



## A revised classification of subtribe Helianthinae (Asteraceae: Heliantheae) II. Derived lineages

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Sequence data for internal transcribed spacer (ITS) and partial external transcribed spacer (ETS) regions were combined in a phylogenetic analysis with previously obtained plastid DNA restriction site data to provide a comprehensive molecular phylogenetic hypothesis for derived members of subtribe Helianthinae. Analyses of the two molecular datasets provided conflicting evidence on relationships among some groups, supporting the hypothesis that hybridization has played a significant role in the divergence of the subtribe. A revised generic-level classification is presented that divides the approximately 350 species of the subtribe among 21 genera. The paraphyletic *Viguiera* is narrowed to embrace only the type species, *V. dentata*. Four newly described genera, *Dendroviguiera*, *Gonzalezia*, *Heiseria* and *Sidneya*, are composed of species formerly included in *Viguiera*. *Aldama* is expanded to include 118 species extending from southwestern North America and Mexico to South America. This requires 116 new combinations, including 58 that were recently transferred into *Rhysolepis*, which is a synonym of *Aldama*, based on molecular phylogenetic results. One species of *Viguiera* is transferred to *Tithonia*, and two combinations in *Hymenostephium* are validated. © 2011 The Linnean Society of London, *Botanical Journal of the Linnean Society*, 2011, 167, 311–331.

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### INTRODUCTION

A general solution to the problem of reassorting the paraphyletic *Viguiera* Kunth (Robinson, 1977; Schilling & Jansen, 1989) and other members of subtribe Helianthinae into monophyletic units for generic-level recognition has remained elusive. Molecular data have provided strong evidence for recognizing the earliest branching lineages of the subtribe at the generic level, although not all of these are strongly differentiated morphologically (Schilling & Panero, 2002). For the derived lineages of the subtribe, however, there is the additional complication that the analysis of plastid and nuclear sequence data

produces phylogenetic trees that are not congruent (Schilling & Panero, 1996b).

Helianthinae includes a number of well-known species that have been the focus of evolutionary studies or are commercially important, and a sound, phylogenetically based, classification is critical for a better understanding of their biology. For example, studies have highlighted the importance of hybridization at the diploid level in generating diversity in *Helianthus* L. (Rieseberg *et al.*, 2003), the genus is the source of a promising pharmaceutical (Mylne *et al.*, 2011), and the origin of the agronomically significant domesticated sunflower, *H. annuus* L., has long been a subject of debate (Harter *et al.*, 2004). The extreme morphological modification in *Lagascea* Cav. that generates one-flowered heads has been the subject of close investigation (Harris, 1994). *Scalesia* Arn. is a

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significant component of the vegetation of the Galápagos Islands (Eliasson, 1974; Schilling, Panero & Eliasson, 1994; Bisconti *et al.*, 2001; Nielsen *et al.*, 2003). The striking divergence between the herbaceous, rosette-forming, *Iostephane* Benth. and the woody members previously classified as *Viguiera* section *Maculatae* (S.F.Blake) Panero & E.E.Schill. (Schilling & Panero, 1991), supported further by the results presented here, still warrants further investigation.

The current study was undertaken to complete the survey of variation in internal transcribed spacer (ITS) sequences in Helianthinae (Schilling & Panero, 2002, 2010), and to combine the resulting data with information from a partial data matrix of external transcribed spacer (ETS) sequences, plastid DNA results and morphology to provide a comprehensive estimate of relationships of the derived lineages of the subtribe. Sampling was extended to include all genera of Helianthinae and all of the major infrageneric units (at the level of series and above) of *Viguiera* as delimited by Blake (1918). A revised generic-level classification is proposed, based on the resulting estimates of phylogenetic relationships.

## MATERIAL AND METHODS

ITS sequences were obtained for 65 accessions representing 54 taxa of Helianthinae to add to previously published sequences from the subtribe (Appendix). Placeholder sequences were utilized for groups that had been analysed previously, including the early branching lineages (Schilling & Panero, 2002), *Helianthus* and *Phoebanthus* S.F.Blake (Schilling & Panero, 1996a) and *Davilanthus* E.E.Schill. & Panero, *Tithonia* Desf. ex Juss. and *Simsia* Pers. (Schilling & Panero, 2010). Partial ETS sequences were also obtained for 63 accessions representing 62 ingroup taxa and one outgroup (Appendix; many of the species are renamed here; see the Taxonomic Treatment section below for the authors). DNA extraction, polymerase chain reaction (PCR) and sequencing protocols followed Schilling & Panero (2010). The primers used for ITS were ITS-4 (5'-TCCTCCGCTTATTGATATGC-3') and ITS-5 (5'-GGAAGTAAAAGTCGTAAC AAGG-3'; White *et al.*, 1990). Amplification and sequencing reactions for the ETS region were performed using the 18-S-ETS (5'-ACTTACACATGCA TGGCTTAATCT-3') primer of Baldwin & Markos (1998), coupled with the Ast-1 primer of Markos & Baldwin (2001) (5'-CGTAAAGGTGTGTGAGTGGTTT-3'). 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, USA). Sequence align-

ment was performed manually. GenBank accession numbers are provided in the Appendix.

A dataset of 132 plastid DNA restriction site characters was taken from Schilling & Panero (1996a). Data were available for many but not all species. Each character represents the presence or absence of a restriction site.

## DATA ANALYSIS

Phylogenetic relationships were analysed 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 1000 random addition replicates and with tree bisection-reconnection (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 jModeltest (Guindon & Gascuel, 2003; Posada, 2008). Plastid DNA restriction site data from Schilling & Panero (1996a) were available for 56 of the 63 samples represented in the ITS/ETS dataset and the outgroup, and these were analysed separately using maximum parsimony and bootstrap approaches. A partition homogeneity analysis of the ITS/ETS and plastid datasets was run using PAUP.

## RESULTS

The ITS region in newly analysed samples of Helianthinae was 639–653 base pairs (bp) in length. Alignment did not present any issues, and most gaps were short insertions or deletions found in single samples. All samples of *Viguiera dentata* (Cav.) Spreng. were characterized by a 13-bp deletion in the ITS2 region. Other groups characterized by indels included *Aldama fruticosa*/*Aldama glomerata* (*Alvordia* Brandegee) + *Aldama purissima* (4-bp deletion in ITS2), *Simsia*/*Davilanthus* (1-bp deletion in ITS2), *Davilanthus* (1-bp deletion in ITS1) and *Pappobolus* S.F.Blake, *Heiseria*, *Syncretocarpus* S.F.Blake and *Scalesia* (1-bp deletion in ITS2).

The ITS sequence of most samples was unambiguous and contained fewer than four polymorphic bp positions. A few samples gave sequence results that were polymorphic for at least one indel and for multiple bp positions. By comparison with other samples, these could be inferred to be of hybrid origin. These included *Gonzalezia rosei*, *Aldama brandegei* (*Alvordia*) and a sample of *Dendroviguiera*. The polymorphisms in the sequence for *G. rosei* appeared to stem from a combination of the sequences from *G. decurrens*, which has an autapomorphic 14-bp deletion, and *G. hypargyrea*, although the pattern of polymorphisms was not exact for this combination. Similarly, the electropherogram obtained for a sample of *A. brandegei* had both indel and bp polymorphisms characteristic of a hybrid origin, and, on the basis of its reported high chromosome number (Carter, 1964; Strother & Panero, 1994), it is likely to be an allopolyploid. A sample that had been identified when collected as a probable hybrid between *Dendroviguiera eriophora* and *D. oaxacana* had an ITS pattern that had the polymorphisms expected from an exact combination of the sequences found in the two parents, including a polymorphism at the site of a 4-bp insertion autapomorphic for *D. oaxacana* (data not shown). Samples with extensive polymorphisms were not included in the phylogenetic analysis.

The results of the Bayesian analysis of ITS sequences for a comprehensive dataset of Helianthinae are shown in Figure 1A–C. The consensus tree from parsimony analysis was nearly identical, but statistical support for individual nodes was lower. Above the previously documented early branching groups, *Calanticaria* (B.L.Rob. & Greenm.) E.E.Schill. & Panero, *Bahiopsis* Kellogg and *Helioneris* Nutt., the remainder of the subtribe formed a well-supported clade (0.96/85%). Within the derived group, there was a split between a group that included all samples of *V. dentata*, *Dendroviguiera* and *Iostephane* (0.63/–), and another with the remainder of the subtribe (1.0/86%). Within the first group, one species of *Dendroviguiera*, *D. sylvatica*, was placed in a clade with *V. dentata*, albeit with weak support (0.86/–). The samples of *V. dentata* formed a strongly supported clade (1.0/100%), with some of the samples included in two subclades (0.89/56% and 1.00/83%). A second group included *Iostephane* and the remaining species of *Dendroviguiera*. Three of the samples of *Iostephane* were placed in a clade (0.90/–), but the sample of *Iostephane papposa* was grouped with members of *Dendroviguiera*. Within *Dendroviguiera*, there were several multispecies clades: one with *D. puruana* and *D. oaxacana*, a second with *D. sphaerocephala*, *D. splendens* and *D. insignis*, and a third with *D. sharpii*, *D. guerrerana*, *D. adeno-*

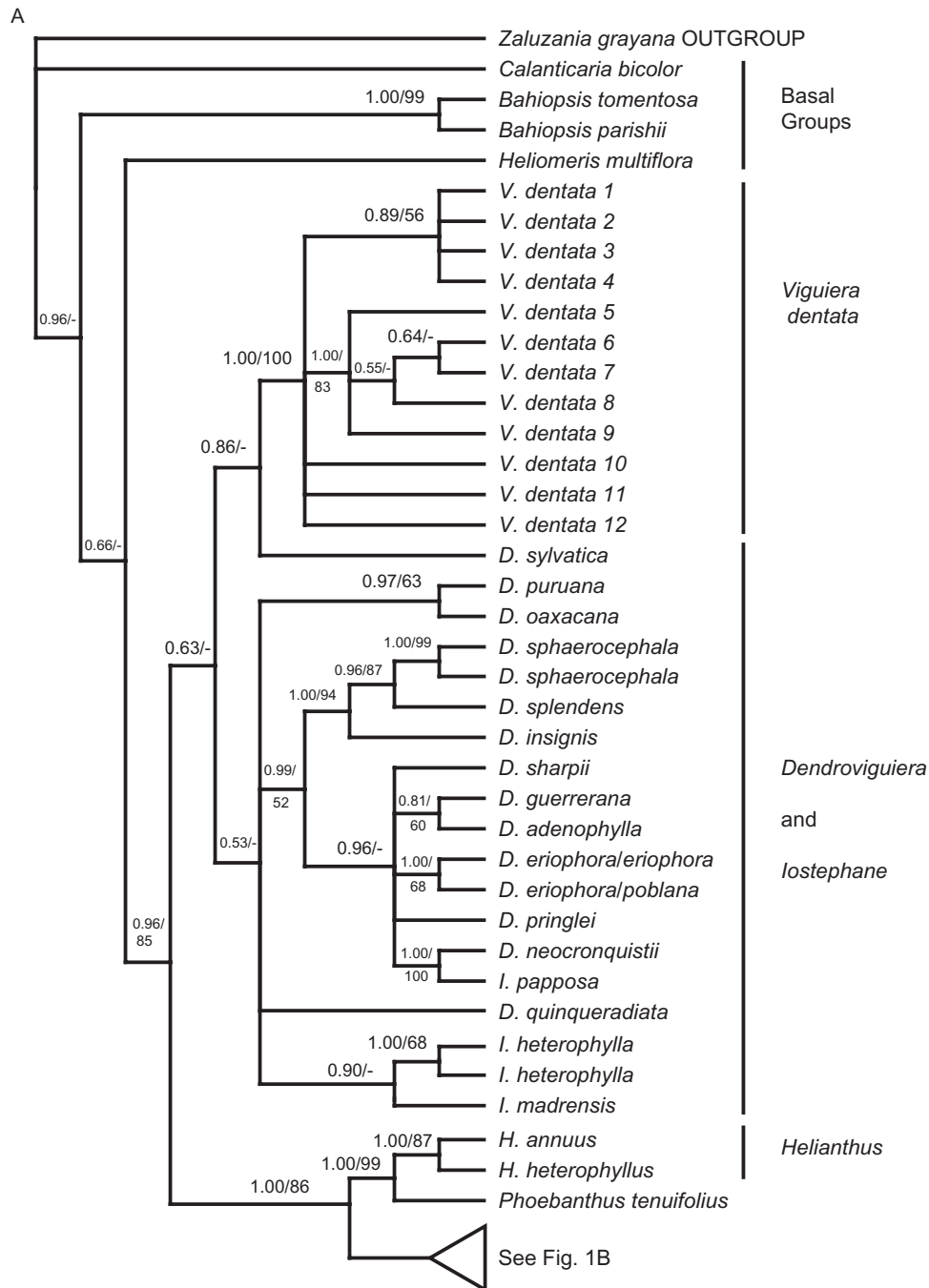
*phylla*, *D. eriophora*, *D. pringlei* and *D. neocronquistii* and *I. papposa* (Fig. 1A).

