*. The species are all at least somewhat shrubby, although the narrowly endemic *D. davilae* is a rhizomatous herb when young (Panero et al., 1993). Molecular evidence, while providing good support for the monophyly of *Davilanthus*, is equivocal regarding its phylogenetic placement. The nuclear ITS sequence analysis placed it as sister to *Simsia* (Fig. 1), whereas plastid DNA-based results (Fig. 2; Schilling and Panero, 1996b) place it with a group of species formerly included in *Viguiera*, including notably *V. pringlei* and members of *V.* subgen. *Amphilepis*. This raises the possibility that *Davilanthus* may be a lineage that was originally of hybrid origin and has subsequently diversified, an hypothesis for which there is some support from morphological observations. The trilobed lowermost leaves of *D. davilae* resemble those found in some species of *Simsia*, but which are not known in other potential relatives of *Davilanthus*, such as species of *Viguiera*. In contrast, the habit and cypsela characteristics of *Davilanthus* are reminiscent of those of species such as *V. pringlei*. Further study will be required to determine whether the distribution of these features represent parallelisms or the results of past reticulation.

The ITS sequence data showed not only that *Davilanthus* is distinct, but also provided information on species relationships within the genus. In addition to the bp changes that are reflected in Fig. 1, the species of *Davilanthus* are also collectively characterized by a 1 bp deletion in ITS1 relative to all other species of Helianthinae that have been examined. ITS data supported recognition of *D. huajuapanus* as distinct from *D. hypargyreus*, and suggested the possibility that *D. hidalgoanus* might be their hybrid derivative. The ITS sequence of *D. huajuapanus* was

distinctive within *Davilanthus* in having a 2 bp deletion in the ITS2 region, and also differed by 5 bp from *D. hypargyreus*, the species (as *Viguiera grammatoglossa*) in which it was placed originally as a variety (Panero and Villaseñor 1996). The ITS sequence of *D. huajuapanus* was actually more similar to that of *D. hidalgoanus*, which differed from it solely in having several bp positions that were polymorphic instead of monomorphic. The ITS sequence of *D. hidalgoanus* also exhibited an indel polymorphism at the position of the 2 bp indel that characterized *D. huajuapanus*. Given the indel and bp polymorphisms, the ITS sequence of *D. hidalgoanus* was nearly what would be expected from combining sequences of *D. huajuapanus* and *D. hypargyreus*. Other data are not consistent, however, with *D. hidalgoanus* being a hybrid derivative from *D. huajuapanus* and *D. hypargyreus*. The geographical location of *D. hidalgoanus* does not overlap with, and is in fact relatively distant from the known occurrences of the other two species, and it is a low subshrub in contrast to the large shrubby habit shared by the other two. Further sampling of each of the species will be necessary to shed light on what might be another example of diploid hybrid speciation in Helianthinae.

The center of diversity of *Davilanthus* is the xeric Tehuacán Valley area, with *D. hidalgoanus* disjunct to calcareous areas in the state of Hidalgo. The Tehuacán Valley region has been noted for its high biological diversity and endemism, but is currently threatened by human activities (Dávila et al. 2002). Most of the species of *Davilanthus* are relatively narrow endemics that, although abundant locally where they occur, may be vulnerable to the impacts of human disturbance. In particular *D. davilae*, *D. hidalgoanus*, *D. huajuapanus*, and *D. purpusii* are known from relatively few sites and should be monitored to detect any threats to their survival.

Key to species of *Davilanthus*

- 1. Cypselae glabrous and epappose *D. sericeus*
- 1. Cypselae pubescent and with a pappus of awns and squamellae.
 - 2. Rhizomatous herbs; involucre bracts lanceolate and appressed *D. davilae*
 - 2. Shrubs or subshrubs; involucre bracts lanceolate to ovate, and loose or appressed.

