

## Nuclear rDNA Evidence for Major Lineages of Helenioid Heliantheae (Compositae)

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**ABSTRACT.** Results of phylogenetic analyses of nuclear 18S–26S rDNA internal transcribed spacer (ITS) region sequences for representatives of most genera of helenioid Heliantheae and various members of Heliantheae s.s. (sensu stricto) and Eupatorieae help to clarify major lineages and relationships in the clade corresponding to Heliantheae s.l. (sensu lato) and Eupatorieae. Most subtribes of helenioid Heliantheae as circumscribed by Robinson (1981) correspond closely with ITS clades. Polygeneric subtribes of helenioid Heliantheae that appear to be monophyletic based on ITS data include Flaveriinae sensu Turner and Powell (1977), Madiinae sensu Carlquist (1959), and Peritylinae sensu Robinson (1981). Chaenactidinae sensu Robinson (1981) is polyphyletic, but most members of the group are encompassed within only four ITS clades. Based on the ITS data and results of combined analyses of ITS variation plus previously published morphological and chloroplast DNA data, we conclude that Heliantheae s.s. and Eupatorieae represent nested clades within helenioid Heliantheae, as previously suggested. Loss of paleae appears to have been a rare occurrence during radiation of Heliantheae s.s.; only one epaleate taxon that we sampled (*Trichocoryne*) was placed within an ITS clade of otherwise paleate taxa, referable to Heliantheae s.s. We conclude that expression of paleae in Heliantheae s.s., Madiinae, and *Marshallia* is homoplasious. We also conclude that pappi of bristles or bristle-like subulate scales have arisen in various lineages of Heliantheae s.l. and in general have received too much weight in previous circumscriptions of suprageneric taxa. Multiple examples of extreme dysploidy from high (putatively polyploid) ancestral chromosome numbers in helenioid Heliantheae are evident from the phylogenetic data. Bidirectional ecological shifts between annual and perennial habits and repeated origins of woodiness from herbaceous ancestors also can be concluded for helenioid Heliantheae. Based on modern distributions of taxa and evident phylogenetic patterns, Baeriinae, Madiinae, and the  $x = 19$  “arnicoid” taxa probably share a common Californian ancestry. To produce a tribal taxonomy for Heliantheae s.l. that better reflects phylogenetic relationships, Eupatorieae and (provisionally) Heliantheae s.s. are retained in essentially the traditional senses, Helenieae is recognized in a restricted sense, Madiaceae and Tageteae are expanded, and three new tribes (**Bahieae**, **Chaenactideae**, and **Perityleae**) are erected. In Madiaceae, three new subtribes (**Arnicinae**, **Hulseinae**, and **Venegasiinae**) are recognized, in addition to Baeriinae and Madiinae. In Peritylinae, a new combination, *Perityle montana*, is proposed for *Correllia montana*.

Uncertainty about relationships in helenioid Heliantheae (= Helenieae sensu Karis and Ryding 1994a) has impeded revision of the tribal and subtribal taxonomy of Compositae (e.g., Karis and Ryding 1994a; Bremer 1996; Jansen and Kim 1996) and has limited our understanding of the evolutionary and biogeographic history of much of western North American Compositae. Helenieae sensu Bentham (1873) has been long regarded as an unnatural assemblage of mostly western North American epaleate Asteroideae belonging to Heliantheae (Cronquist 1955) or to various tribes such as Anthemideae, Astereae, Heliantheae, or Senecioneae (e.g., Turner and Powell 1977). In his revision of Heliantheae, Robinson (1981) presented evidence from micro- and macro-morphology, secondary chemistry, and chromosomes for “more phyletic integrity among the epaleaceous Heliantheae than is generally recognized by recent workers.” Robinson (1981) recognized epaleate groups referable to Helenieae s.l. as subtribes of Heliantheae and incorporated some taxa previously assigned to other tribes, such as Senecioneae (e.g., *Arnica*; also see Nordenstam 1977), into Heliantheae. In a recent review, Karis and Ryding (1994a) largely adopted Robinson’s (1981) subtribal taxonomy for helenioid taxa and resurrected Helenieae as a provisional

paraphyletic tribe for the mostly-epaleate subtribes plus Madiinae.

An incentive for gaining finer-scale resolution of relationships of helenioid Heliantheae has been generated by molecular phylogenetic evidence for nested placement of Eupatorieae within Heliantheae s.l. (i.e., including Helenieae; see Jansen and Kim 1996; Bayer and Starr 1998). Reconciling rank-based botanical nomenclature with a taxonomic system of monophyletic groups in Heliantheae s.l. + Eupatorieae demands either submergence of Eupatorieae into Heliantheae, the name with priority, or dissection of Heliantheae s.l. into coordinate monophyletic tribes. Sinking Eupatorieae into Heliantheae would result in a tribe containing ca. 25% of all species of Compositae and, in general, has been resisted by synantherologists (see Bremer 1996; Robinson 1996; but see also Jeffrey 1995). The break-up of Heliantheae s.l. into monophyletic tribes is complicated in part by morphological and molecular evidence for parphyly or polyphyly of helenioid Heliantheae (Karis 1993a; Jansen and Kim 1996). Karis and Ryding (1994a) instituted a practical compromise by recognizing Helenieae s.l. as a provisional, non-monophyletic group to maintain recognition of the putatively monophyletic Heliantheae s.s. and the

putatively monophyletic Eupatorieae as tribes. Elevation of helenioid subtribes, or groups of subtribes, to the tribal level was not considered practical by Karis and Ryding (1994a), who expressed doubts about monophyly of some taxa, particularly Chaenactidinae and Hymenopappinae, and noted the need for further study of helenioid relationships in general.

Previous phylogenetic studies of morphological (Karis 1993a) and molecular (Jansen and Kim 1996) data for Heliantheae s.l. provided evidence for monophyly of a group corresponding to the helenioid subtribe Gaillardinae sensu Robinson (1981) plus *Marshallia* [= Gaillardinae sensu Karis and Ryding (1994a)]. Analyses of chloroplast DNA (cpDNA) data from restriction sites and *ndhF* sequences resolved a sister-group relationship between a clade including representatives of Gaillardinae sensu Karis and Ryding (1994a) and a clade including the remaining sampled taxa of Heliantheae s.l. + Eupatorieae (see Jansen and Kim 1996). Previous phylogenetic studies have provided minimal support for other higher-level relationships within helenioid Heliantheae. Fortunately, outgroup choice for further phylogenetic investigation of the Heliantheae s.l. + Eupatorieae clade has been simplified by *ndhF* evidence (Kim and Jansen 1995; Eldenäs et al. 1999) for a robust clade comprising three well-supported subclades: Heliantheae s.l. + Eupatorieae, the Old World genus *Anisopappus* Hook. & Arn., and a clade identified earlier by Eriksson (1991) that includes the Old World genera *Athroisma* and *Blepharispermum* [and *Leucoblepharis*—not sampled by Kim and Jansen (1995) or Eldenäs et al. (1999)].

Herein, we examine nuclear 18S–26S ribosomal DNA data on major clades of helenioid Heliantheae in the context of previous morphological and molecular studies and discuss the implications of our findings for evolution and historical biogeography of Heliantheae s.l. + Eupatorieae. Baldwin here proposes a revised taxonomy for helenioid Heliantheae that is based on putatively monophyletic groups and preserves tribal status of Eupatorieae.