In the sister clade to *Viguiera/Dendroviguiera/Iostephane* (Fig. 1A), there was an initial split that separated the samples of *Helianthus* + *Phoebanthus* (1.00/99%). At the next level (Fig. 1B), there was a trichotomy, with one branch including the samples of *Sidneya* (1.00/70%), a second including those of *Gonzalezia* (1.00/82%) and the third with all remaining samples (0.98/–).

At the next level, there was another trichotomy, with each branch receiving posterior probability ranging from 0.65 to 1.00, but no bootstrap support. The first branch (Fig. 1B) split again into two highly supported branches, one (1.00/86%) containing *Lagascea* (1.00/94%) and *Tithonia* (0.80/–), and the other (1.00/–) containing *Simsia* (1.00/99%) and *Davilanthus* (1.00/95%). The second branch (Fig. 1C) contained primarily South American samples, including *Pappobolus*, *Heiseria*, *Syncretocarpus* and *Scalesia*, with the Mexican *Aldama canescens* (*Viguiera potosina* S.F.Blake) and *A. cordifolia* splitting off at the base. The third major clade (Fig. 1C) had all other samples of *Aldama* La Llave. This clade included all samples previously placed in *Aldama*, *Alvordia*, *Rhysolepis* S.F.Blake, *Stuessya* B.L.Turner & F.G.Davies, *Viguiera* section *Leighia* (Cass.) Gardner and *Viguiera* subgenus *Amphilepis* S.F.Blake, as well as some species formerly of *Viguiera* section *Grammatoglossae* and most of the South American species once placed in *Viguiera* and, more recently, in *Rhysolepis*.

For a subset of the samples, sequences were obtained for the initial part of the ETS region. As with the ITS region, there was little length variation within subtribe Helianthinae and alignment was straightforward. All samples of the subtribe exhibited a 73-bp deletion near the beginning of the ETS region relative to the outgroup, *Zaluzania grayana* B.L.Rob. & Greenm., and to all other samples of Heliantheae for which ETS data are available in GenBank. The sequence of this region, however, suggested that it actually represented a duplication for the non-Helianthinae samples of Heliantheae. Excluding the 73-bp deletion, the aligned length of the ETS region analysed for Helianthinae was 425 bp.

The tree obtained from Bayesian analysis of the combined ITS/ETS dataset is shown in Figure 2. Also shown in this figure for comparison is the tree obtained from plastid DNA restriction site analysis (Schilling & Panero, 1996a). The ITS/ETS and plastid datasets were shown to be incongruent ( $P < 0.01$ ) using the partition homogeneity analysis in PAUP, and were thus analysed separately. The tree obtained with the ITS/ETS dataset was almost identical in topology to that obtained from ITS alone. The major



**Figure 1.** Estimation of phylogenetic relationships among members of subtribe Helianthinae based on the Bayesian analysis of internal transcribed spacer (ITS) sequence data. A, Early diverging clades, with *Zaluzania grayana* as outgroup and selected species of *Calanticaria*, *Bahiopsis* and *Heliomeris* as placeholders. B, Derived clades including *Tithonia* and *Simsia*. C, Derived clades including *Pappobolus* and *Aldama*. Support values shown as Bayesian posterior probabilities/bootstrapped percentages (faststep search option of PAUP; -, less than 50%).

difference was the placement of *D. sylvatica*, which was placed as the sister to *D. puruana* rather than in a clade with the samples of *V. dentata*. There were several notable areas of disagreement in the place-

ment of samples or groups of samples between the plastid- and ITS/ETS-based trees. These all involved species that were in the more derived branches of the tree, above the split of the *Helianthus/Phoebanthus*



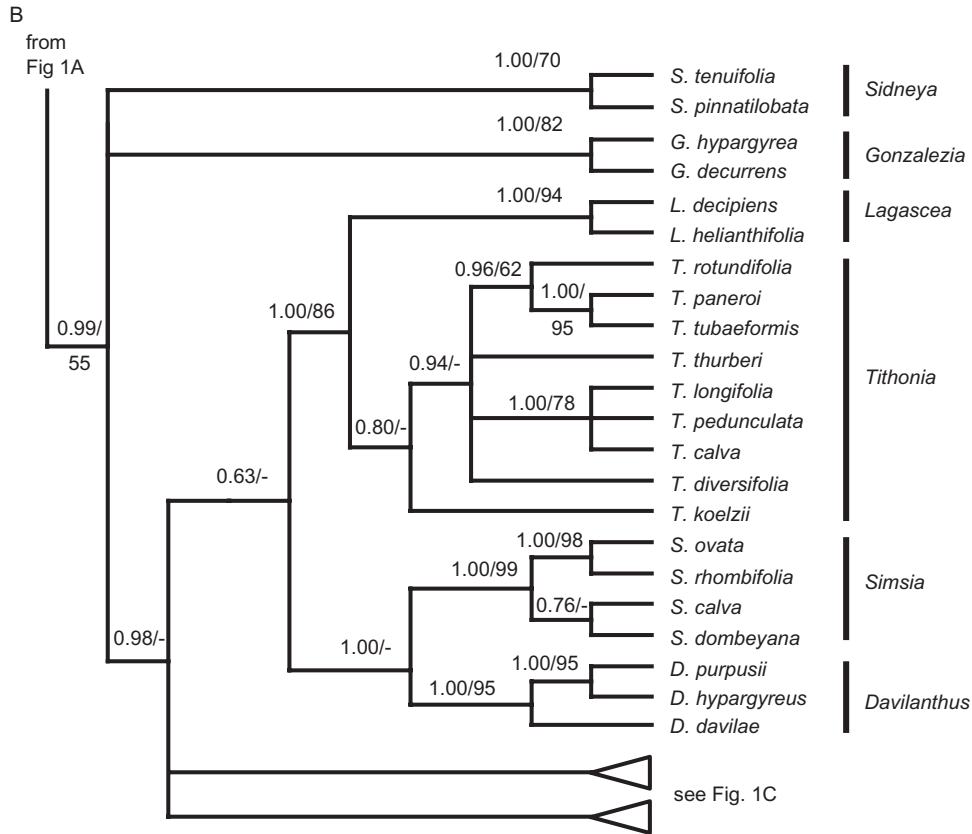


Figure 1. Continued.

lineage. The clade that included the South American *Pappobolus/Syncretocarpus/Scalesia* lineage was placed in the plastid tree as the first diverging branch above *Helianthus + Phoebanthus*, rather than being embedded higher up as part of the trichotomy with *Aldama* and *Tithonia/Lagascea/Simsia/Davilanthus*. Neither *A. canescens* nor *A. cordifolia* was placed with the *Pappobolus* clade, but rather they were separated with *A. canescens* sister to a clade of South American *Aldama*, and *A. cordifolia* in a clade with the *Gonzalezia* samples. The plastid DNA-based tree had a major split between one lineage that included all *Simsia* spp. (except *S. dombeyana* DC.) and a second that contained all *Davilanthus* spp.; *Aldama* spp. were split between these two clades, as were *Tithonia* spp. Clades that were strongly supported in both plastid and ITS/ETS trees, but were placed in different parts of the tree, included *Sidneya*, *Gonzalezia* and *Lagascea*.

## DISCUSSION

The analysis of an expanded set of ITS sequences for Helianthinae and a subset for which partial ETS sequence data were added helped to clarify some,

but not all, of the problems of phylogenetic relationships within the subtribe. In general, the ITS and ITS/ETS sequence data provided additional information to characterize many of the groups that are recognizable from morphology or from previous plastid DNA analyses. There remain, however, a number of points of striking incongruence between the ITS/ETS and plastid DNA results (Fig. 2). This incongruence is found primarily in the derived lineages of the subtribe, which also exhibit a large amount of species-level diversity of the subtribe, and thus invites the search for a possible causal relationship. The lack of concordance among trees based on ITS/ETS and plastid sequences and the incomplete concordance with morphological observations make decisions on how to erect a generic-level taxonomy somewhat arbitrary, but the results show clearly that changes must be made to the existing classification.

Almost all of the incongruence between ITS/ETS and plastid DNA results was present in the more derived lineages of the tree, particularly above the split between *V. dentata + Dendroviguiera/Iostephane* and the remainder of the tree (Fig. 2). Below this split, the majority of species are woody, but above this

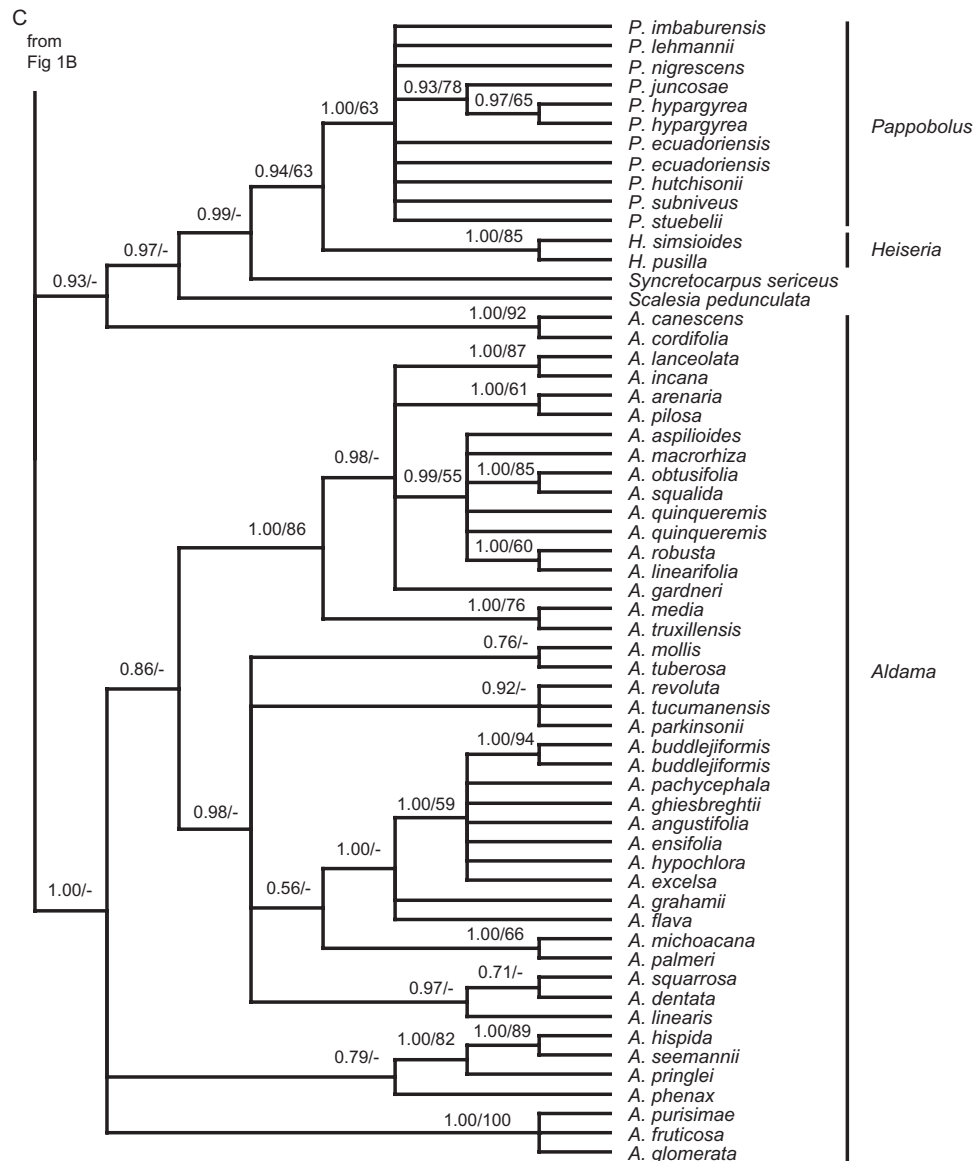
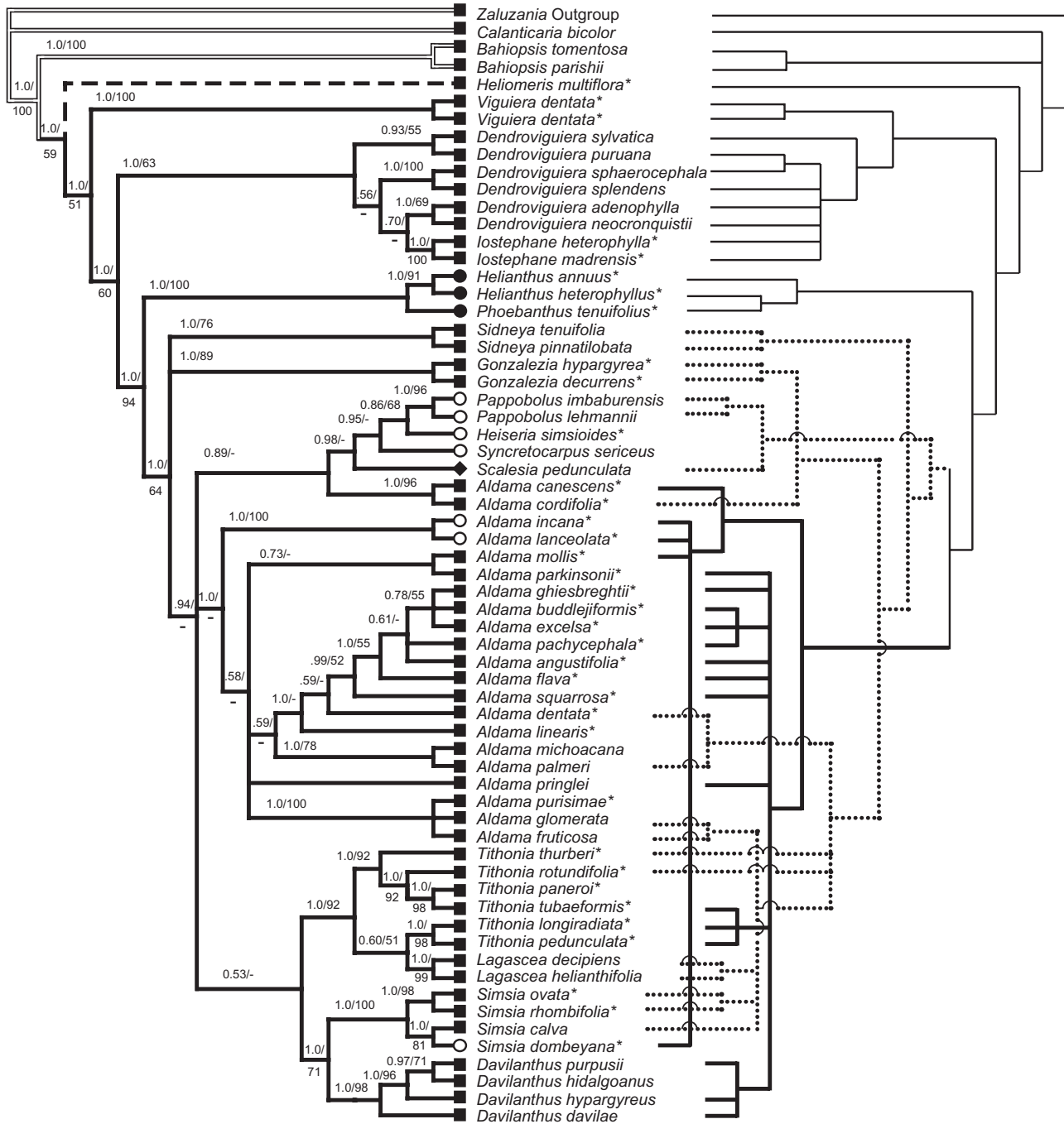