3. Leaves hispid-pilose and greenish abaxially *D. purpusii*
 3. Leaves densely sericeous and silvery abaxially.
 4. Subshrubs 1–1.5 m tall. *D. hidalgoanus*
 4. Shrubs, usually more than 1.5 m tall.
 5. Cypselae and pappus awns each less than 4 mm long; phyllaries ovate to lance-ovate, covering the head in bud. *D. huajuapanus*
 5. Cypselae and usually also pappus awns both 4 mm or more long; phyllaries lanceolate, not covering the head in bud. *D. hypargyreus*

Davilanthus davilae (Panero & Villaseñor)

E. E. Schill. & Panero, **comb. nov.** *Viguiera davilae* Panero & Villaseñor, Contr. Univ. Michigan Herb. 19: 191. 1993. Type: Mexico. Puebla: Summit of Cerro Tepoxtla Grande, 1 Nov 1991, *J. L. Panero, P. Dávila & P. Tenorio 2581* (holotype: MEXU; isotypes: ENCB, MEXU, MICH, NY, TENN, TEX, UC, US).

Geographic Range: Known only from the type locality in the state of Puebla, Mexico.

Davilanthus hidalgoanus (E. E. Schill. & Panero)

E. E. Schill. & Panero, **comb. nov.** *Viguiera hidalgoana* E. E. Schill. & Panero, Brittonia 42: 57. 1990. Type: Mexico. Hidalgo: 16 Sep 1988, *E. E. Schilling & J. L. Panero 88-28* (holotype: MEXU; isotypes: ENCB, F, LP, MA, TENN, TEX, US).

Geographic Range: Known only from a limited area in the state of Hidalgo, Mexico.

Additional specimen examined. MEXICO. Hidalgo: 2 km NE barranca de Venados, 11 Jan 1980, *Hernández 3937* (ENCB, GH).

Davilanthus huajuapanus (Panero & Villaseñor)

E. E. Schill. & Panero, **comb. et stat. nov.** *Viguiera grammatoglossa* DC. var. *huajuapana* Panero & Villaseñor, Brittonia 48: 571. 1996 [publ. 1997]. Type: Mexico. Oaxaca: Dist. Huajuapán de León, 29 Sep 1995, *J. L. Panero, I. Calzada & C. Clevinger 6141* (holotype: MEXU; isotypes: IEB, MICH, MSC, NY, TENN, TEX, UC).

Geographic Range: Known only from the type locality in the state of Oaxaca, Mexico.

Davilanthus hypargyreus (B. L. Rob. & Greenm.)

E. E. Schill. & Panero, **comb. nov.** *Encelia hypargyrea* B. L. Rob. & Greenm., Amer. J. Sci. 50: 155. 1895. Type: Mexico. Oaxaca: La Hoya Canyon, 2 Nov 1894, *C. G. Pringle 6142* (lectotype, **here designated**: MEXU; isolectotypes: AC-n.v.,

BM-n.v., CM-n.v., GH, JE-n.v., K, MEXU, MINN, MO, MSC, NY, UC, US, Z).

Geographic Range: In or near the Tehuacán Valley area in the states of Oaxaca and Puebla, Mexico.

Additional specimens examined. MEXICO.

Oaxaca: 5 km al E de Teotitlán del Camino, 21 Oct 1979, *Arias 181* (TEX-LL); About 40 km NNW of Telixtlahuaca, along road to Tehuacán, 13 Nov 1970, *Cronquist & Fay 10922* (NY); Mountains along route 175, ca. 27 mi N of the junction with route 190, 26 Jul 1960, *King 3504* (DS, MICH, NY, TEX, UC, US) - voucher for n=17, Turner et al. 1962; Tomellin Cañon, 15 Jun 1899, *J. Rose & Hough 4563* (US); 6 km NE de Chilapa de Díaz, 2 Nov 1976, *Rzedowski 34497* (CAS, MICH, RSA); ca 4 mi N of Jayacatlán, 27 Nov 1984, *Spooner 2832* (UC, WIS). **Puebla:** 7 km SE Cañada Morelos, 10 Jul 1974, *Powell 1168* (UC); Vicinity of San Luis Tultitlanapa, Jul 1908, *Purpus 2525* (MO, NY, US); Cerro de Coatepec, Aug 1907, *Purpus 2528* (UC); Tehuacán, Sep 1911, *Purpus 5615* (UC); Esperanza, Oct 1911, *Purpus 5615* (MO, NY, UC, US); ca 10 km SW of Tehuacán on road to Huajuapán del León, 8 Oct 1988, *Turner 15905* (TEX-LL); 7 km al E de Zinacatepec, 3 Nov 1980, *Villaseñor & Jaramillo 85* (TEX-LL).