## MATERIALS AND METHODS

We sampled ITS sequences from representatives of all genera of helenioid Heliantheae or Helenieae s.l. recognized by Robinson (1981) or Karis and Ryding (1994a) except the monospecific genera *Leucoblepharis*, *Lycapsus*, and *Welwitschiella* (material unavailable), and most genera of Pectidinae sensu Robinson (1981) [= Tageteae sensu Strother (1977, 1986)] (see Table 1). We obtained sequence data for only six of the 23 genera of Pectidinae sensu Robinson (1981) because ITS sequences of the group have already been examined in a phylogenetic study by Loockerman (1996). Karis (1998) suggested that *Apostates* is helenioid; unfortunately, no material was available for our study. Type species were sampled for the majority of helenioid genera included in our study (see Table 1). We also sampled ITS sequences from representatives of Eupatorieae and the monospecific *Pelucha* because both groups are nest-

ed in Heliantheae s.l. [Eupatorieae—see Jansen and Kim (1996); *Pelucha*—see Baldwin and Wessa (2000a)].

Our sampling of Heliantheae s.s. and Eupatorieae was much less thorough than for helenioid Heliantheae (see Table 1). For Heliantheae s.s., ITS sequences were included from representatives of Ambrosiinae, Coreopsidinae, Engelmanniinae, Galinsoginae, Helianthinae, Melampodiinae, Rudbeckiinae, and Zaluzaniinae (see Robinson 1981; Karis and Ryding 1994b; Panero et al. 1999b; Clevinger and Panero 2000; Urbatsch et al. 2000). Members of Eupatorieae included in our analyses span four of King and Robinson's (1987) 18 subtribes and represent four major groups in Bremer et al.'s (1994) morphological cladograms of Eupatorieae (also see Schilling et al. 1999).

The choice of outgroup species in *Athroisma* and *Blepharispermum* was based on results from the *ndhF* study of Kim and Jansen (1995), which provided strong bootstrap support for a sister-group relationship between a Heliantheae s.l. + Eupatorieae clade and an *Athroisma*—*Blepharispermum* clade. *Anisopappus*, subsequently shown by Eldenäs et al. (1999) to be sister to *Athroisma*—*Blepharispermum* and/or Heliantheae s.l. + Eupatorieae, was unavailable for our study.

We isolated total DNA from leaves of live plants, silica-gel-dried leaf material, or herbarium specimens using a modification of Doyle and Doyle's (1987) CTAB procedure (adding a phenol extraction, RNase digestion, and two ethanol precipitations) or the method of Palmer (1986), without separation of organelles. The ITS region (i.e., ITS-1, 5.8S, ITS-2) of 18S–26S nuclear rDNA was amplified by PCR using primers ITS-1 [5'-GTCCACTGAACCTTAT-CATTAG-3'; Urbatsch et al. (2000)] and ITS4 (White et al. 1990) in 25 µL reactions as described by Baldwin (1992), with equimolar primer concentrations. PCR reaction conditions in a Perkin-Elmer 9600 thermal cycler included 40 cycles of denaturation at 97°C for 10 seconds, primer annealing at 48°C for 30 seconds, and primer extension at 72°C, initially for 20 seconds (with an increase of 4 seconds to each successive extension). Thermal-cycling was followed by a final extension at 72°C for 7 minutes. PCR products were visualized by agarose gel electrophoresis and purified by filtration using Millipore Ultrafree-MC tubes (UFC3 LTK 00).

Cycle-sequencing reactions were conducted using Amersham Pharmacia Biotech's Thermo Sequenase Dye Terminator Cycle Sequencing Kit (US79765) using the manufacturer's protocol, with half-volume reactions and addition of 5% DMSO. Cycle-sequencing reaction products were purified using Princeton Separations Centri-seps columns (CS-901). DNA sequences were resolved on 4.8% polyacrylamide gels (using Amresco's Page-Plus acrylamide E562) using an Applied Biosystems, Inc. (ABI) 377 automated sequencer. DNA sequences were analyzed using ABI Sequence Analysis software and examined using ABI Sequence Navigator software. Nucleotide sequences of both DNA strands were compared to ensure accuracy. Amplified copies of the ITS-region were cloned (using the TOPO TA cloning kit: K4550-01) for samples of *Arnica cernua*, *Bartlettia*, *Blepharispermum*, *Hypericophyllum*, *Pelucha*, and *Platyschukria* because of difficulties in obtaining high-quality sequences directly from pooled PCR products. Cloned ITS-region sequences were re-amplified (prior to sequencing) directly from plated, transformed colonies with M13 primers. Cells were lysed at 94°C for 12 minutes prior to 30 cycles of PCR at 94°C for 1 minute, 58°C for 1 minute, and 72°C for 2 minutes, followed by a final extension period (72°C for 7 minutes).

We aligned the ITS-1, 5.8S, and ITS-2 nrDNA sequences using a manual, iterative process. Groups well-supported (≥85%) on the basis of "fast heuristic" bootstrap values (10,000 replicates) from an analysis of the initial sequence matrix were used to guide subsequent refinement of the alignment. Alignment was optimized within each group prior to reconciliation of alignment among the groups (see below). Alignment was also refined by further compartmentalization (Mishler 1994), wherein well-supported phylogenetic structure was used to reduce a group of sequences to an

archetype (ancestral) sequence (see below). Elimination of apomorphic insertion/deletion mutations (indels) within each group simplified alignment among groups.

Gaps were inserted in regions of variable length, bounded by conserved sequence. Considerations in alignment included maximizing sequence similarity (considering a higher likelihood of transitions than transversions) while minimizing the number of inferred indels. A general exception to the standard procedure was to position gaps to minimize creation of potentially informative sites (for parsimony analysis) in areas of uncertain alignment. Gaps were treated as missing data in phylogenetic analyses. Inferred insertion/deletion mutations (indels) were recoded as separate characters using simple and complex gap coding (Simmons and Ochoterena 2000).

Nucleotide states were recoded as "N" (any of four nucleotide states) if other equally likely alignments have different phylogenetic implications. The "N" recoding process preserves phylogenetic information in unambiguously aligned taxa (see Bruns et al. 1992), unlike elimination of entire characters from the analyses. Seven characters (sites 83–89 in the ITS-1 alignment) were excluded altogether from analyses because of extensive alignment uncertainty. The percentage of potentially informative data matrix cells scored as missing data was 4.3%, including gaps, or 0.8%, excluding gaps.

We sought to improve speed and accuracy of parsimony analyses by using a data compartmentalization approach that effectively reduces the number of taxa and amount of homoplasy in the data set (Mishler 1994). We produced archetype sequences of well-supported ( $\geq 85\%$  bootstrap) clades using MacClade (Maddison and Maddison 1992) to estimate ancestral character states under the option of "almost all possible changes; approximate maximum number." We compensated for any topological uncertainty by estimating ancestral states under different branch arrangements and using the union of the estimates as the set of possible archetype states. Uncertainties were coded using IUPAC symbols, which were treated as nucleotide ambiguities rather than polymorphisms in the phylogenetic analyses (see Maddison and Maddison 1992). We also estimated ancestral states of indel regions for construction of archetype sequences using the same approach implemented in MacClade. The data-matrix was reduced from 157 original sequences to 30 archetypes and 49 original sequences. Again, nucleotide states were recoded as "N" if other equally likely alignments have different phylogenetic implications. Five characters (sites 83–87 in the ITS-1 alignment) were excluded altogether from analyses because of extensive alignment uncertainty. The percentage of potentially informative data matrix cells scored as missing data was 3.9%, including gaps, or 1.3%, excluding gaps.

In an attempt to improve our estimate of broad-scale phylogenetic patterns and our understanding of morphological character evolution in Heliantheae s.l. + Eupatorieae, we conducted parsimony analyses of original and archetype ITS sequences combined with Karis's (1993a) matrix of morphological and anatomical characters (hereafter, referred to as morphological characters). The combined matrix comprises only a subset of taxa because of differences in taxon sampling between our study and Karis's (1993a) analysis. Two other limitations of combining the molecular and morphological data sets are that Karis's taxa are genera and some of the genera treated by Karis have been shown subsequently not to be monophyletic (e.g., *Hemizonia* and *Madia*; see Baldwin 1999b). We consulted generic descriptions in Karis and Ryding (1994a) to ensure that we assigned our sequences to genera corresponding to Karis's (1993a) circumscriptions if we did not sample the type species. An ITS archetype for all congeneric sequences was used in the combined analyses if the ITS analyses provided strong support for monophyly of the genus. Given non-overlap in generic sampling of Eupatorieae, we combined an archetype ITS sequence for members of the tribe sampled in our study (based on the tree

and data in Fig. 1) with the character-consensus of morphological data (i.e., with internally variable characters scored as ambiguous for the included states) from taxa of Eupatorieae sampled by Karis (1993a). The percentage of potentially informative data matrix cells scored as missing data was 7.0%, including gaps, or 1.9%, excluding gaps.