Figure 1. Continued.

split over half of the species are herbaceous (Fig. 2), and many occur in disturbed or successional habitats. This suggests that a fundamental shift to the herbaceous perennial habit occurred, probably correlated with the drying and cooling of the environment during the Pliocene (Ravelo *et al.*, 2004, which would have led to an expansion of the relatively open grassland and savanna habitats (Retallack, 2001; Strömberg & McInerney, 2011) favoured by many derived Helianthinae. Associated with this shift is an apparent increase in hybridization, between both congeneric species, as has been well documented for *Helianthus* (e.g. Heiser *et al.*, 1969; Kane *et al.*, 2009), but also between lineages that had already begun to

diverge significantly, such as *Simsia* and *Tithonia* (Schilling & Panero, 1996b). The possibility for wide hybridization to be successful may have been enhanced by the stability in chromosome number ( $x = 17$ ) that is achieved in the derived clade (Fig. 2).

A further striking feature of divergence in Helianthinae is the movement of the subtribe out of the region of northwest Mexico, where most of the early diverging lineages occur, to colonize other areas, not only in Mexico but also extending into both North and South America (Fig. 2). Invasion into eastern North America is limited to the sister genera *Helianthus* and *Phoebanthus*, which together have > 50 species.



**Figure 2.** Estimation of phylogenetic relationships among members of subtribe Helianthinae based on the Bayesian analysis of combined internal transcribed spacer (ITS) and external transcribed spacer (ETS) sequence data (left; support values shown as Bayesian posterior probabilities/bootstrap percentages; -, less than 50%; line type differentiates chromosome base number: open,  $x = 18$ ; broken,  $x = 8$ ; full,  $x = 17$ ; symbol at branch tip shows area of geographical origin: square, Mexico; filled circle, North America; open circle, South America; diamond, Galápagos Islands; asterisk, herbaceous habit), with comparison of relationships from plastid DNA restriction site data (right; based on Schilling & Panero, 1996a); bold branches highlight derived clades which exhibited significant incongruence between plastid and ITS/ETS results, and dotted/full lines differentiate the two major clades present among these samples.

In contrast, several lineages appear to have penetrated and diversified in South America, and two different lineages have produced high levels of species diversity. One with >50 species includes *Pappobolus*, *Scalesia*, *Syncretocarpus* and *Heiseria*, and is shown by the ITS and ITS/ETS data (although not plastid DNA data) to be sister to the Mexican *A. canescens* (*V. potosina*) and *A. cordifolia*. The second is clearly derived from within *Aldama*, and includes >70 species in South America that occur in diverse habitats ranging from the cerrado and campo rupestre regions of Brazil (Schilling *et al.*, 2000; Magenta, Pirani & Mondin, 2010) to the montane areas of the Andes from Ecuador to Chile and Argentina and in the savannas and grasslands of Argentina (Sáenz, 1979). This is an amazing radiation that deserves further study, especially in the light of the relatively short time during which it has been suggested to have occurred (Schilling *et al.*, 2000).

The lack of concordance between nuclear and plastid markers appears to provide evidence for the importance of phylogenetic reticulation through hybridization in diversification of the subtribe. This phenomenon has previously been suggested for the striking nonconcordance of ITS and plastid DNA trees in *Simsia* and *Tithonia* (Schilling & Panero, 1996b). The studies of Rieseberg (e.g. Rieseberg *et al.*, 2003) have clearly documented the importance of interspecific hybridization in generating new species within a genus. The results of Timme, Simpson & Linder (2007) for ETS sequences from *Helianthus* provide further evidence that interspecific hybridization is widespread in Helianthinae. Additional examples are noted in the current study for *Gonzalezia* and *Dendroviguiera*. Although naturally occurring intergeneric hybrids have not been documented, Cristov & Panayotov (1991), Reyes-Valdés *et al.* (2005) and Luévanos-Escareño *et al.* (2010) have produced crosses between *Helianthus* and *Tithonia*, showing that hybridization at this level of divergence could occur. Hybridization thus appears to be more widespread than previously recognized as an evolutionary phenomenon contributing to divergence in the subtribe.

The phylogenetic results suggest that features of the heads have been subject to homoplasy or extreme modification. For example, the syndrome involving reduction to one- to few-flowered, clustered heads appears to have developed independently at least three times: in *Calanticaria* (González Elizondo, González Elizondo & Rzedowski, 2000), *Lagascea* (Harris, 1994) and *Aldama* (*Alvordia*; Carter, 1964). Similarly, the development of paleae that have stiff, attenuate, elongate tips has occurred in *Heliomeris*, *Viguiera*, *Aldama* and *Tithonia*. The highly modified

paleae that led previously to narrow delimitations of both *Aldama* and *Rhysolepis* appear in each case to involve autapomorphic changes. The collective pattern is that there is significant evolutionary pressure on the heads, which is probably the result of the activities of seed predators. Seed predation has been documented to be severe in Asteraceae (Pilson, 2000; Prado *et al.*, 2002), and we have often noted extensive damage to developing cypselae in many Helianthinae.

Erecting a generic-level classification for Helianthinae on the basis of the molecular phylogenetic results is challenging because of the lack of consensus for the placement of some species or groups of species. Even more difficult is the task of preparing a key to distinguish groups selected for recognition because of the numerous exceptional cases in which even groups well supported by molecular data lack unambiguous morphological synapomorphies to define them. For example, *Helianthus* appears to be clearly monophyletic, on the basis of molecular results, and is mostly characterized by a caducous pappus and trilobed paleae. The species *H. porteri*, however, which is clearly a *Helianthus* on the basis of molecular and genetic data (chromosome number and crossing results), completely lacks a pappus and has unlobed paleae; its morphology is so similar to that exhibited by species of *Heliomeris* that a dissertation study examining it closely came to the conclusion that it should be retained in *Heliomeris* (Storbeck, 1985). One solution to the problem of generic delimitation would be to place many or all of the species of the subtribe in a single large genus. This would, however, obscure the considerable morphological variation that occurs in the subtribe, and would also simply shift the problem to the next level in recognizing infrageneric taxa. The classification proposed here is viewed as a provisional attempt to recognize groups that can be the focus of more detailed study, the results of which may suggest modifications or realignments. Individual lineages that are suggested for generic recognition are discussed below, and a key to genera and taxonomic adjustments follows.

#### VIGUIERA S.S

The suggestion made initially by Robinson (1977) that the circumscription of *Viguiera* could be narrowed to this single species appears to be the most accurate way to reflect the phylogenetic hypotheses generated by molecular analyses (Figs 1 and 2). *Viguiera dentata* has special nomenclatural status as the type species of *Viguiera*, and is quite distinctive in both morphology and at the molecular level. Morphologi-



cally, *V. dentata* has a distinctive apomorphy as the only species of Helianthinae with conspicuously pubescent anther filaments (Robinson, 1977). The ITS results were congruent with plastid DNA results in placing it as one of the relatively early diverging clades of Helianthinae (Figs 1 and 2). In addition to sequence differences, all 12 samples of *V. dentata* that were analysed exhibited a distinctive 13-bp deletion in the ITS2 region. Plastid DNA data had earlier shown this species to be highly distinctive (Schilling & Jansen, 1989; Schilling & Panero, 1996a). In contrast with the plastid DNA results, there was intraspecific variation for ITS and ETS sequences which divided the samples of *V. dentata* into two or more groups (Figs 1 and 2). There was not, however, an easily discernible correlation with the morphological features, such as leaf pubescence and prominence of the paleae, which have been used to split this group into multiple species. A more detailed study of variability is needed to assess whether this widespread entity contains more than a single species.

*DENDROVIGUIERA* (VIGUIERA SECTION *MACULATAE*)  
AND *IOSTEPHANE*

The ITS results supported the distinctiveness of the woody group previously recognized as *Viguiera* section *Maculatae* (Panero & Schilling, 1988) and its seemingly improbable close, sister group, relationship to the herbaceous, rosulate *Iostephane* (Schilling & Panero, 1991). Continued recognition of *Iostephane*, which is quite distinctive morphologically (Strother, 1983), requires the recognition of *Viguiera* section *Maculatae* at the genus level and is proposed here. Although *Dendroviguiera* + *Iostephane* were placed near *V. dentata*, there was only limited support in the ITS data and none in the ITS/ETS data (Figs 1 and 2) for the collective monophyly of these suggested by plastid DNA restriction site data (Fig. 2; Schilling & Jansen, 1989; Schilling & Panero, 1996a). The placement of the Costa Rican *D. sylvatica* varied slightly between the ITS-based tree, where it was placed with *V. dentata*, albeit with low support, and the ITS/ETS- and plastid-based trees, where it was placed within *Dendroviguiera* (Fig. 2). It is included here in *Dendroviguiera*, but the analysis of its relationships requires further study.

*HELIANTHUS* + *PHOEBANTHUS*

*Helianthus* and *Phoebanthus* are the only two genera of Helianthinae that have native geographical distributions primarily or exclusively in eastern North America and, on the basis of both ITS and plastid DNA results (Schilling & Panero, 1996a; Schilling

*et al.*, 1998), they formed a strongly supported lineage that is the sister group to the rest of the terminal clade (Figs 1 and 2).

*SIDNEYA* (VIGUIERA SERIES *PINNATILOBATAE*)

The placement and monophyly of *Sidneya* were supported by both ITS/ETS and plastid DNA data (Figs 1 and 2). Morphologically, this is a well-marked group characterized by a shrubby habit with pinnately lobed leaves and small, epappose cypselae.

*GONZALEZIA* (VIGUIERA SECTION *HYPARGYREA*)

The species of *Gonzalezia* formed a well-supported clade in both the ITS and plastid DNA trees (Figs 1 and 2). Morphologically, *Gonzalezia* can be distinguished by its robust herbaceous habit, leaves that are silky or tomentose abaxially, and heads that are solitary or few, and relatively large. The ITS and ETS results showed that *G. rosei* is of a probable hybrid origin involving the other two species, based on the pattern of base and indel polymorphisms.