The name *Viguiera grammatoglossa* DC. was previously used for this species (e.g. Blake 1918), but the type locality in Michoacan (Tlalpujahuá; “Tlapujahuá,” variant spelling) is distant from all other known sites for it, and examination of an image of the type (*F. W. Keerl s.n.*, G-DC) shows it to be *Viguiera dentata* Kunth., a widespread species in Mexico. The next available name, *Encelia hypargyrea*, is adopted here.

Davilanthus purpusii (Brandege)

E. E. Schill. & Panero, **comb. nov.** *Viguiera purpusii* Brandege, Univ. Calif. Publ. Bot. 3: 393. 1909. Type: Mexico. Puebla: San Luis Tultitlanapa, Aug 1908, *Purpus 3089* (lectotype, **here designated**: GH; isolectotypes: BM-n.v., MO, UC, US).

Geographic Range: restricted to a limited area in the state of Puebla, Mexico.

Additional specimens examined. MEXICO. Puebla: Cerro el Gavilán, 22 Nov. 1985, *Dorado & Salinas F-3066* (TENN); base del Cerro el Gavilán, 10 Sep 1991, *Panero & Salinas 2313* (TENN); Caltepec, Santa Lucia, Coatepec, 19 Oct 1984, *Tenorio et al.* (TEX); Coxcatlán, 3 km al S de Calipan, rumbo a Teotitlán del Camino, 3 Nov 1980, *Villaseñor & Jaramillo* (TEX).

Davilanthus sericeus (Klatt) E. E. Schill. & Panero, **comb. nov.** *Gymnolomia sericea* Klatt, *Leopoldina* 23: 90. 1887. (= *Viguiera bombycina* S. F. Blake). Type: Mexico, without locality, *F. M. Liebmann 609* (lecto-type, **here designated**: C; isolectotype: GH). Geographic Range: known from the states of Puebla and Veracruz in Mexico.

Additional specimens examined. MEXICO. Puebla: 10 km S of Esperanza, 5 Jan 1970, *Anderson & Anderson 5306* (MICH); 13 mi S of Esperanza on Mex 28 to Tehuacán, 21 Nov 1976, *Olsen & Lane 360* (TEX-LL); Esperanza, Oct 1911, *Purpus 5615* (US); 22 km S of Esperanza, sobre la carretera a Chapulco, 22 Nov 1973, *Rzedowski 30383* (CAS); ca 10 km SW Tehuacán on road to Huajuapán de León, 8 Oct 1988, *Turner 15899* (TEX-LL); 3.2 km SSW of Pto. del Aire, near state line between Chapulco and Acultzingo on Hwy 150 (Tehuacán to Orizaba) at km 277.5, 28 Sep 1962, *Ugent & Flores 2544* (WIS). **Veracruz:** Cumbres de Acultzingo, cerca de Puerto del Aire, 30 Oct 1986, *Chazaro & Hernández 4179* (WIS); Between Tehuacán and Acultzingo, 16 Oct 1965, *Cronquist & Sousa 10351* (CAS, MICH, NY, TEX-LL, WIS); 1.5 km S of Cd. Mendoza on road to Tehuacán near Azumbilla at F 150, 13 Jan 1987, *Kim et al 10056* (TEX-LL); Along rte 150, ca 20 mi N of Tehuacán, 26 Jan 1960, *King 2327* (US); Mun. Acultzingo, along old Hwy Mex 150, 1.5 km above and WSW of Acultzingo, 8 Feb 1984, *Nee & Taylor 29503* (NY, TEX-LL); Cumbres de Acultzingo, 30 Nov 1967, *Rosas 855* (MICH); 4.4 mi W of Acultzingo along hwy 150, 25 Aug 1983, *Turner 15156* (TEX-LL).

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