We also sought to obtain an improved phylogenetic estimate of overall relationships in Heliantheae s.l. + Eupatorieae by simultaneous analysis of our ITS data combined with Kim and Jansen's (1995) cpDNA *ndhF* sequences for taxa in common between the two studies. We combined data from congeneric or conspecific taxa except for Eupatorieae, wherein lack of overlap in generic sampling led us to combine our archetype of all ITS sequences of the tribe with Kim and Jansen's (1995) *ndhF* sequence of *Bartlettina sordida* (Less.) R. M. King & H. Rob. [= *Eupatorium atrorubens* Nicholson]. The percentage of potentially informative data matrix cells scored as missing data was 2.6%, including gaps, or 1.0%, excluding gaps.

We conducted a combined analysis of ITS, morphological, and *ndhF* data for the smaller subset of congeneric taxa in common among the three studies and for Eupatorieae (treated as indicated above for the other combined analyses). Archetype ITS sequences for Flaveriinae sensu Turner and Powell (1977) (for *Flaveria* and a clade comprising *Adenophyllum*, *Tagetes*, and *Thymophylla* (for *Tagetes*)) were used in the simultaneous analysis of all three lines of evidence in an attempt to offset potential problems with homoplasy from the low density of taxon sampling. The percentage of potentially informative data matrix cells scored as missing data was 4.7%, including gaps, or 0.4%, excluding gaps. Prior to conducting parsimony analyses of any combined data matrix, we assessed data sets for combinability using the partition homogeneity test (Farris et al. 1995), as implemented in PAUP\*.

Parsimony analyses were conducted using a beta-test version of PAUP\* 4.0 (b2) (D. L. Swofford, Smithsonian Institution). Analyses of the entire aligned sequence matrix with recoded indel characters were first conducted to identify well-supported clades for subsequent compartmentalization. Following compartmentalization, the archetype ITS matrix with recoded indel characters was analyzed.

For parsimony analyses in general, we attempted to find all minimum-length trees by performing heuristic searches with 100 random addition sequences of the taxa. We estimated reliability of clades for the original ITS data set by a full heuristic bootstrap analysis (100 replicates), with "simple" stepwise addition of taxa. For the archetype ITS data set and combined data sets we conducted both bootstrap and decay analyses, with 20 heuristic searches and random addition sequences of the taxa for each of the 100 bootstrap replicates and for the decay analyses. Decay of clades with relaxation of parsimony was assessed by strict consensus of all trees up to a particular tree length using the reverse-constraints approach as implemented in AutoDecay 4.0 (Eriksson 1998).

Parsimony analysis of character-state evolution on the maximally parsimonious archetype trees was conducted with MacClade 3.1 (Maddison and Maddison 1992) using the "trace character" option and resolution of "all most parsimonious states at each node." Morphological, ecological, and chromosomal characteristics assigned to terminal taxa are the union of states for members of the putatively monophyletic group in question (not just for the sampled species if the group includes additional diversity). Historical biogeographic patterns were examined using the same methods used for estimating character evolution and, for subsets of taxa, dispersal-vicariance analysis (DIVA1.1; Ronquist 1997).

## RESULTS

**Sequence Variation.** Alignment of the 157 ITS-region sequences of Heliantheae s.l. + Eupatorieae re-



TABLE 1. Collection information for taxa sampled in the molecular phylogenetic study of ITS-region sequence variation in Heliantheae s.l. + Eupatorieae. Asterisks (\*) denote type species of generic names. Collections are from the U.S.A. unless otherwise indicated. Collector abbreviations: BGB = Bruce G. Baldwin; JLP = Jose L. Panero; SJB = Susan J. Bainbridge.

**Athroisma-Blepharispermum group** (outgroup). *Athroisma hastifolium* Mattf.; KENYA, Oloitokitok; *Rauh Ke277* (UC); GenBank no. AF229258. \**Blepharispermum zanguebaricum* Oliv. & Hiern; KENYA, Machakos Dt; *Eriksson 604* (EA, S); Clone 1, GenBank no. AF229259; Clone 2, GenBank no. AF229260.

**Tribe Bahieae B. G. Baldwin**

**Subtribe Bahiinae Rydb.**

“**Bahia clade**”. \**Achyropappus anthemoides* Kunth; MEXICO, Mexico State, 4.5 mi W of Santa Maria del Monte; *Keil 15420*, *Luckow* (UC); GenBank no. AF374894. \**Amauriopsis dissecta* (A. Gray) Rydb. [= *Bahia dissecta* (A. Gray) Britton]; Arizona, Coconino Co.; *Scott 1258* (ASC, UC); GenBank no. AF374889. *Bahia absinthifolia* Benth.; New Mexico, Eddy Co.; *BGB 967*, *SJB* (UC); GenBank no. AF374892. *Bahia oppositifolia* (Nutt.) DC. [= *Picradeniopsis oppositifolia* (Nutt.) Rydb.]; Wyoming, Fremont Co.; *Hartman 3153* (UC); GenBank no. AF374893. *Florestina platyphylla* (B. L. Rob. & Greenm.) B. L. Rob. & Greenm.; MEXICO, Oaxaca, 7.3 mi NW of Totolapan; *Keil 15532*, *Luckow* (UC); GenBank no. AF374883. *Florestina tripteris* DC.; MEXICO, Nuevo León, between Nuevo Laredo and Monterrey; *BGB 970*, *JLP*, *SJB*, *Francisco-Ortega* (UC); GenBank no. AF374884. \**Hymenothrix wislizeni* A. Gray; Arizona, Pima Co.; *SJB s. n.* (UC); GenBank no. AF374887. *Hymenothrix wrightii* A. Gray; Arizona, Cochise Co.; *BGB 964*, *SJB* (UC); GenBank no. AF374888. *Palafoxia arida* B. L. Turner & M. I. Morris; California, San Diego Co.; *BGB 784*, *Kyhos*, *Martens* (JEPS); GenBank no. AF374881. *Palafoxia texana* DC. var. *texana*; MEXICO, Nuevo León, between Nuevo Laredo and Monterrey; *BGB 969*, *JLP*, *SJB*, *Francisco-Ortega* (UC); GenBank no. AF374882. \**Platyschukhria integrifolia* (A. Gray) Rydb. var. *integrifolia*; Wyoming, Fremont Co.; *BGB 938*, *SJB* (UC); Clone 1, GenBank no. AF374890; Clone 2, GenBank no. AF374891. *Schkuhria pinnata* (Lam.) Kuntze ex Thell. var. *wislizeni* (A. Gray) B. L. Turner; Arizona, Santa Cruz Co.; *Keil 19020*, *Pinkava* (UC); GenBank no. AF374885; MEXICO, Durango, Kilometer 93 along Highway 40; *BGB 974*, *JLP*, *SJB*, *Francisco-Ortega* (UC); GenBank no. AF374886.

“**Chaetymenia clade**”. \**Chaetymenia peduncularis* Hook. & Arn.; MEXICO, Jalisco, road between Ameca and Atenguillo at Puente El Rialito; *BGB 978*, *JLP*, *SJB*, *Francisco-Ortega* (UC); GenBank no. AF374900. \**Espejoa mexicana* DC.; MEXICO, Oaxaca, 6.4 mi NW of Jalapa de Marquez; *Keil 15549*, *Luckow* (UC); GenBank no. AF374901. *Hypericophyllum angolense* (O. Hoffm.) N. E. Br.; MALAWI, North Province, Karonga District; *Pawek 5290* (UC); Clone 1, GenBank no. AF374898; Clone 2, GenBank no. AF374899.