*ALDAMA* (VIGUIERA SECTION *LEIGHIA*, V. SUBGENUS *AMPHILEPIS*, V. *SESSILIFOLIA*, V. *PARKINSONII*, V. SECTION *PARADOSA* S.F.BLAKE, V. SUBGENUS *YERBALESIA* S.F.BLAKE, *RHYSOLEPIS*, *STUESSYA* AND *ALVORDIA*)

*Aldama* is expanded as the oldest available generic name to accommodate a group of species that include various infrageneric taxa of *Viguiera* and three other genera, *Alvordia*, *Rhysolepis* and *Stuessya*, and were placed together in a terminal clade in the ITS and ITS/ETS results (Figs 1 and 2). Although there is no unambiguous morphological apomorphy to define *Aldama*, most of its species are herbaceous perennials with a stiff, upright habit. The genus that results is still possibly paraphyletic or even polyphyletic, but the conflict between the ITS and plastid DNA results raises the likelihood that it will be difficult unambiguously to discriminate smaller clades for recognition as genera. As originally defined, *Aldama* included two species that were characterized morphologically by having paleae that completely enclosed the associated cypselae at maturity (Feddem, 1966, 1971; Harriman, 1989). The molecular phylogenetic results suggested that this syndrome is autapomorphic.

Haps the most surprising result from the ITS/ETS data was the extremely close similarity between *Aldama* spp. formerly placed in *Alvordia* and *Aldama purisimae* (*Viguiera purisimae* Brande-

gee). The only apparent unifying theme for these species is geography, as they occur primarily in the Baja California peninsula. The four species formerly placed in *Alvordia* are characterized by the reduction of heads to one or a few flowers and their condensation into secondary heads (Carter, 1964; Turner, 1998), but molecular phylogenetic results suggested that this lineage is embedded within *Aldama* (Figs 1 and 2).

The two molecular datasets provided conflicting evidence for the phylogenetic placements of *A. cordifolia* (*V. cordifolia*) and *A. canescens* (*V. potosina*), for which morphological data offer little insight. These two species were placed together with strong support in the ITS/ETS tree (Figs 1C and 2), and as sister to the group containing *Pappobolus*, *Scalesia* and *Syncretocarpus*. In contrast, the species were placed in separate parts of the plastid DNA tree, where *A. cordifolia* was placed sister to *Gonzalezia* as part of a larger clade that included *Simsia* and some species of *Aldama* and *Tithonia*, and *A. canescens* as sister to a clade with South American members of *Aldama* (Fig. 2). Morphologically, the stiff herbaceous habit of *A. cordifolia* is similar to many other species of *Aldama*, where it is provisionally placed. In contrast, *A. canescens* is morphologically quite distinctive, with long pubescent petioles and narrow cylindrical heads, and further study may show the desirability of segregating it as a separate genus.

#### DAVILANTHUS AND SIMSIA

The sister group relationship of *Davilanthus* and *Simsia* was the focus of Schilling & Panero (2010), and no further nomenclatural adjustments are needed.

#### TITHONIA AND LAGASCEA

Schilling & Panero (1996b, 2010) presented comprehensive data on the relationships of *Tithonia* and *Lagascea* to one another, and to *Simsia* and *Davilanthus*. *Lagascea* is a small genus characterized by reduction and condensation of its heads into tertiary units (Stuessy, 1978; Harris, 1994), and a close relationship to *Tithonia* is not suggested by morphology. The close sister group relationship of *T. paneroi* (*V. paneroi*) and *T. tubaeformis* (Figs 1 and 2) suggests that the former be transferred to *Tithonia*, despite the lack of the fistulose peduncle that otherwise characterizes *Tithonia*.

#### PAPPOBOLUS, SCALEZIA, SYNCRETOCARPUS AND HEISERIA

*Pappobolus*, *Scalesia* and the small Andean genus *Syncretocarpus* formed a monophyletic group based on the ITS/ETS results (Fig. 1), in agreement with previous results from plastid DNA data (available only for *Pappobolus* and *Scalesia*; Schilling *et al.*, 1994). Surprisingly, the two Andean species formerly placed in *Viguiera* as subseries *Pusillae* S.F.Blake [*V. pusilla* (A.Gray) S.F.Blake and *V. simsioides* S.F.Blake; Blake, 1918] were also included in this clade, as sister to *Pappobolus* (Figs 1 and 2). The subseries, characterized among South American species of the subtribe primarily by annual habit, is elevated here to *Heiseria*. There was an overall low level of sequence divergence within *Pappobolus* which suggests that, despite having a relatively large number of species (Panero, 1992), its divergence, like that of other members of the subtribe in South America, has been relatively recent.

### TAXONOMIC TREATMENT

#### KEY TO GENERA OF HELIANTHINAE

1. Staminal filaments pubescent.....*Viguiera*
1. Staminal filaments glabrous.....2
2. Capitula in dense clusters, with one to eight florets per head.....3
2. Capitula not in dense clusters, usually with more than eight florets per head.....6
3. Annual herb; florets greenish-white; cypselae with a pappus of a short ciliolate-fimbriate rim.....*Hymenostephium rivularis*
3. Shrubs or herbs; florets yellow, white or purple; cypselae epappose or with a pappus of 2–15 barbellate awns, scales or a ring of bristles.....4
4. Cypselae epappose, glabrous.....*Calanticaria oligocephala*
4. Cypselae usually with a pappus of awns or bristles, usually pubescent at least at the apex.....5
5. Primary involucre scarious; clusters of heads not subtended by a secondary involucre; shrubs.....*Aldama*
5. Primary involucre herbaceous; clusters of heads subtended by a secondary involucre; shrubs or herbs.....*Lagascea*

6. Mature marginal paleae enlarged to completely and closely enclose the disc cypselae, the margins overlapping adaxially.....7
6. Mature marginal paleae not enlarged, typically conduplicate and at most loosely enclosing the disc cypselae....8
7. Mature marginal paleae thickened and sclerified, the surface frequently tuberculate.....*Sclerocarpus*
7. Mature marginal paleae membranaceous or chartaceous, the surface irregularly wrinkled and pitted.....*Aldama*
8. Disc florets (and ray florets, if present) white; paleae three-lobed.....*Scalesia*
8. Disc florets and ray florets not white, typically yellow or purplish, pinkish, reddish or brownish; paleae lobed or unlobed.....9
9. Disc cypselae with a conspicuous elaiosome, often also with corky margins.....*Syncretocarpus*
9. Disc cypselae without an elaiosome, and margins not corky.....10
10. Peduncles fistulose; paleae usually rigid, acuminate to aristate.....*Tithonia*
10. Peduncles not fistulose; paleae various.....11
11. Ray ovaries long and narrow (> 4 mm long and 4–20 times as long as wide); style branches long and tapering, but with only a short terminal appendage; disc corolla lobes with sclerified cells; anther connectives often setose; cypselae sometimes conspicuously flattened and with a broad marginal rim; nodal discs sometimes present.....*Simsia*
11. Ray ovaries shorter and broader (typically < 4 mm long and 2.0–3.8 times as long as wide); style branches either deltate or with a conspicuous terminal appendage; disc corolla lobes lacking sclerified cells; anther connectives glabrous; cypselae not conspicuously flattened; nodal discs absent.....12
12. Involucre one- to two-seriate; heads subglobose to campanulate, the discs 5.5–10.0 mm high and 3–12 mm wide; leaves usually with a slender petiole and an ovate, serrate blade.....*Hymenostephium*
12. Involucre two- to seven-seriate; heads broadly campanulate to hemispheric or cylindrical, the discs usually > 12 mm wide; leaves various, but rarely with a slender petiole and an ovate, serrate blade.....13
13. Plants herbaceous.....14
13. Plants woody, shrubs or trees.....21
14. Plants with a rosette of leaves from a stout, woody caudex; cypselae strongly quadrate.....*Iostephane*
14. Plants not rosulate or, if rosulate, caudex not stout and woody, and cypselae biconvex.....15
15. Style branches long and tapering, and with a conspicuous terminal appendage; paleae usually three-lobed (unlobed in *Helianthus porteri*).....16
15. Style branches shorter and broader, with a deltate apex and only a short terminal appendage; paleae unlobed.....17
16. Lateral lobes of paleae almost as long as terminal one; pappus persistent, of one or two short awns and an indefinite number of minute bristles; plants from small, slender tubers.....*Phoebanthus*
16. Lateral lobes of paleae much shorter than terminal one; pappus deciduous, usually of two conspicuous awns, sometimes also with a few, short additional scales, or epappose (*H. porteri*); tubers if present stout..*Helianthus*
17. Cypselae with a pappus of two awns and intermediate scales.....18
17. Cypselae epappose.....20
18. Annuals, involucre two- or three-seriate.....*Heiseria*
18. Perennials, involucre (two-) three- to five-seriate.....19
19. Stout perennial herbs with one to a few large heads, the discs > 2.5 cm across; leaves sessile, softly and densely pubescent beneath.....*Gonzalezia*
19. Perennial herbs with varied habit, but usually not stout, often with a branched capitulescence of heads with discs < 2 cm across; leaves petiolate or sessile, glabrous to densely pubescent beneath.....*Aldama*
20. Involucre two-seriate, phyllary apices acute, leaves usually linear or lanceolate.....*Heliomeris*
20. Involucre three- to five-seriate, inner phyllaries usually with rounded, amplified, membranaceous apices.....*Aldama*
21. Cypselae epappose and leaves pinnately lobed, the lobing sometimes obscure.....*Sidneya*
21. Cypselae usually with a pappus, if epappose, then leaves unlobed.....22
22. Heads solitary at the ends of branches.....*Calanticaria*
22. Heads in a branched inflorescence of two or three or more heads.....23
23. Leaf petioles < 3 mm long in combination with blades > 40 mm long, blades entire or subentire.....*Aldama*
23. Leaf petioles typically > 3 mm long, if shorter, blades < 35 mm long; blades entire or serrate.....24
24. Leaves lacking sessile glandular trichomes on the undersurface, the lower ones usually ovate or deltoid and trinerved with basal naked veins.....*Davilanthus*
24. Leaves with sessile glandular trichomes on the undersurface or, if lacking sessile glandular trichomes, then leaves not with basal naked veins.....25

25. Disc pappus caducous, either of several awns or of two awns with or without squamellae; shrubs and subshrubs from South America.....*Pappobolus*
25. Disc pappus persistent, usually of two awns and intermediate squamellae; shrubs and trees of southwestern North America and Mexico to Central America.....26
26. Phyllaries with oblong, indurated bases and short, triangular herbaceous apices; pappus awns usually broad, > 0.3 mm across; abaxial leaf surfaces usually not densely pubescent; shrubs and trees usually of tropical deciduous forest of central to southern Mexico, with one species in Costa Rica and Panama.....*Dendroviguiera*
26. Phyllaries with ovate, indurated bases and abruptly narrowed and usually elongate (except in *B. microphylla*) herbaceous apices; pappus awns usually narrow, < 0.2 mm across; abaxial surfaces of leaves usually either densely pubescent or resinous; xerophytic shrubs of Baja California, Mexico and nearby areas.....*Bahiopsis*

*New combinations in Aldama La Llave*

**Aldama adenotricha** (S.F.Blake) E.E.Schill. & Panero, **comb. nov.** Basionym: *Viguiera adenotricha* S.F.Blake. Contr. Gray Herb. 54: 120, 1918.

**Aldama amphichlora** (S.F.Blake) E.E.Schill. & Panero, **comb. nov.** Basionym: *Viguiera amphichlora* S.F.Blake. Contr. Gray Herb. 54: 166, 1918.

**Aldama anchusifolia** (DC.) E.E.Schill. & Panero, **comb. nov.** Basionym: *Leighia anchusifolia* ('*anchusaefolia*') DC. Prodr. 5: 580, 1836.

**Aldama angustifolia** (Hook. & Arn.) E.E.Schill. & Panero **comb. nov.** Basionym: *Tithonia angustifolia* Hook. & Arn. Bot. Beech. Voy. 299, 1840.

**Aldama angustissima** (S.F.Blake) E.E.Schill. & Panero, **comb. nov.** Basionym: *Viguiera angustissima* S.F.Blake. Contr. Gray Herb. 54: 118, 1918.

**Aldama apiculata** (S.F.Blake) E.E.Schill. & Panero, **comb. nov.** Basionym: *Viguiera apiculata* S.F.Blake. Contr. U.S. Natl. Herb. 22: 620, 1924.

**Aldama arenaria** (Baker) E.E.Schill. & Panero, **comb. nov.** Basionym: *Viguiera arenaria* Baker in Martius. Fl. Bras. 6(3): 226, 1884.

**Aldama aspilioides** (Baker) E.E.Schill. & Panero, **comb. nov.** Basionym: *Viguiera aspilioides* Baker in Martius. Fl. Bras. 6(3): 228, 1884.

**Aldama atacamensis** (Phil.) E.E.Schill. & Panero, **comb. nov.** Basionym: *Viguiera atacamensis* Phil. Anales Mus. Nac. Chile, Segunda Secc., Bot. 1891: 48, 1891.

**Aldama australis** (S.F.Blake) E.E.Schill. & Panero, **comb. nov.** Basionym: *Viguiera australis* S.F.Blake. Contr. Gray Herb. 54: 148, 1918.