“**Peucephyllum clade**”. \**Peucephyllum schottii* A. Gray; California, San Bernardino Co.; *BGB 916*, *Strother* (JEPS); GenBank no. AF374880. *Psathyrotopsis hintoniiorum* B. L. Turner; MEXICO, Coahuila, Municipio Parras; *Nesom 7648*, *Mayfield*, *Hinton* (UC); GenBank no. AF374879.

**Other clades**. \**Bartlettia scaposa* A. Gray; MEXICO, Chihuahua, 25 km. SE of Nuevo Casas Grandes; *Spellenberg*, *Corral 8582* (UC); Clone 1, GenBank no. AF374896; Clone 2, GenBank no. AF374897. \**Chamaechaenactis scaposa* (Eastw.) Rydb.; Wyoming, Sweetwater Co.; *BGB 942*, *SJB* (UC); GenBank no. AF374895. *Hymenopappus artemisiifolius* DC.; Louisiana, Bienville Parish; *Urbatsch 7029* (LSU); GenBank no. AF374877. *Hymenopappus filifolius* Hook. var. *filifolius*; Washington, Grant Co.; *BGB 876*, *Hufford*, *Sanderson*, *Wojciechowski* (UC); GenBank no. AF374876. \**Loxothysanus sinuatus* (Less.) B. L. Rob.; MEXICO, Oaxaca, Municipio de Santa Maria Chimalapa; *Calzada and Hernández G. 22348* (UC); GenBank no. AF374875. *Thymopsis thymoides* (Griseb.) Urb. subsp. *polyantha* (Urb.) Borhidi & O. Muñoz; CUBA, Las Villas Province, south of Santa Clara; *Howard et al. 334* (UC); GenBank no. AF374878.

**Tribe Chaenactideae B. G. Baldwin**

**Subtribe Chaenactidinae Rydb.** *Chaenactis macrantha* D. C. Eaton; Nevada, Nye Co.; *Ertter 9987* (UC); GenBank no. AF374904. *Chaenactis santalinoides* Greene; California, Kern Co./Ventura Co. border (Mt. Pinos); *BGB 953*, *SJB* (JEPS); GenBank no. AF374905. \**Dimeresia howellii* A. Gray; California, Lassen Co.; *BGB 925*, *SJB* (JEPS); GenBank no. AF374902. \**Orochaenactis thysanocarpa* (A. Gray) Coville; California, Inyo Co.; *BGB 934*, *SJB* (JEPS); GenBank no. AF374903.

**Tribe Eupatorieae Cass.**

**Subtribe Ageratinae Less.** *Piqueria trinervia* Cav.; MEXICO, Mexico State, Municipio El Oro; *JLP et al. 7343* (TEX); GenBank no. AF374911. *Stevia pelophila* S. F. Blake; MEXICO, Durango, La Rumorosa; *BGB 973*, *JLP*, *SJB*, *Francisco-Ortega*, *Gonzalez* (UC); GenBank no. AF374912.

**Subtribe Alomiinae Less.** *Brickellia californica* A. Gray; California, Tehama Co.; *SJB s. n.* (JEPS); GenBank no. AF374910.

**Subtribe Hofmeisteriinae R. M. King & H. Rob.** *Hofmeisteria schaffneri* (A. Gray) R. M. King & H. Rob.; MEXICO, Jalisco, Municipio Mascota; *JLP et al. 5594* (TEX); GenBank no. AF374907. *Hofmeisteria urenifolia* Walp.; MEXICO, Jalisco, Municipio Talpa de Allende; *JLP et al. 5598* (TEX); GenBank no. AF374906.

**Subtribe Oxylobinae R. M. King & H. Rob.** *Ageratina adenophora* (Spreng.) R. M. King & H. Rob.; California, Alameda Co.; *BGB s.n.* (JEPS); GenBank no. AF374909. *Ageratina glechonophylla* (Less.) R. M. King & H. Rob.; CHILE, Valparaíso Province; *Hartwig s.n.* (UC); GenBank no. AF374908.

**Tribe Helenieae Benth. & Hook.**

**Subtribe Gaillardiiinae Less.** \**Balduina uniflora* Nutt.; Louisiana, St. Tammany Parish; *Urbatsch 7579* (LSU, UC); GenBank no. AF229270. \**Gaillardia pulchella* Foug.; unknown source (commercial wildflower seed); *BGB s.n.* (JEPS); GenBank no. AF229271. *Helenium bigelovii* A. Gray; California, Siskiyou Co.; *BGB 681* (DAV); GenBank no. AF229269.

**Subtribe Marshalliinae H. Rob.** *Marshallia caespitosa* Nutt. ex DC.; Texas, Travis Co.; *JLP 7426* (TEX); GenBank no. AF229262.

TABLE 1. Continued.