**Aldama bakeriana** (S.F.Blake) E.E.Schill. & Panero, **comb. nov.** Basionym: *Viguiera bakeriana* S.F.Blake. Contr. Gray Herb. 54: 130, 1918.

**Aldama bishopii** (H.Rob.) E.E.Schill. & Panero, **comb. nov.** Basionym: *Viguiera bishopii* H.Rob. Phytologia 45: 458, 1980.

**Aldama bracteata** (Gardner) E.E.Schill. & Panero, **comb. nov.** Basionym: *Viguiera bracteata* Gardner. Lond. J. Bot. 7: 404, 1848.

**Aldama brandegeei** (A.M.Carter) E.E.Schill. & Panero, **comb. nov.** Basionym: *Alvordia brandegeei* A.M.Carter. Proc. Calif. Acad. Sci. (ser. 4) 30: 163, 1964.

**Aldama breviflosculosa** (S.F.Blake) E.E.Schill. & Panero, **comb. nov.** Basionym: *Viguiera breviflosculosa* S.F.Blake. Contr. Gray Herb. 54: 158, 1918.

**Aldama brittonii** (Hochr.) E.E.Schill. & Panero, **comb. nov.** Basionym: *Viguiera brittonii* Hochr. Bull. New York Bot. Gard. 6: 294, 1910.

**Aldama buddlejiformis** (DC.) E.E.Schill. & Panero **comb. nov.** Basionym: *Helianthus buddlejiformis* [as *buddlieaeformis*] DC. Prodr. 5: 588, 1836.

**Aldama canescens** (B.Rob.) E.E.Schill. & Panero, **comb. nov.** Basionym: *Gymnolomia canescens* B.Rob. Proc. Amer. Acad. Arts 27: 174, 1892 (= *Viguiera potosina* S.F.Blake).

**Aldama congesta** (Rose ex Hoffmann) E.E.Schill. & Panero, **comb. nov.** Basionym: *Agiabampoa congesta* Rose ex Hoffmann. Nat. Pflanzenfam. 4: 390, 1893.

**Aldama coraniana** (A.A.Sáenz) E.E.Schill. & Panero, **comb. nov.** Basionym: *Viguiera coraniana* A.A.Sáenz. Parodiana 5: 26, 1987 [1988].

**Aldama cordifolia** (A.Gray) E.E.Schill. & Panero, **comb. nov.** Basionym: *Viguiera cordifolia* A.Gray. Smiths. Contr. Knowl. 3 (5): 107, 1852.

**Aldama cornifolia** (Kunth) E.E.Schill. & Panero **comb. nov.** Basionym: *Helianthus cornifolius* Kunth, Nov. Gen. Sp. 4: 223, 1820.

**Aldama densifolia** (Baker) E.E.Schill. & Panero, **comb. nov.** Basionym: *Viguiera densifolia* Baker in Martius. Fl. Bras. 6(3): 219, 1884.

**Aldama dillonorum** (A.J.Moore & H.Rob.) E.E.Schill. & Panero, **comb. nov.** Basionym: *Rhysolypis dillonorum* A.J.Moore & H.Rob. Proc. Biol. Soc. Wash. 117: 432, 2004.

**Aldama discolor** (Baker) E.E.Schill. & Panero, **comb. nov.** Basionym: *Viguiera discolor* Baker in Martius. Fl. Bras. 6(3): 225, 1884.



- Aldama ellenbergii** (Cuatrec.) E.E.Schill. & Panero, **comb. nov.** Basionym: *Viguiera ellenbergii* Cuatrec. Proc. Biol. Soc. Wash. 77: 146, 1964.
- Aldama emaciata** (H.Rob. & A.J.Moore) E.E.Schill. & Panero, **comb. nov.** Basionym: *Rhysol-epis emaciata* H.Rob. & A.J.Moore. Proc. Biol. Soc. Wash. 117: 434, 2004.
- Aldama ensifolia** (Sch.Bip.) E.E.Schill. & Panero **comb. nov.** Basionym: *Montagnea ensifolia* Sch.Bip. in Seeman. Botany Herald 304, 1856.
- Aldama excelsa** (Willd.) E.E.Schill. & Panero **comb. nov.** Basionym: *Helianthus excelsus* Willd. Sp. Pl. 3: 2243, 1803.
- Aldama fabrisii** (A.A.Sáenz) E.E.Schill. & Panero, **comb. nov.** Basionym: *Viguiera fabrisii* A.A.Sáenz. Darwiniana 22: 50, 1979.
- Aldama filifolia** (Sch.Bip. ex Baker) E.E.Schill. & Panero, **comb. nov.** Basionym: *Viguiera filifolia* Sch.Bip. ex Baker in Martius. Fl. Bras. 6(3): 219, 1884.
- Aldama flava** (Hemsl.) E.E.Schill. & Panero **comb. nov.** Basionym: *Gymnolomia flava* Hemsl. Biol. Centr.-Am. Bot 2: 161, 1881.
- Aldama fruticosa** (Brandegee) E.E.Schill. & Panero, **comb. nov.** Basionym: *Alvordia fruticosa* Brandegee. Erythea 7: 5, 1899.
- Aldama fusiformis** (S.F.Blake) E.E.Schill. & Panero, **comb. nov.** Basionym: *Viguiera fusiformis* S.F.Blake. Contr. Gray Herb. 54: 145, 1918.
- Aldama gardneri** (Baker) E.E.Schill. & Panero, **comb. nov.** Basionym: *Viguiera gardneri* Baker in Martius. Fl. Bras. 6(3): 224, 1884.
- Aldama gentryi** (B.L.Turner) E.E.Schill. & Panero, **comb. nov.** Basionym: *Viguiera gentryi* B.L.Turner. Phytologia 66: 458, 1989.
- Aldama ghiesbreghtii** (Hemsl.) E.E.Schill. & Panero **comb. nov.** Basionym: *Gymnolomia ghiesbreghtii* Hemsl. Biol. Centr.-Am. Bot. 2: 162, 1881 (= *Viguiera hemsleyana* S.F.Blake).
- Aldama gilliesii** (Hook. & Arn.) E.E.Schill. & Panero, **comb. nov.** Basionym: *Leighia gilliesii* Hook. & Arn. Hooker's J. Bot. 3: 313, 1841.
- Aldama glomerata** (Brandegee) E.E.Schill. & Panero, **comb. nov.** Basionym: *Alvordia glomerata* Brandegee. Proc. Calif. Acad. Sci. (ser. 2) 2: 174. 1889.
- Aldama goldmanii** (Greenm.) E.E.Schill. & Panero, **comb. nov.** Basionym: *Viguiera goldmanii* Greenm. Proc. Amer. Acad. Arts 39: 104, 1903.
- Aldama goyasensis** (H.Rob. & A.J.Moore) E.E.Schill. & Panero, **comb. nov.** Basionym: *Rhysol-epis goyasensis* H.Rob. & A.J.Moore. Proc. Biol. Soc. Wash. 117: 434, 2004.
- Aldama goyazii** E.E.Schill. & Panero nom. nov. *Viguiera hispida* Baker in Martius. Fl. Bras. 6(3): 220, 1884, non *Aldama hispida* (Kunth) E.E.Schill. & Panero (*Ximenesia hispida* Kunth Nov. Gen. Sp. 4: 227, 1820).
- Aldama grahamii** (McVaugh) E.E.Schill. & Panero **comb. nov.** Basionym: *Viguiera gra-hamii* McVaugh Contr. Univ. Michigan Herb. 9: 456, 1972.
- Aldama grandiflora** (Gardner) E.E.Schill. & Panero, **comb. nov.** Basionym: *Viguiera grandiflora* Gardner. London J. Bot. 7: 404, 1848.
- Aldama guaranitica** (Chodat) E.E.Schill. & Panero, **comb. nov.** Basionym: *Viguiera guarantica* Chodat. Bull. Herb. Boissier ser. 2, 3: 724, 1903.
- Aldama hatschbachii** (H.Rob. & A.J.Moore) E.E.Schill. & Panero, **comb. nov.** Basionym: *Rhysol-epis hatschbachii* H.Rob. & A.J.Moore. Proc. Biol. Soc. Wash. 117: 438, 2004.
- Aldama helianthoides** (Rich.) E.E.Schill. & Panero **comb. nov.** Basionym: *Sanvitalia helian-thoides* Rich. in Willd. Sp. Pl. 3: 2190, 1803.
- Aldama hilairei** (S.F.Blake) E.E.Schill. & Panero, **comb. nov.** Basionym: *Viguiera hilairei* S.F.Blake. Contr. Gray Herb. 54: 153, 1918.
- Aldama hispida** (Kunth) E.E.Schill. & Panero, **comb. nov.** Basionym: *Ximenesia hispida* Kunth. Nov. Gen. Sp. 4: 227. 1820 (= *Viguiera sessilifolia* DC).
- Aldama hypochlora** (S.F.Blake) E.E.Schill. & Panero, **comb. nov.** Basionym: *Gymnolomia hypochlora* S.F.Blake. Proc. Amer. Acad. Arts 51: 516, 1916.
- Aldama hypoleuca** (S.F.Blake) E.E.Schill. & Panero, **comb. nov.** Basionym: *Viguiera hypoleuca* S.F.Blake. Contr. Gray Herb. 54: 165, 1918.
- Aldama incana** (Pers.) E.E.Schill. & Panero, **comb. nov.** Basionym: *Helianthus incanus* Pers. Syn.Pl. 2: 475, 1807.
- Aldama imbricata** (Baker) E.E.Schill. & Panero, **comb. nov.** Basionym: *Viguiera imbricata* Baker in Martius. Fl. Bras. 6(3): 220, 1884.
- Aldama kingii** (H.Rob.) E.E.Schill. & Panero, **comb. nov.** Basionym: *Rhysol-epis kingii* H.Rob. Phy-tologia 24: 210, 1972.
- Aldama knobiana** (Mondin & Magenta) E.E.Schill. & Panero, **comb. nov.** Basionym: *Viguiera knobiana* Mondin & Magenta. Rodriguésia 61: 2, 2010.
- Aldama kunthiana** (Gardner) E.E.Schill. & Panero, **comb. nov.** Basionym: *Viguiera kunthiana* Gardner. Lond. J. Bot. 7: 399, 1848.
- Aldama lanceolata** (Britton) E.E.Schill. & Panero, **comb. nov.** Basionym: *Viguiera lanceolata* Britton. Bull. Torrey Bot. Club 19: 149, 1892.
- Aldama latibracteata** (Hemsl.) E.E.Schill. & Panero, **comb. nov.** Basionym: *Gymnolomia latibrac-teata* Hemsl. Biol. Centr.-Am. Bot 2: 162, 1881.
- Aldama laxicymosa** (H.Rob. & A.J.Moore) E.E.Schill. & Panero, **comb. nov.** Basionym: *Rhysol-epis laxicymosa* H.Rob. & A.J.Moore. Proc. Biol. Soc. Wash. 117: 440, 2004.