- \**Marshallia obovata* (Walter) Beadle & Boynton var. *obovata*; North Carolina, Durham Co.; *BGB s.n.*, *SJB* (UC); GenBank no. AF229261.
- Subtribe Plateileminae B. G. Baldwin.** \**Plateilema palmeri* (A. Gray) Cockerell; MEXICO, Nuevo León, Galeana; *Hinton 25344* (TEX); GenBank no. AF229272.
- Subtribe Psathyrotinae B. G. Baldwin.** \**Pelucha trifida* S. Watson; MEXICO, Sonora, Isla San Pedro Mártir; *Moran 21745* (UC); Clone 1, GenBank no. AF229267; Clone 2, GenBank no. AF229268. \**Psathyrotes annua* (Nutt.) A. Gray; California, Inyo Co.; *BGB 930*, *SJB* (JEPS); GenBank no. AF229264. *Psathyrotes ramosissima* A. Gray; California, Inyo Co.; *BGB 1062*, *Sanderson*, *Wojciechowski* (JEPS); GenBank no. AF229263. \**Trichoptilium incisum* (A. Gray) A. Gray; California, San Diego Co.; *BGB 785*, *Martens* (JEPS); GenBank no. AF229266.
- Subtribe Tetraneurinae Rydb.** \**Amblyolepis setigera* DC.; Oklahoma, Kimble Co.; *Boke & Massey 401* (UC); GenBank no. AF229281. \**Baileya multiradiata* Harv. & A. Gray; California, San Bernardino Co.; *BGB 834*, *SJB* (JEPS); GenBank no. AF229273. *Baileya pauciradiata* Harv. & A. Gray; California, San Bernardino Co.; *BGB 836*, *SJB* (JEPS); GenBank no. AF229275. *Baileya pleniradiata* Harv. & A. Gray; California, San Bernardino Co.; *BGB 835*, *SJB* (JEPS); GenBank no. AF229274. *Hymenoxys ambigens* (S. F. Blake) Bierner var. *floribunda* (A. Gray) W. L. Wagner [= *Plummera floribunda* A. Gray]; Arizona, Cochise Co.; *BGB 963*, *SJB* (UC); GenBank no. AF229278. *Hymenoxys hoopesii* (A. Gray) Bierner [= *Dugaldia hoopesii* (A. Gray) Rydb.]; California, Tuolumne Co.; *BGB 954*, *SJB* (JEPS); GenBank no. AF229279. *Hymenoxys lemmonii* (Greene) Cockerell; California, Mono Co.; *BGB 931*, *SJB* (JEPS); GenBank no. AF229280. *Psilostrophe cooperi* (A. Gray) Greene; California, San Bernardino Co.; *Wisura 4797*, *Wall, Brooks* (UC); GenBank no. AF229276. *Psilostrophe tagetina* (Nutt.) Greene; New Mexico, Eddy Co.; *BGB 968*, *SJB* (UC); GenBank no. AF229277. *Tetraneuris acaulis* (Pursh) Greene var. *acaulis* [= *Hymenoxys acaulis* (Pursh) K. F. Parker var. *acaulis*]; Wyoming, Fremont Co.; *BGB 937*, *SJB* (UC); GenBank no. AF229282.
- Tribe Heliantheae Cass.**
- Subtribe Ambrosiinae Less.** *Ambrosia artemisiifolia* L.; see Urbatsch et al. (2000); GenBank nos. U73794, U74437.
- Subtribe Coreopsidinae Less.** *Bidens alba* DC.; see Ganders et al. (2000); GenBank no. U67107. *Coreopsis tinctoria* Nutt.; see Urbatsch et al. (2000); GenBank nos. U74393, U74442. *Cosmos bipinnatus* Cav.; see Ganders et al. (2000); GenBank no. U67114.
- Subtribe Engelmanniinae Stuessy.** *Wyethia amplexicaulis* Nutt.; see Urbatsch et al. (2000); GenBank nos. U73159, U74429.
- Subtribe Galinsoginae Benth. & Hook.** *Galinsoga parviflora* Cav.; Tennessee, Cumberland Co.; *Urbatsch s.n.* (LSU); GenBank no. AF374917.
- Subtribe Helianthinae Dumort.** *Helianthus simulans* E. Watson; see Urbatsch et al. (2000); GenBank nos. U73796, U74439.
- Subtribe Melampodiinae Less.** *Melampodium divaricatum* DC.; Louisiana, East Baton Rouge Parish; *Urbatsch 7021* (LSU); GenBank no. AF374915. *Smallanthus uvedalia* Mack. ex Small; Louisiana, East Baton Rouge Parish; *Urbatsch 7020* (LSU); GenBank no. AF374916.
- Subtribe Rudbeckiinae H. Rob.** *Rudbeckia alpicola* Piper; see Urbatsch et al. (2000); GenBank nos. U59382, U71097.
- Subtribe Zaluzaniinae H. Rob.** *Chromolepis heterophylla* Benth.; MEXICO, Durango, Kilometer 93 of Highway 40; *BGB 977*, *JLP, SJB, Francisco-Ortega, Gonzalez* (UC); GenBank no. AF374913.
- Incertae Sedis.** *Trichocoryne connata* S. F. Blake; MEXICO, Durango, La Rumorosa; *BGB 972*, *JLP, SJB, Francisco-Ortega, Gonzalez* (UC); GenBank no. AF374914.
- Tribe Madieae Jeps.**
- Subtribe Arnicinae B. G. Baldwin.** *Arnica cernua* Howell; California, Mendocino Co.; *Fauver s. n.* (JEPS); Clone 1, GenBank no. AF229303; Clone 2, GenBank no. AF229304; Clone 3, GenBank no. AF229305. *Arnica dealbata* (A. Gray) B. G. Baldwin [= *Whitneya dealbata* A. Gray]; California, Tehama Co.; *BGB 920*, *SJB, Sanderson* (JEPS); GenBank no. AF229307. *Arnica longifolia* D. C. Eaton; California, Tuolumne Co.; *BGB 955*, *SJB* (JEPS); GenBank no. AF229302. *Arnica mallotopus* (Franch. & Sav.) Makino [= *Mallotopus japonicus* Franch. & Sav.]; JAPAN, Toyama Prefecture, Mt. Sougatake; *Ono s. n.* (UC); GenBank no. AF229308. *Arnica mollis* Hook.; California, Alpine Co.; *BGB 680* (DAV); GenBank no. M93789. *Arnica unalaschcensis* Less.; JAPAN, Aomori Prefecture, Mt. Akakuradake; *BGB 1036*, *Crawford, Yahara* (UC); GenBank no. AF229306.
- Subtribe Baeriinae Benth. & Hook.** \**Amblyopappus pusillus* Hook. & Arn.; MEXICO, Baja California, Isla San Martín; *BGB s. n.* (UC); GenBank no. AF229292. \**Baeriopsis guadalupensis* J. T. Howell; MEXICO, Baja California, Isla Guadalupe, Islote Negro; *Moran 17424* (UC); GenBank no. AF229291. Outer Islet (Islote Zapato); *Rebman 6869* (SD); GenBank no. AF378090. \**Constancea nevini* (A. Gray) B. G. Baldwin [= *Eriophyllum nevini* A. Gray]; California, Santa Catalina Island; *Junak SCA-833* (SBBG); GenBank no. AF229296; California, San Clemente Island; *Mistretta, O'Brien, Hayduk s.n.* (JEPS); GenBank no. AF229297. *Eriophyllum congdonii* Brandegee; California, Mariposa Co.; *Mooring 3884* (SACL); GenBank no. AF229288. *Eriophyllum lanatum* (Pursh) J. Forbes; California, Fresno Co.; *Mooring 3452* (SACL); GenBank no. AF229283. \**Eriophyllum staechadifolium* Lag.; California, San Luis Obispo Co.; *BGB 895* (JEPS); GenBank no. AF229284. *Lasthenia burkei* (Greene) Greene; California, Sonoma Co.; *Ornduff 9280-96* (JEPS); GenBank no. AF229290. *Lasthenia californica* Lindl.; California, Contra Costa Co.; *Ornduff 10079* (UC); GenBank no. AF229289. *Monolopia congdonii* (A. Gray) B. G. Baldwin [= *Lembertia congdonii* (A. Gray) Greene]; California, San Luis Obispo Co.; *BGB 814*, *SJB* (JEPS); GenBank no. AF229295. *Monolopia gracilis* A. Gray; California, Santa Clara Co.; *BGB 944*, *SJB* (JEPS); GenBank no. AF229293. \**Monolopia major* DC.; California, San Benito Co.; *D'Alcamo s. n.*, *deGeofroy, Markos* (JEPS); GenBank no. AF229294. \**Pseudobahia bahiifolia* (Benth.) Rydb.; California, Madera Co.; *BGB 945*, *SJB* (JEPS); GenBank no. AF229285. *Pseudobahia peirsonii* Munz; California, Kern Co.; *BGB 913*, *Strother* (JEPS); GenBank no. AF229286. \**Syntrichopappus fremontii* A. Gray; California, San Bernardino Co.; *BGB 915*, *Strother* (JEPS); GenBank no. AF229287.

TABLE 1. Continued.