- Aldama linearifolia** (Chodat) E.E.Schill. & Panero, **comb. nov.** Basionym: *Viguiera linearifolia* Chodat. Bull. Herb. Boissier ser. 2: 2: 392, 1902.
- Aldama linearis** (Cav.) E.E.Schill. & Panero, **comb. nov.** Basionym: *Helianthus linearis* Cav. Icon 3: 9, 1795.
- Aldama macbridei** (S.F.Blake) E.E.Schill. & Panero, **comb. nov.** Basionym: *Viguiera macbridei* S.F.Blake. J. Wash. Acad. Sci. 16: 218, 1926.
- Aldama macrocalyx** (S.F.Blake) E.E.Schill. & Panero, **comb. nov.** Basionym: *Viguiera macrocalyx* S.F.Blake. Contr. Gray Herb. 54: 171, 1918.
- Aldama macropoda** (S.F.Blake) E.E.Schill. & Panero, **comb. nov.** Basionym: *Viguiera macropoda* S.F.Blake. Contr. Gray Herb. 54: 128, 1918.
- Aldama macrorhiza** (Baker) E.E.Schill. & Panero, **comb. nov.** Basionym: *Viguiera macrorhiza* Baker in Martius. Fl. Bras. 6(3): 225, 1884.
- Aldama media** (S.F.Blake) E.E.Schill. & Panero, **comb. nov.** Basionym: *Viguiera media* S.F.Blake. Contr. Gray Herb. 54: 138, 1918.
- Aldama meridionalis** (Magenta) E.E.Schill. & Panero, **comb. nov.** Basionym: *Viguiera meridionalis* Magenta. Rodriguésia 61: 4, 2010.
- Aldama michoacana** (B.L.Turner & F.Davies) E.E.Schill. & Panero, **comb. nov.** Basionym: *Stuessya michoacana* B.L.Turner & F.Davies. Brittonia 32: 212, 1980.
- Aldama mollis** (Griseb.) E.E.Schill. & Panero, **comb. nov.** Basionym: *Viguiera mollis* Griseb. Abh. Königl. Ges. Wiss. Göttingen 19: 183, 1874.
- Aldama montana** (Rose) E.E.Schill. & Panero, **comb. nov.** Basionym: *Viguiera montana* Rose. Contr. U. S. Natl. Herb. 1: 103, 1891.
- Aldama morelensis** (S.F.Blake) E.E.Schill. & Panero, **comb. nov.** Basionym: *Rhysolepis morelensis* S.F.Blake. Contr. Gray Herb. 52: 36, 1917.
- Aldama nervosa** (Gardner) E.E.Schill. & Panero, **comb. nov.** Basionym: *Viguiera nervosa* Gardner. Lond. J. Bot. 7: 403, 1848.
- Aldama nesomii** (B.L.Turner) E.E.Schill. & Panero, **comb. nov.** Basionym: *Viguiera nesomii* B.L.Turner. Phytologia 67: 339, 1989.
- Aldama nudicaulis** (Baker) E.E.Schill. & Panero, **comb. nov.** Basionym: *Viguiera nudicaulis* Baker in Martius. Fl. Bras. 6(3): 228, 1884.
- Aldama nudibasilaris** (S.F.Blake) E.E.Schill. & Panero, **comb. nov.** Basionym: *Viguiera nudibasilaris* S.F.Blake. Contr. Gray Herb. 54: 149, 1918.
- Aldama oblongifolia** (Gardner) E.E.Schill. & Panero, **comb. nov.** Basionym: *Viguiera oblongifolia* Gardner. London J. Bot. 7: 402, 1848.
- Aldama obtusifolia** (Baker) E.E.Schill. & Panero, **comb. nov.** Basionym: *Viguiera obtusifolia* Baker in Martius. Fl. Bras. 6(3): 226, 1884.
- Aldama ovatifolia** (DC.) E.E.Schill. & Panero, **comb. nov.** Basionym: *Leighia ovatifolia* DC. Prodr. 5: 583, 1836.
- Aldama pachycephala** (DC.) E.E.Schill. & Panero, **comb. nov.** Basionym: *Tithonia pachycephala* DC. Prodr. 5: 585, 1836.
- Aldama palmeri** (A.Gray ex S.Watson) E.E.Schill. & Panero, **comb. nov.** Basionym: *Viguiera palmeri* A.Gray ex S.Watson. Proc. Amer. Acad. Arts 22: 427, 1887.
- Aldama palmeri** (A.Gray ex S.Watson) E.E.Schill. & Panero var. **rzedowskii** (McVaugh) E.E.Schill. & Panero **comb. nov.** Basionym: *Viguiera palmeri* A.Gray ex S.Watson var. *rzedowskii* McVaugh. Contr. Univ. Mich. Herb. 9: 459, 1972.
- Aldama parkinsonii** (Hemsl.) E.E.Schill. & Panero, **comb. nov.** Basionym: *Gymnolomia parkinsonii* Hemsl. Biol. Centr.-Am. Bot. 2: 163, 1881.
- Aldama perennans** (B.L.Turner & F.Davies) E.E.Schill. & Panero, **comb. nov.** Basionym: *Stuessya perennans* B.L.Turner & F.Davies. Brittonia 32: 211, 1980.
- Aldama peruviana** (A.Gray) E.E.Schill. & Panero, **comb. nov.** Basionym: *Viguiera peruviana* A.Gray. Proc. Amer. Acad. Arts 5: 124, 1861.
- Aldama phenax** (S.F.Blake) E.E.Schill. & Panero, **comb. nov.** Basionym: *Viguiera phenax* S.F.Blake. Proc. Biol. Soc. Wash. 54: 19, 1941.
- Aldama pilicaulis** (S.F.Blake) E.E.Schill. & Panero, **comb. nov.** Basionym: *Viguiera pilicaulis* S.F.Blake. Contr. Gray Herb. 54: 164, 1918.
- Aldama pilosa** (Baker) E.E.Schill. & Panero, **comb. nov.** Basionym: *Viguiera pilosa* Baker in Martius. Fl. Bras. 6(3): 223, 1884.
- Aldama pringlei** (B.Rob. & Greenm.) E.E.Schill. & Panero, **comb. nov.** Basionym: *Viguiera pringlei* B.Rob. & Greenm. Proc. Amer. Acad. Arts 29: 387, 1894.
- Aldama purisimae** (Brandege) E.E.Schill. & Panero, **comb. nov.** Basionym: *Viguiera purisimae* Brandege. Proc. Calif. Acad., ser. 2: 2: 173, 1889.
- Aldama quinqueremis** (S.F.Blake) E.E.Schill. & Panero, **comb. nov.** Basionym: *Viguiera quinqueremis* S.F.Blake. Contr. Gray Herb. 54: 168, 1918.
- Aldama radula** (Baker) E.E.Schill. & Panero, **comb. nov.** Basionym: *Viguiera radula* Baker in Martius. Fl. Bras. 6(3): 223, 1884.
- Aldama retroflexa** (S.F.Blake) E.E.Schill. & Panero, **comb. nov.** Basionym: *Viguiera retroflexa* S.F.Blake. Contr. Gray Herb. 54: 146, 1918.
- Aldama revoluta** (Meyen) E.E.Schill. & Panero, **comb. nov.** Basionym: *Helianthus revolutus* Meyen. Reise 1: 311, 1834.
- Aldama robusta** (Gardner) E.E.Schill. & Panero, **comb. nov.** Basionym: *Viguiera robusta* Gardner. Lond. J. Bot. 7: 403, 1848.

**Aldama rojasii** (S.F.Blake) E.E.Schill. & Panero, **comb. nov.** Basionym: *Viguiera rojasii* S.F.Blake. Contr. Gray Herb. 54: 179, 1918.

**Aldama rubra** (Magenta & Pirani) E.E.Schill. & Panero, **comb. nov.** Basionym: *Viguiera rubra* Magenta & Mirani. Rodriguésia 61: 6, 2010.

**Aldama salicifolia** (Hassl.) E.E.Schill. & Panero, **comb. nov.** Basionym: *Viguiera salicifolia* Hassl. Repert. Spec. Nov. Regni Veg. 14: 274, 1916.

**Aldama santacatarinensis** (H.Rob. & A.J.Moore) E.E.Schill. & Panero, **comb. nov.** Basionym: *Rhysolypis santacatarinensis* H.Rob. & A.J.Moore. Proc. Biol. Soc. Wash. 117: 442, 2004.

**Aldama seemannii** (Sch.Bip.) E.E.Schill. & Panero, **comb. nov.** Basionym: *Viguiera seemannii* Sch.Bip. in Seemann. Bot. Herald 305, 1856.

**Aldama sodiroi** (Hieron.) E.E.Schill. & Panero, **comb. nov.** Basionym: *Helianthus sodiroi* Hieron. Bot. Jahrb. Syst. 29: 41, 1900.

**Aldama speciosa** (Hassl.) E.E.Schill. & Panero, **comb. nov.** Basionym: *Viguiera speciosa* Hassl. Repert. Spec. Nov. Regni Veg. 14: 272, 1916.

**Aldama squalida** (S.Moore) E.E.Schill. & Panero, **comb. nov.** Basionym: *Viguiera squalida* S.Moore. J. Bot. 42: 37, 1904.

**Aldama squarrosa** (Sch.Bip.) E.E.Schill. & Panero, **comb. nov.** Basionym: *Zaluzania squarrosa* Sch.Bip. Flora 47: 217, 1864 (= *Viguiera schultzi*).

**Aldama subcanescens** (S.F.Blake) E.E.Schill. & Panero, **comb. nov.** Basionym: *Viguiera subcanescens* S.F.Blake. Contr. Gray Herb. 54: 49, 1918.

**Aldama subdentata** (S.F.Blake) E.E.Schill. & Panero, **comb. nov.** Basionym: *Viguiera subdentata* S.F.Blake. Contr. Gray Herb. 54: 131, 1918.

**Aldama subtruncata** (H.Rob. & A.J.Moore) E.E.Schill. & Panero, **comb. nov.** Basionym: *Rhysolypis subtruncata* H.Rob. & A.J.Moore. Proc. Biol. Soc. Wash. 117: 442, 2004.

**Aldama tenuifolia** (Gardner) E.E.Schill. & Panero, **comb. nov.** Basionym: *Viguiera tenuifolia* Gardner. Lond. J. Bot. 7: 400, 1848.

**Aldama torresii** (B.L.Turner) E.E.Schill. & Panero, **comb. nov.** Basionym: *Viguiera torresii* B.L.Turner. Phytologia 66: 456, 1989.

**Aldama truxillensis** (Kunth) E.E.Schill. & Panero, **comb. nov.** Basionym: *Helianthus truxillensis* Kunth. Nov. Gen. Sp. 4: 223, 1820.

**Aldama tuberculata** (S.F.Blake) E.E.Schill. & Panero, **comb. nov.** Basionym: *Viguiera tuberculata* S.F.Blake. Contr. Gray Herb. 54: 151, 1918.

**Aldama tuberosa** (Griseb.) E.E.Schill. & Panero, **comb. nov.** Basionym: *Viguiera tuberosa* Griseb. Abh. Königl. Ges. Wiss. Göttingen 24: 192, 1879.

**Aldama tucumanensis** (Hook. & Arn.) E.E.Schill. & Panero, **comb. nov.** Basionym: *Leighia tucumanensis* Hook. & Arn. Hooker's J. Bot. 3: 314, 1841.

**Aldama veredensis** (Magenta & Pirani) E.E.Schill. & Panero, **comb. nov.** Basionym: *Viguiera veredensis* Magenta & Pirani. Rodriguésia 61: 6, 2010.

**Aldama vernonioides** (Baker) E.E.Schill. & Panero, **comb. nov.** Basionym: *Viguiera vernonioides* Baker in Martius. Fl. Bras. 6(3): 223, 1884.

**Aldama weddellii** (S.F.Blake) E.E.Schill. & Panero, **comb. nov.** Basionym: *Viguiera weddellii* S.F.Blake. Contr. Gray Herb. 54: 126, 1918.

*New combination in Tithonia Desf.*

**Tithonia paneroi** (B.L.Turner) E.E.Schill. & Panero, **comb. nov.** Basionym: *Viguiera paneroi* B.L.Turner. Phytologia 89: 353, 2007.

*Validation of two combinations in Hymenostephium Benth. (because the place of publication of the basionym was not cited, the following combinations were invalidly made in Schilling & Panero, 2002)*

**Hymenostephium kingii** (McVaugh) E.E.Schill. & Panero, **comb. nov.** Basionym: *Viguiera kingii* McVaugh. Contr. Univ. Michigan Herb. 9: 458, 1972.

**Hymenostephium lepidostephanum** (Cuatrec.) E.E.Schill. & Panero, **comb. nov.** Basionym: *Viguiera lepidostephana* Cuatrec. Proc. Biol. Soc. Washington 77: 147, 1964.

**Dendroviguiera** E.E.Schill. & Panero, **stat. & nom. nov.** Replaced synonym: *Viguiera* Kunth series *Maculatae* S.F.Blake, Contr. Gray Herb. n.s. 54: 62, 1918. – *Viguiera* section *Maculatae* (S.F.Blake) Panero & E.E.Schill., Syst. Bot. 13: 377, 1988. – Type species: *Dendroviguiera eriophora* (Greenm.) E.E.Schill. & Panero (= *Viguiera eriophora* Greenm.)

The taxonomy of *Dendroviguiera* was thoroughly covered as *Viguiera* section *Maculatae* in Panero & Schilling (1988), and additional discussion is not needed. The only species added is *Dendroviguiera sylvatica*, which extends the range of the genus to Costa Rica. The following combinations are required.

**Dendroviguiera adenophylla** (S.F.Blake) E.E.Schill. & Panero, **comb. nov.** Basionym: *Viguiera adenophylla* S.F.Blake. Proc. Amer. Acad. Arts 51: 518, 1916.

**Dendroviguiera eriophora** (Greenm.) E.E.Schill. & Panero, **comb. nov.** Basionym: *Viguiera eriophora* Greenm. Proc. Amer. Acad. Arts 39: 104, 1903.

**Dendroviguiera eriophora** (Greenm.) E.E.Schill. & Panero ssp. **poblana** (Panero & E.E.Schill.) E.E.Schill. & Panero, **comb. nov.** Basionym: *Viguiera eriophora* Greenm. ssp. *poblana* Panero & E.E.Schill. Syst. Bot. 13: 389, 1988.

**Dendroviguiera guerrerana** (Panero & E.E.Schill.) E.E.Schill. & Panero, **comb. nov.** Basionym: *Viguiera guerrerana* Panero & E.E.Schill. Syst. Bot. 13: 396, 1988.

**Dendroviguiera insignis** (Miranda) E.E.Schill. & Panero, **comb. nov.** Basionym: *Viguiera insignis* Miranda. *Anales Inst. Biol. Univ. Nac. Mexico* 15: 32, 1944.

**Dendroviguiera mirandae** (Panero & E.E.Schill.) E.E.Schill. & Panero, **comb. nov.** Basionym: *Viguiera mirandae* Panero & E.E.Schill. *Syst. Bot.* 13: 392, 1988.

**Dendroviguiera neocronquistii** (B.L.Turner) E.E.Schill. & Panero, **comb. nov.** Basionym: *Viguiera neocronquistii* B.L.Turner. *Phytologia* 58: 229, 1985.

**Dendroviguiera oaxacana** (Greenm.) E.E.Schill. & Panero, **comb. nov.** Basionym: *Helianthus oaxacanus* Greenm. *Proc. Amer. Acad. Arts* 39: 107, 1903.

**Dendroviguiera pringlei** (Fernald) E.E.Schill. & Panero, **comb. nov.** Basionym: *Encelia pringlei* Fernald. *Proc. Amer. Acad. Arts* 35: 573, 1900 (= *Viguiera trachyphylla* S.F.Blake).

**Dendroviguiera puruana** (Paray) E.E.Schill. & Panero, **comb. nov.** Basionym: *Viguiera puruana* Paray. *Bol. Soc. Bot. México* 22: 4, 1958.

**Dendroviguiera quinqueradiata** (Cav.) E.E.Schill. & Panero, **comb. nov.** Basionym: *Helianthus quinque-radiatus* Cav. *Icon.* 3: 36, 1795.

**Dendroviguiera sharpii** (Panero & E.E.Schill.) E.E.Schill. & Panero, **comb. nov.** Basionym: *Viguiera sharpii* Panero & E.E.Schill. *Syst. Bot.* 13: 393, 1988.

**Dendroviguiera sphaerocephala** (DC.) E.E.Schill. & Panero, **comb. nov.** Basionym: *Leighia sphaerocephala* DC. *Prodr.* 5: 582, 1836.

**Dendroviguiera splendens** (Panero & E.E.Schill.) E.E.Schill. & Panero, **comb. nov.** Basionym: *Viguiera splendens* Panero & E.E.Schill. *Syst. Bot.* 13: 404, 1988.

**Dendroviguiera sylvatica** (Klatt) E.E.Schill. & Panero, **comb. nov.** Basionym: *Viguiera sylvatica* Klatt. *Bull. Soc. Roy. Bot. Belgique* 31: 204, 1892.

***Gonzalezia* E.E.Schill. & Panero, *stat. & nom.***

**nov.** Replaced synonym: *Viguiera* Kunth section *Hypargyrea* S.F.Blake, *Contr. Gray Herb. n.s.* 54:59. 1918. – Type species: *Gonzalezia hypargyrea* (Greenm.) E.E.Schill. & Panero (= *Viguiera hypargyrea* Greenm.)

Coarse, erect perennial herbs, 0.6–1.0 m tall; stems densely pubescent; leaves alternate, sessile, blades 4–22 cm long, 1–8 cm wide, triplinerved or penninerved, lanceolate to lance-ovate, densely pubescent abaxially and with numerous subsessile glandular trichomes ('resin dots'), apices acute to acuminate, base rounded to clasping or decurrent along stem, margin entire; heads terminal, solitary, campanulate to hemispherical, discs 25–40 mm across and 15–27 mm high, on pubescent 1.0–10.5-cm-long peduncles; phyllaries about 30, in two or three slightly graduated series, the outer series often sur-

passing disc, inner series appressed, oblong to elliptical, acuminate, pubescent; ray flowers 13–18, corolla dull brownish orange to golden yellow, limb oval-oblong, 10–20 mm long, 1.6–5.0 mm wide, abaxially pubescent and with subsessile glandular trichomes, tube 2.0–2.5 mm long, sparsely pubescent; disc flowers 125–250, corollas yellow–orange to yellow or dull orange–brown, tube essentially glabrous, 0.7–1.0 mm long; throat cylindrical, 1–2 mm long, sparsely pubescent, lobes deltoid, glabrous or pubescent, 0.8–1.0 mm long; anthers dark brown, 1.5–2.0 mm long, appendages yellow, lanceolate, 0.5–0.8 mm long; styles 2–3 mm long; paleae oblong-rectangular, 7–9 mm long, with acute or truncate apices, abaxial surfaces moderately to densely pubescent, adaxial surfaces glabrous, partly folded about cypselae; disc cypselae oblong or obovate, 5.5–7.0 mm long, pubescent, with a pappus of two awns and 3–12 deeply lacerated squamellae, awns 2.0–4.5 mm long, squamellae unequal, 0.2–1.5 mm long; ray ovaries trigonal, 1.5–2.5 mm long, pubescent, pappus a ring of squamellae, 0.3–0.5 mm long. Chromosome number,  $x = 17$ .

The genus name honours Socorro González Elizondo for her many botanical contributions that have increased our understanding of the diversity and distribution of the flora of the state of Durango in northwest Mexico and in the family Cyperaceae.

*Gonzalezia* is a genus of three species of robust herbaceous perennials, characterized by alternate, sessile, entire and penninerved or weakly triplinerved leaves, which are densely pubescent abaxially and have subsessile glandular trichomes on both leaves and rays, solitary or a few large heads, and a pappus that is present on both disc and ray flowers. It is most similar to some *Tithonia* spp., which differ by having the peduncle fistulose and the abaxial leaf surface subglabrous or at most pilose, and to some *Aldama* spp., which were formerly placed in *Viguiera* subgenus *Amphilepis*, most specifically *A. excelsa* and *A. pachycephala*, and differ in having leaves with triplinerved venation and a setose-hispid pubescence on the abaxial surfaces of the leaves. The species of *Gonzalezia* occur in northwestern Mexico, ranging from Zacatecas to Durango and Chihuahua. Molecular data suggest that *G. rosei* is of hybrid origin, probably descended from some combination of the other two species or their precursors. The chemistry of *Gonzalezia* and, in particular, of *G. decurrens*, has been of interest, in part because of the use of the latter as a fish poison by indigenous Mexican peoples (Wollenweber *et al.*, 1995; Marquina *et al.*, 2001.) The only published chromosome count is for *G. decurrens* (Keil & Pinkava, 1976, as *Viguiera decurrens*) and suggests that the genus has the base number of  $x = 17$ , typical of derived Helianthinae.



KEY TO SPECIES OF *GONZALEZIA*

1. Leaves strongly decurrent.....*G. decurrens*  
 1. Leaves sessile.....2  
 2. Stems densely silky-lanate; leaves > 8.0 cm long.....*G. rosei*  
 2. Stems pilose-strigose; leaves < 7.5 cm long.....*G. hypargyrea*

***Gonzalezia decurrens*** (A.Gray) E.E.Schill. & Panero **comb. nov.** Basionym: *Tithonia decurrens* A.Gray. Pl. Fendl. 85, 1849. Type: MEXICO, CHIHUAHUA: common on mountains around Cosiquiriachi, x.1846, A. F. Wislizenus 193 (Holotype: GH).

***Gonzalezia hypargyrea*** (Greenm.) E.E.Schill. & Panero **comb. nov.** Basionym: *Viguiera hypargyrea* Greenm. Proc. Amer. Acad. 39: 105, 1903. Type: MEXICO, DURANGO: city of Durango and vicinity, iv–xi.1896, E. Palmer 816 (Lectotype, here designated: GH; isolectotypes: K, MO, US).

***Gonzalezia rosei*** (Greenm.) E.E.Schill. & Panero **comb. nov.** Basionym: *Viguiera rosei* Greenm. Proc. Am Acad. 39: 105, 1903. Type: MEXICO, ZACATECAS: near Plateado, on the road from Colotlan, 31.viii.1897, J. N. Rose 2710 (Lectotype, here designated: US; isolectotypes: GH, K).

***Heiseria* E.E.Schill. & Panero, stat. & nom. nov.**

Replaced synonym: *Viguiera subseries Pusillae* S.F.Blake. Contr. Gray Herb. n.s. 54: 159. 1918. – Type species: *Heiseria pusilla* (A.Gray) E.E.Schill. & Panero (= *Viguiera pusilla* A.Gray)

Annuals, 1.1–6 dm tall; stems striate, glabrate to sparsely hispid-pilose; leaves opposite, blades ovate to lanceolate, 15–70 mm long, 4–27 mm wide, dentate or subentire, trinerved, tuberculate-strigillose adaxially, tuberculate-hispid abaxially, subsessile glandular trichomes absent, apices acute or obtuse, base acuminate to cuneate, petioles 10–20 mm long; heads 1–4, hemispherical; phyllaries in two or three graduated series, 5–8 mm long, oblong to linear, indurated at base, sparsely to densely hispid-pilose, apices free, herbaceous; ray flowers 8–12, corollas yellow, limb oval-oblong, 6–12 mm long; disc flowers numerous, 75 or more, corolla lobes yellow–orange or purplish, tube sparsely pubescent, 1.0–1.1 mm long, throat proximally globose and densely pubescent, throat distally subcylindrical and glabrate, 2.2–263.0 mm long, lobes deltate, c. 0.7 mm long; anthers dark brown, 1.5–1.7 mm long, appendage ovate, 0.5–0.6 mm long; paleae oblong-rectangular, 6.0–7.5 mm long, apices obtuse or three-toothed; disc cypselae black or mottled, pilose, 3.5–4.0 mm long, pappus of two awns, 1.3–3.5 mm long, and four intermediate scales, 1.0–1.5 mm long. Chromosome number, not known.

The genus name honours the late Charles B. Heiser, long-time student of sunflowers who had a special fondness for the Andean Mountain region.

*Heiseria* includes two poorly known species found in the Andean region of Peru. Although one was named for its resemblance in involucre features to *Simsia*, and the other was originally placed in *Tithonia*, molecular data (Figs 1 and 2) suggest that the genus is closely related to the geographically proximate *Pappobolus*. Further study is needed to clarify this remarkable and unanticipated relationship.

***Sidneya* E.E.Schill. & Panero, stat. & nom. nov.**

Replaced synonym: *Viguiera Kunth series Pinnatilibatae* S.F.Blake. Contr. Gray Herb. n.s. 54:95, 1918. – Type species: *Sidneya pinnatilibata* (Sch.Bip.) E.E.Schill. & Panero (= *Zaluzania pinnatilibata* Sch.Bip.)

Compact, rounded shrubs, 5–15 dm tall; stems striate, strigose when young, becoming glabrous with age; leaves opposite or alternate, blades 15–110 mm long, 10–90 mm wide across basal lobes, entire or pinnately three- to nine-lobed, margins revolute, subglabrate to pubescent adaxially, densely pubescent abaxially, with numerous subsessile glandular trichomes ('resin dots'), apices acute to obtuse, margin entire to crenate, petiole 3–40 mm long, densely pubescent; heads terminal, solitary or three to seven

KEY TO SPECIES OF *HEISERIA*

- Disc corollas purplish at apex; cypselae black.....*H. simsioides*  
 Disc corollas yellow throughout; cypselae mottled black and white.....*H. pusilla*

***Heiseria pusilla*** (A.Gray) E.E.Schill. & Panero, **comb. nov.** Basionym: *Tithonia pusilla* A.Gray. Proc. Amer. Acad. 5: 124, 1848. Type: PERU: Obrajillo, 1838–1842, W. Rich s.n. (Holotype: GH).

***Heiseria simsioides*** (S.F.Blake) E.E.Schill. & Panero, **comb. nov.** Basionym: *Viguiera simsioides* S.F.Blake. Bot. Jahrb. Syst. 119: 48, 1916. Type: PERU: mountains north of Chosica, 17.iv.1910, Weberbauer 5355 (Holotype: B, destroyed; fragment GH; isotypes: GH, US).

in cymose panicles, hemispherical, 6–20 mm across and 6–12 mm high, on densely pubescent 2–5-cm-long peduncles; phyllaries 15–30, in two or three series, 4–13 mm long, appressed, obovate, indurated at base, sparsely to moderately pubescent, somewhat greenish, apices free, herbaceous and slightly narrowed; ray flowers 13–18, corolla golden yellow, limb oval-oblong, 6–15 mm long, moderately pubescent and with subsessile glandular trichomes along abaxial veins, tube 0.9–2.0 mm long, sparsely to densely pubescent; disc flowers 70–100+, tightly packed, corollas yellow–orange, tube pubescent and sometimes glandular, widening to form a cap over the cypselae, 0.4–1.1 mm long, throat widened abruptly above tube, subcylindrical, 1.6–2.3 mm long, sparsely pubescent, lobes pubescent, 0.5–0.8 mm long; anthers dark brown, 1.3–1.5 mm long, appendage ovate to lanceolate, 0.3–0.5 mm long; styles 3–4 mm long; paleae elliptical or oblong-rectangular, 4–5 mm long, with shortly acuminate apices, pubescent abaxially mainly along the midrib; disc cypselae black, obovate, 1.7–3 mm long, glabrous and epappose; ray ovaries trigonal, 1.8–3 mm long, glabrous and epappose.

Chromosome number,  $N = 17, 34$ .

The genus name honours Sidney F. Blake, monographer of *Viguiera* and long-time student of Asteraceae systematics.