- Subtribe Hulseinae B. G. Baldwin.** \**Eatonella nivea* (D. C. Eaton) A. Gray; Nevada, Esmeralda Co., near Boundary Peak; *Taylor s.n.* (JEPS); GenBank no. AF229300. *Hulsea algida* A. Gray; California, Alpine Co.; *BGB 678* (DAV); GenBank no. M93792. \**Hulsea californica* Torr. & A. Gray; California, San Diego Co., Laguna Mountains; *BGB s.n., SJB* (JEPS); GenBank no. AF229298. *Hulsea vestita* A. Gray subsp. *parryi* (A. Gray) Wilken; California, San Bernardino Co., San Bernardino Mountains; *BGB s.n., SJB* (JEPS); GenBank no. AF229299.
- Subtribe Madiinae Benth. & Hook.** \**Achyrachaena mollis* Schauer; California, Solano Co.; *BGB 651* (DAV); GenBank no. AF229318. \**Adenothamnus validus* (Brandegee) D. D. Keck; MEXICO, Baja California, Punta Banda; *Witter 86-99* (DAV); GenBank no. M93787. *Anisocarpus scabridus* (Eastw.) B. G. Baldwin [= *Raillardiopsis scabrida* (Eastw.) Rydb.]; California, Lake Co.; *BGB 676* (DAV); GenBank no. M93799. \**Argyroxiphium sandwicense* DC. subsp. *sandwicense*; Hawaii, Mauna Kea; *BGB 657* (DAV); GenBank no. AF061883. \**Blepharipappus scaber* Hook.; Idaho, Washington Co.; *BGB 882, Sanderson, Wojciechowski* (UC); GenBank no. AF229316. \**Blepharizonia plumosa* (Kellogg) Greene; California, Alameda Co.; *BGB 982H, Preston* (JEPS); GenBank no. AF229323. \**Calycadenia truncata* DC.; California, Tehama Co.; *BGB 605* (DAV); GenBank no. U04261. \**Carlquistia muirii* (A. Gray) B. G. Baldwin [= *Raillardiopsis muirii* (A. Gray) Rydb.]; California, Monterey Co.; *BGB 618* (DAV); GenBank no. M93798. *Centromadia perennis* Greene [= *Hemizonia perennis* (Greene) D. D. Keck]; MEXICO, Baja California, between Colonet and San Antonio del Mar; *Kyhos s.n.* (DAV); GenBank no. U04265. \**Deinandra fasciculata* (DC.) Greene [= *Hemizonia fasciculata* (DC.) Torr. & A. Gray]; California, Orange Co.; *BGB s.n., Weller* (JEPS); GenBank no. AF229320. \**Dubautia plantaginea* Gaudich. subsp. *plantaginea*; Hawaii, Oahu, Koolau Range; *G. Carr 1180* (HAW); GenBank no. AF061889. \**Hemizonella minima* (A. Gray) A. Gray [= *Madia minima* (A. Gray) D. D. Keck]; California, Plumas Co.; *SJB s.n.* (JEPS); GenBank no. AF229317. \**Hemizonia congesta* DC. subsp. *calyculata* Babc. & H. M. Hall; California, Mendocino Co.; *BGB 622* (DAV); GenBank no. AF229322. \**Holocarpha virgata* (A. Gray) D. D. Keck subsp. *virgata*; California, Solano Co.; *BGB 499* (DAV); GenBank no. AF229321. \**Holozonia filipes* (Hook. & Arn.) Greene; California, Monterey Co.; *Neese & Painter HL823* (JEPS); GenBank no. AF229312. \**Kyhosia bolanderi* (A. Gray) B. G. Baldwin [= *Madia bolanderi* (A. Gray) A. Gray]; California, El Dorado Co.; *BGB 509* (DAV); GenBank no. M93793. *Lagophylla minor* (D. D. Keck) D. D. Keck; California, Napa Co.; *BGB 600* (DAV); GenBank no. AF229311. \**Lagophylla ramosissima* Nutt.; California, San Luis Obispo Co.; *BGB 536* (JEPS); GenBank no. AF229310. \**Layia gaillardoides* (Hook. & Arn.) DC.; California, Santa Cruz Co.; *Buck 217* (JEPS); GenBank no. AF229315. *Layia heterotricha* (DC.) Hook. & Arn.; California, Fresno Co.; *BGB 794, Delgado* (JEPS); GenBank no. AF229313. *Layia munzii* D. D. Keck; California, San Luis Obispo Co.; *BGB 571* (DAV); GenBank no. AF229314. \**Madia sativa* Molina; California, San Mateo Co.; *BGB s.n.* (JEPS); GenBank no. AF229319. \**Osmadenia tenella* Nutt.; California, San Diego Co.; *G. Carr 1365* (DAV); GenBank no. U04266. \**Raillardella argentea* (A. Gray) A. Gray; California, El Dorado Co.; *BGB 625* (DAV); GenBank no. AF229309. \**Wilkesia gymnoxiphium* A. Gray; Hawaii, Kauai, Waimea Canyon; *Char 76.022* (HAW); GenBank no. M93800.
- Subtribe Venegasiainae B. G. Baldwin.** \**Venegasia carpesioides* DC.; California, San Luis Obispo Co.; *BGB 893, SJB, R. Baldwin, S. Baldwin* (JEPS); GenBank no. AF229301.
- Tribe Perityleae B. G. Baldwin**
- Subtribe Peritylinae Rydb.** \**Amauria rotundifolia* Benth.; MEXICO, Baja California, Isla San Martín; *BGB s.n.* (UC); GenBank no. AF378089. \**Eutetras palmeri* A. Gray; MEXICO, Aguascalientes, Kilometer 39.8 along Highway 54; *BGB 977, JLP, SJB, Francisco-Ortega* (UC); GenBank no. AF374871. \**Pericome caudata* A. Gray; California, Inyo Co.; *BGB 958, SJB* (JEPS); GenBank no. AF374866. *Perityle cochisensis* (Niles) A. M. Powell; Arizona, Cochise Co.; *BGB 962, SJB* (UC); GenBank no. AF374867. *Perityle emoryi* Torr.; California, San Bernardino Co.; *BGB 917, Strother* (JEPS); GenBank no. AF374868. *Perityle incana* A. Gray; MEXICO, Baja California, Isla Guadalupe, Outer Islet (Islote Zapato); *Rehman 6871* (SD); GenBank no. AF374869. *Perityle megaloccephala* (S. Watson) J. F. Macbr.; California, Inyo Co.; *BGB 957, SJB* (JEPS); GenBank no. AF374870. *Perityle montana* (A. M. Powell) B. G. Baldwin [= *Correllia montana* A. M. Powell]; MEXICO, Chihuahua, Turuachi Canyon; *Nesom 5139, Lewis* (UC); GenBank no. AF374872.
- Tribe Tageteae Cass.**
- Subtribe Flaveriinae Less.** *Flaveria trinervia* (Spreng.) C. Mohr; MEXICO, Veracruz, Municipio Acultzingo; *Nee 33131* (UC); GenBank no. AF374918. \**Haploësthes greggii* A. Gray; Oklahoma, Woods Co.; *Nighswonger 862* (UC); GenBank no. AF374920. \**Sartwellia flaveriae* A. Gray; Texas, Ward Co.; *Correll 33654* (UC); GenBank no. AF374919.
- Subtribe Jaumeinae Benth. & Hook.** *Jaumea carnosa* (Less.) A. Gray; California, Alameda Co.; *BGB 940, SJB* (JEPS); GenBank no. AF374928.
- Subtribe Pectidinae Less.** *Adenophyllum cooperi* (A. Gray) Strother; California, Inyo Co.; *Wisura 4768, Hayduk, Husar* (UC); GenBank no. AF374935. *Arnicastrum guerrerense* Villaseñor; MEXICO, Guerrero, Cerro Teotepec; *Villaseñor 976, Martinez* (UC); GenBank no. AF374924. \**Clappia suaeifolia* Wooton & Standl.; Texas, Hidalgo Co.; *Webster 31464, Benn, McDonald, McWhorter* (LL, TEX); GenBank no. AF374922. \**Jamesianthus alabamensis* S. F. Blake & Sherff; Alabama, Colbert Co.; *Gunn s.n.* (UC); GenBank no. AF374923. \**Nicolettia occidentalis* A. Gray; California, Kern Co.; *Charlton 1574* (UC); GenBank no. AF374931. \**Oxyppappus scaber* Benth.; MEXICO, Colima, Municipio Comala; *Sanders 10377, Phillips, Rothschild* (UC); GenBank no. AF374929. *Pectis papposa* Harv. & A. Gray; California, San Bernardino Co.; *BGB 630, Martens* (JEPS); GenBank no. AF374933. *Porophyllum gracile* Benth.; California, San Bernardino Co.; *BGB 190* (UCSB); GenBank no. AF374932. \**Pseudoclappia arenaria* Rydb.; New Mexico, Otero Co.; *BGB 966, SJB* (UC); GenBank no. AF374921. *Tagetes lucida* Cav.; MEXICO, Durango, Kilometer 93 on Highway 40; *BGB 975, JLP, SJB, Francisco-Ortega* (UC); GenBank no. AF374930. *Thymophylla pentachaeta* (DC.) Small var. *belenidium* (DC.) Strother; California, San Bernardino Co.; *Thorne, Wisura, Davidson 49093* (UC); GenBank no. AF374934.



TABLE 1. Continued.

**Subtribe Varillinae** B. L. Turner & A. M. Powell. \**Coulterella capitata* Vasey & Rose; MEXICO, Baja California Sur, ca. 10 km NE of La Paz; JLP, Campos, Cabrera 2841 (UC); GenBank no. AF374927. \**Varilla mexicana* A. Gray; MEXICO, Durango, 9.9 miles N of Rio Nazas bridge along Highway 45; BGB 971, JLP, SJB, Francisco-Ortega (UC); GenBank no. AF374925. *Varilla texana* A. Gray; Texas, Webb Co.; Nesom 6896, Gilbert, Crutchfield (CAS); GenBank no. AF374926.

#### **Incertae Sedis**

“**Villanova clade**”. *Galeana pratensis* Rydb.; MEXICO, Mexico State, near Temascaltepec; BGB 980, JLP, SJB, Francisco-Ortega (UC); GenBank no. AF374873. *Villanova achillaeoides* Less.; MEXICO, Veracruz, southwest of Perote; BGB 981, JLP, SJB, Calzada, Francisco-Ortega (UC); GenBank no. AF374874.

sulted in a matrix of 943 characters (495 in ITS-1, 167 in the 5.8S gene, and 281 in ITS-2), of which 443 are potentially informative for parsimony analysis (217 in ITS-1, 29 in the 5.8S gene, and 197 in ITS-2) after exclusion of seven characters (83–89) of ambiguous alignment from ITS-1. Recoding of potentially informative indels yielded another 73 characters. The data matrix is available from B. G. Baldwin.

Length variable regions are interspersed throughout ITS-1 and ITS-2, with pronounced length variation between positions 39–58, 68–89, 141–166, 195–216, and 289–470 in ITS-1 and between positions 678–733, 754–762, and 863–902 in ITS-2. Length variation in the ITS region is most extreme in ITS-1, ranging from 213 bp in *Thymopsis thymoides* to 410 bp in *Arnicastrum guerrense*. A 120 bp segment of inserted sequence in *A. guerrense* and an approximately 50 bp deletion in *T. thymoides* account for much of the ITS-1 length variation. ITS-2 length variation ranges from 195 bp in *Athroisma hastifolium* to 229 bp in *Ageratina glechonophylla*. Length of the 5.8S rDNA is nearly uniform, between 163–166 bp.

Pairwise sequence divergence, assuming a two-parameter model of sequence evolution (i.e., HKY85; Hasegawa et al. 1985), ranges widely in the study group. Pairwise distances of 21.5% to 34.0% were found between the outgroup species *Athroisma hastifolium* and each member of the ingroup and from 21.9% to 34.4% between the outgroup species *Blepharismum zanguebaricum* and each ingroup member. Pairwise divergence is even higher between certain taxa in the ingroup (e.g., 37.2% between *Oxypappus scaber* and *Hofmeisteria urenifolia*). Our decisions to sample most of the genera within helenioid Heliantheae and to compartmentalize the sequence data were in part based on the need to reduce potential for spurious branch attraction between highly divergent sequences (see Mishler 1994; Hillis 1998).

**Phylogenetic Analysis of ITS Data.** Parsimony analyses of the full ITS-region sequence matrix plus recorded indels yielded trees with 62 clades supported by  $\geq 85\%$  bootstrap values. Well-supported clades are mostly apical in the tree ( $\leq 7$  nodes in from terminal branches). Robust lineages (with  $\geq 85\%$  bootstrap support) chosen as compartments for reduction to arche-

type sequences included clades corresponding to the following sets of taxa (top to bottom in Fig. 1): (1) *Blepharismum zanguebaricum* (both clones) (2) *Marshallia*, (3) *Pelucha* (both clones), (4) *Psathyrotes* and *Trichoptilium*, (5) *Balduina*, *Gaillardia*, and *Helenium* s.s., (6) *Psilostrophe*, (7) *Baileya*, (8) *Hymenoxys* (including *Dugaldia* and *Plummera*), (9) *Varilla*, (10) *Haploësthes* and *Sartwellia*, (11) *Adenophyllum* and *Thymophylla*, (12) *Chaenactis*, *Dimeresia*, and *Orochaenactis*, (13) *Perityle* (including *Correllia*), (14) *Hymenopappus*, (15) *Bartlettia* (both clones), (16) *Chaetymenia*, *Espejoa*, and *Hypericophyllum*, (17) *Schkuhria*, (18) *Bahia* s.s., (19) *Palafoxia*, (20) *Amauriopsis* (*Bahia*) *dissecta*, *Hymenothrix*, and *Platyschkuhria*, (21) *Hofmeisteria* Walp., (22) *Ageratina* Spach, (23) *Constancea* (*Eriophyllum*) *nevinii* (both sequences), (24) *Eriophyllum lanatum*, *E. staechadifolium*, and *Pseudobahia*, (25) *Amblyopappus* and *Baeriopsis*, (26) *Hulsea*, (27) *Arnica* (including *Mallotopus* and *Whitneya*), and (28) *Madiinae*. The clade comprising members of *Monolopia* (including *Lembertia*) is not well-supported based on the analyses conducted here, but we chose to treat the group as a compartment based on shared, unusual morphological characteristics and consistent recovery of the clade in analyses involving a more thorough sampling of taxa in *Monolopia* and *Baeriinae* in general (Baldwin and Wessa, unpubl. data). We also treated the 84%-bootstrap clade corresponding to *Lasthenia* as a compartment based on additional molecular evidence for monophyly of genus (Chan 2000).

Phylogenetic analyses of the archetype ITS matrix (available from B. G. Baldwin) yielded additional clade resolution and higher bootstrap values for clades than was obtained from analyses of the original ITS matrix (compare Figs. 1 and 2). For example, in the archetype tree (Fig. 2), unlike in the tree based on the original ITS matrix, *Baeriinae* is resolved as a monophyletic group, as is a mostly Californian clade comprising *Baeriinae*, *Madiinae*, *Arnica*, *Eatonella*, *Hulsea*, and *Venegasia*. Also, *Psathyrotes* and *Trichoptilium* are placed with *Pelucha* in the archetype trees, but not in the strict consensus of trees based on the original ITS matrix. Clades receiving elevated bootstrap values in the archetype ITS trees include the following groups (top to bottom on Fig. 2): (1) *Tetranneurinae* except *Psilostrophe*, (2) the ingroup except *Helenieae* s.s., (3) *Coreopsidinae*