Blake (1918) first recognized the distinctiveness of the lineage formed by *Sidneya* when he segregated the species of his *Viguiera* series *Pinnatilobatae* from among epappose elements that had been grouped under *Gymnolomia* or *Heliomeris*. Molecular studies supported both the monophyly and distinctiveness of this lineage (Figs 1 and 2). Morphologically, *Sidneya* is characterized by its shrubby habit, pinnately lobed leaves, disc flower corollas which are broadened at the base to form a cap over the apices of the cypselae, and glabrous, epappose cypselae. Blake (1918) included four species in *Viguiera* series *Pinnatilobatae*, three of which are considered here to form a single species, *S. pinnatilobata*, which occurs in the states of Oaxaca and Puebla, Mexico. The transfer of the other species of the genus unfortunately results in the need to abandon a widely used species epithet in favour of that under which it was originally described (in *Heliomeris*). This species, *Sidneya tenuifolia*, has been documented to include both diploid and tetraploid cytotypes (Butterworth, 1975), and it is morphologically variable, particularly in leaf shape; no correlation has been demonstrated, however, between chromosome number and morphology.

***Sidneya pinnatilobata*** (Sch.Bip.) E.E.Schill. & Panero, **comb. nov.** Basionym: *Zaluzania pinnatilobata* Sch.Bip. *Flora* 47: 219, 1864. Type: MEXICO,

PUEBLA: Tehuacan, v.1842, *F. M. Liebmann* 384 (Lectotype, here designated: C; isolectotypes: C, G-DC, GH).

***Sidneya pinnatilobata*** (Sch.Bip.) E.E.Schill. & Panero var. ***megaphylla*** (Butterw. ex B.L.Turner) E.E.Schill. & Panero, **comb. nov.** Basionym: *Viguiera pinnatilobata* Sch.Bip. var. *megaphylla* Butterw. ex B.L.Turner. *Phytologia* 66: 461, 1989. Type: MEXICO, OAXACA: dry subtropical deciduous low forest 57 miles southeast of Oaxaca and 20 miles northwest of Nejapa. 30.x.1965, A. Cronquist & M. Sousa 10448 (Holotype: LL; isotypes: MICH, US).

***Sidneya tenuifolia*** (A.Gray) E.E.Schill. & Panero, **comb. nov.** Basionym: *Heliomeris tenuifolia* A.Gray. *Pl. Fendl.* 84, 1848 (= *Viguiera stenoloba* S.F.Blake). Type: MEXICO, COAHUILA: west of Mapimi, 9.v.1847, *J. Gregg* 21 (Holotype: GH).

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## APPENDIX

Samples of subtribe Helianthinae and outgroup used for DNA data. Specimens at TENN, unless otherwise noted; GenBank number (ITS, ETS) or (ITS).

**Aldama angustifolia**: Mexico, *Panero* 2447 (GQ864133, HQ688906); **A. arenaria**: Brazil, *Da Costa* 7 (AF162286); **A. aspilioides**: Brazil, *Da Costa* 89 (AF162287); **A. buddlejiformis**: Mexico, *Panero* 2383 (GQ864134, HQ688900); **A. canescens**: Mexico, *Schilling s.n.* (HQ688848, HQ688899); **A. cordifolia**: Mexico, *Schilling & Panero* 88-11 (GQ864143, HQ688918); **A. dentata**: Mexico, *Panero* 3070 (HQ688852, HQ688912); **A. ensifolia**: Mexico, *Panero* 2781 (GQ864135); **A. excelsa**: Mexico, *Panero* 2461 (GQ864136, HQ688904); **A. flava**: Mexico, *Schilling & Panero* 88-51 (GQ864137, HQ688901); **A. fruticosa**: Mexico, *Panero* 2846 (GQ864155, HQ688925); **A. gardneri**: Brazil, *Da Costa* 72 (AF162291); **A. ghiesbreghtii**: Mexico, *Panero* 2399 (GQ864139, HQ688905); **A. glomerata**: Mexico, *Panero* 2833 (GQ864156, HQ688924); **A. grahamii**: Mexico, *Panero* 3155 (GQ864138); **A. helianthoides**: Bolivia, *Feuerer* 22106a (HQ688843); **A. hispida**: Mexico, *Schilling* 85-25 (GQ864147, HQ688919); **A. hypochlora**: Mexico, *Panero* 2560 (GQ864140); **A. incana**: Peru, *Panero* 885 (HQ688896); **A. lanceolata**: Peru, *Panero* 863 (HQ688841, HQ688898); **A. linearifolia**: Brazil, *Da Costa* 70 (AF162307); **A. linearis**: Mexico, *Schilling & Panero* 88-17 (HQ688849, HQ688916); **A. macrorrhiza**: Brazil, *Da Costa* 24 (AF162292); **A. media**: Ecuador, *Panero* 1443 (HQ688846); **A. michoacana**: Mexico, *Panero* 3161, *TEX/LL* (HQ688851, HQ688911); **A. mollis**: Argentina, *Schilling & Panero* 90-1 (HQ688842, HQ688897); **A. obtusifolia**: Brazil, *Da Costa* 91 (AF162295); **A. pachycephala**: Mexico, *Panero* 2443 (GQ864141, HQ688902); **A. palmeri**: Mexico, *Panero* 2442 (HQ688853, HQ688913); **A. parkinsonii**: Mexico, *Schilling & Panero* 88-45 (GQ864146, HQ688907); **A. phenax**: Mexico, *Schilling & Spring* 318 (HQ688854); **A. pilosa**: Argentina, *Schilling & Panero* 90-23 (AF162293); **A. pringlei**: Mexico, *Panero* 2861 (GQ864144, HQ688934); **A. purisimae**: Mexico, *Schilling* 51 (HQ688850); **A. quinqueremis**: Brazil, *Da Costa* 65 (AF162298); **A. revoluta**: Chile, *Spooner* 4475 (HQ688845); **A. robusta**: Brazil, *Da Costa* 66 (AF162302); **A. seemannii**: Mexico, *Panero* 2780 (GQ864145); **A. squalida**: Brazil, *Da Costa* 88 (AF162305); **A. squarrosa**: Mexico, *Schilling & Panero* 88-47 (GQ864142, HQ688908); **A. truxillensis**: Peru, *Sagastegui* 14149 (HQ688844); **A. tuberosa**: Argentina, *Schilling & Panero* 90-17 (HQ688847); **A. tucumanensis**: Argentina, *Schilling & Panero* 90-6 (AF162288).

- Bahiopsis tomentosa*: Mexico, Schilling 83-18 (AF496930, HQ688861); *B. parishii*: USA, Schilling 129 (AF496934, HQ688862).
- Calanticaria bicolor*: Mexico, Schilling & Panero 88-29 (HQ688793, HQ688863).
- Davilanthus davilae*: Mexico, Panero 2581 (GQ864149, HQ688932); *D. hidalgoanus*: Mexico, Schilling & Panero 88-28 (GQ864151, HQ688930); *D. huajuapanus*: Mexico, Panero et al. 6141 (GQ053571, HQ688931); *D. hypargyreus*: Mexico, Panero 2832 (GQ864150, HQ688929); *D. purpusii*: Mexico, Panero 2313 (GQ864152, HQ688933); *D. sericeus*: Mexico, Panero 2595 (GQ864148).
- Dendroviguiera adenophylla*: Mexico, Panero 2 (HQ688813, HQ688874); *D. eriophora*: Mexico, Panero 649 (HQ688809); *D. eriophora* ssp. *poblana*: Tenorio 15293 (HQ688810); *D. guerrerana*: Mexico, Panero 514 (HQ688808); *D. insignis*: Mexico, Schilling et al. 85-17 (HQ688811); *D. neocronquistii*: Mexico, Panero 2484 (HQ688817); *D. oaxacana*: Mexico, Panero & Panero 5 (HQ688812, HQ688878); *D. pringlei*: Mexico, Panero 2297 (HQ688814, HQ688875); *D. puruana*: Mexico, Panero et al. 864 (AF047973, HQ688873); *D. quinqueradiata*: Mexico, Panero 2435 (HQ688818, HQ688879); *D. sphaerocephala*: Mexico, Panero 527 (HQ688806); Panero 2404 (HQ688815, HQ688876); *D. splendens*: Mexico, Panero 2432 (HQ688816, HQ688877); *D. sharpii*: Mexico, Sharp 441512 (HQ688807); *D. sylvatica*: Costa Rica, Panero 2717 (HQ688819, HQ688880).
- Gonzalezia decurrens*: Mexico, Schilling & Spring 328 (HQ688856, HQ688915); *G. hypargyrea*: Mexico, Schilling & Panero 88-12 (HQ688855, HQ688914); *G. rosei*: Mexico, Schilling & Panero 88-19 (HQ688857, HQ688858).
- Heiseria pusilla*: Peru, MacBryde & Featherstone 434, F (HQ688839); *H. simsioides*: Peru, Sagastegui 14138 (HQ688838, HQ688894).
- Helianthus annuus*: USA, Schilling 660 (AF047924, HQ688886); *H. heterophyllus*: USA, Schilling 04-53: (AF047970, HQ688887).
- Heliomeris multiflora*: USA, Schilling NM-13 (AF496919, HQ688865).
- Iostephane heterophylla*: Mexico, Schilling & Panero 88-53 (HQ688820, HQ688881); Panero & Schilling 1549 (HQ688821); *I. madrensis*: Mexico, Schilling & Panero 88-22 (HQ688822, HQ688882); *I. papposa*: Mexico, Panero et al. 617 (HQ688823, HQ688883); *I. trilobata*: Mexico, Calzada 20355 (HQ688824); Schilling & Panero 88-34 (HQ688825, HQ688884).
- Lagascea decipiens*: USA, Schilling & Spring 297 (GQ864100, HQ688909); *L. helianthifolia*: Mexico, Panero 3061 (GQ864099, HQ688910).
- Pappobolus ecuadoriensis*: Ecuador, Panero 1475 (HQ688832); *P. ecuadoriensis* var. *lancifolius*: Ecuador, Panero 1465 (HQ688834); *P. hutchisonii*: Peru, Panero 1241 (HQ688833); *P. hypargyreus*: Ecuador, Panero 1414 (HQ688831); Panero 733 (HQ688830); *P. imbaburensis*: Ecuador, Panero 711 (HQ688826, HQ688891); *P. lehmannii*: Ecuador, Panero 720 (HQ688827, HQ688892); *P. juncosae*: Ecuador, Panero 1094 (HQ688829); *P. nigrescens*: Ecuador, Panero 755 (HQ688828); *P. stuebelii*: Peru, Panero 955 (HQ688836); *P. subniveus*: Peru, Panero 1282 (HQ688835).
- Phoebanthus tenuifolius*: USA, Schilling & Spring 204 (AF047971, HQ688888).
- Scalesia pedunculata*: Ecuador, Eliasson 649, GB (HQ688840, HQ688895).
- Sidneya pinnatilobata*: Mexico, Schilling et al. 85-28 (GQ864153, HQ688890); *S. tenuifolia* (*Viguiera stenoloba*): USA, Schilling & Spring 267 (GQ864154, HQ688889).
- Simsia calva*: USA, Schilling & Spooner 84-1 (GQ864107, HQ688922); *S. dombeyana*: Ecuador, Panero 1336 (GQ864109, HQ688923); *S. ovata*: Mexico, Schilling & Panero 88-36 (GQ864102, HQ688920); *S. rhombifolia*: Mexico, Schilling & Panero 88-31 (GQ864102, HQ688921).
- Syncretocarpus sericeus*: Peru, Panero 1361 (HQ688837, HQ688893).
- Tithonia calva*: Mexico, Panero 2213 (GQ864125); *T. diversifolia*: Mexico, Panero & Schilling 620 (GQ864126); *T. koelzii*: Mexico, LaDuke et al. 477, OS (GQ864127); *T. longiradiata*: Mexico, Panero 2523 (GQ864128); *T. paneroi*: Mexico, Saynes 3951, TEX/LL (HQ688859, HQ688928); *T. pedunculata*: Mexico, Panero 2505 (GQ864129); *T. rotundifolia*: Mexico, Panero 2395 (GQ864130, HQ688926); *T. thurberi*: USA, Schilling & Spring 296 (GQ864131, HQ688927); *T. tubaeformis*: Mexico, Panero 2417 (GQ864132).
- Viguiera dentata*: Guatemala, Spooner 2750 (HQ688804); Mexico, Schilling VD-1 (AF496918, HQ688870); Schilling & Spring 325 (HQ688800, HQ688872); Panero 8863 (HQ688794, HQ688866); Sharp 441502 (HQ688799); Villaseñor 400 (HQ688802); Spooner 2825 (HQ688805); Spooner 2771 (HQ688797, HQ688869); Panero 5035 (HQ688803); Spooner 2408 (HQ688796, HQ688868); Spooner 2422 (HQ688795, HQ688867).
- Zaluzania grayana*: USA, Spring & Schilling 298 (AF496912, HQ688860).