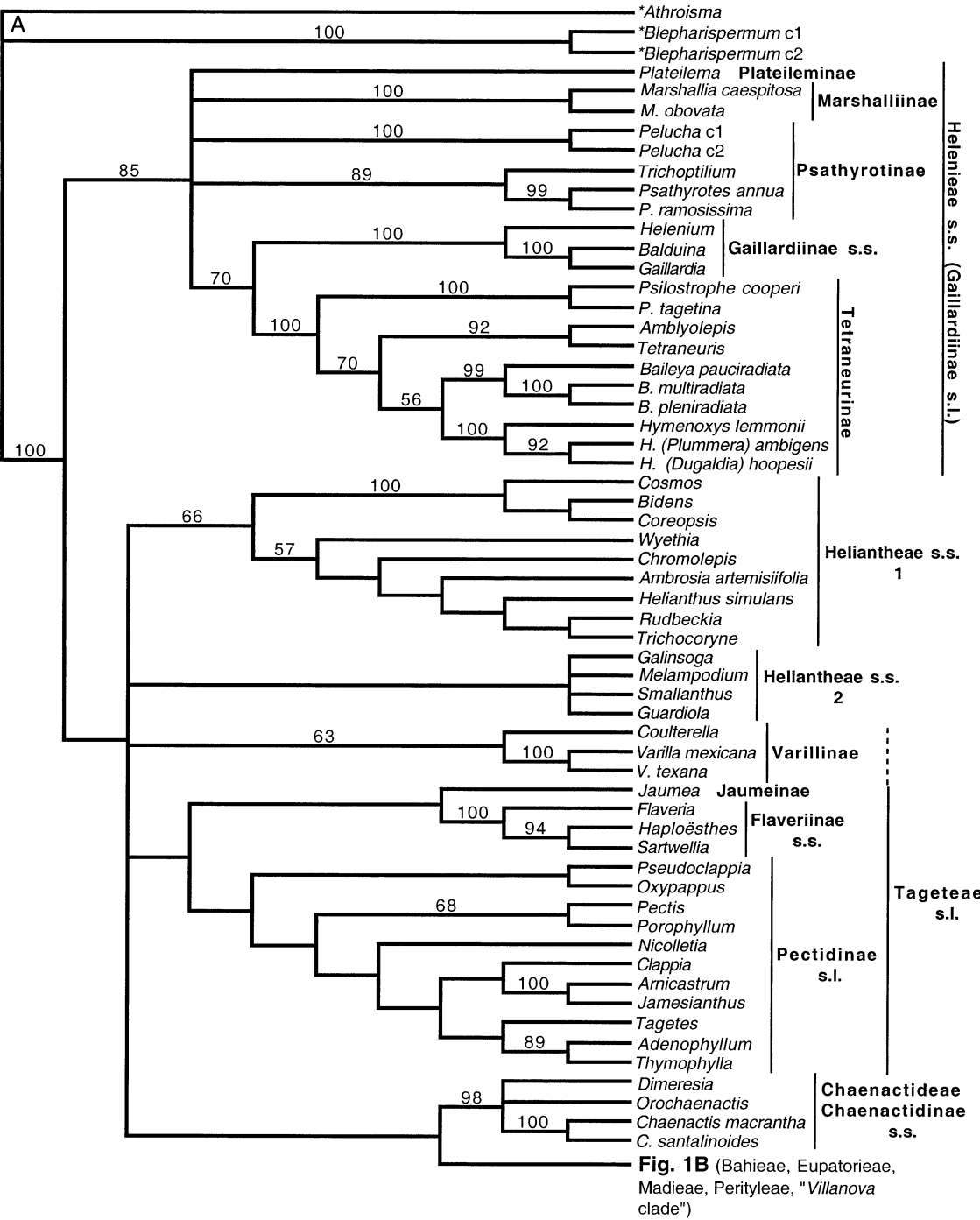


FIG. 1A, B. Strict consensus of 1492 minimum-length trees from parsimony analysis of ITS-region sequences and recoded insertion/deletion (indel) characters for 157 representatives of Heliantheae s.l. + Eupatorieae. Consistency index (excluding uninformative characters) = 0.19. Retention index = 0.57. Tree-length = 6298 steps. Numbers above branches are bootstrap values (above 50%). Asterisks (\*) denote outgroup sequences (from the *Athroisma*—*Blepharispermum* clade). Abbreviations: c = clone; SCA = Santa Catalina Island; SCL = San Clemente Island; s.l. = sensu lato; s.s. = sensu stricto. See Table 2 for new taxonomy of helenioid Heliantheae followed here.



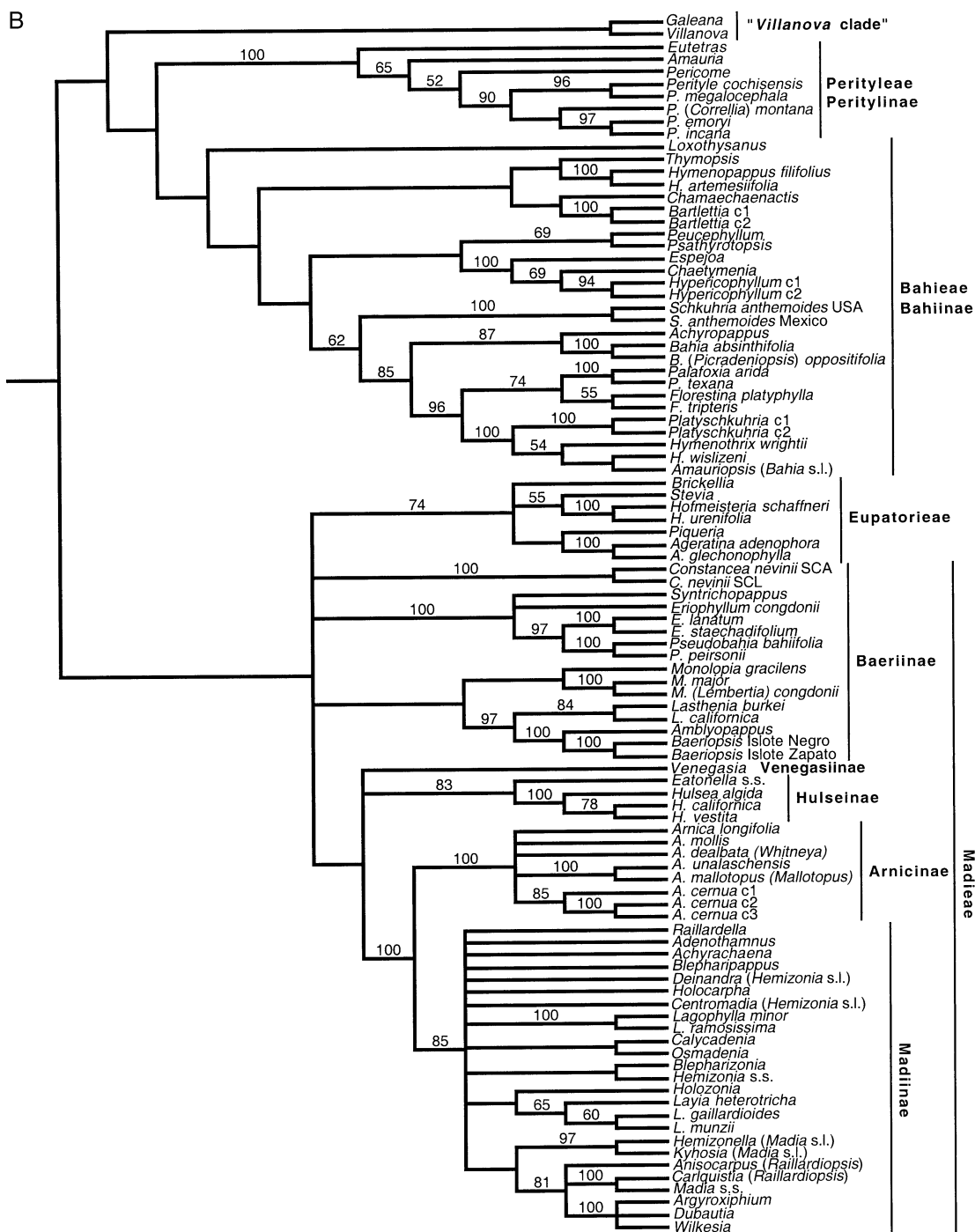


FIG. 1A, B. Continued.

with other Heliantheae s.s. except *Galinsoga* Ruiz & Pav., *Melampodium* L., and *Smallanthus* Mack., (4) *Coulterella* with *Varilla*, (6) *Tagetes* with *Adenophyllum* and *Thymophylla*, (7) Eupatorieae, (8) *Eatonella* with *Hulsea*, (9) *Perityle* (including *Correllia*) with *Pericome*, (10) *Amauria* with *Perityle* and *Pericome*, (11) *Peucephyllum*

with *Psathyrotopsis*, and (12) *Schkuhria* with *Achryopappus*, *Amauriopsis* (*Bahia*) *dissecta*, *Bahia* s.s., *Florestina*, *Hymenothrix*, *Palafoxia*, and *Platyschkuhria*.

Separate parsimony analyses of major clades shown in Fig. 2 yielded results (not shown) almost completely congruent with those obtained from analyses of the

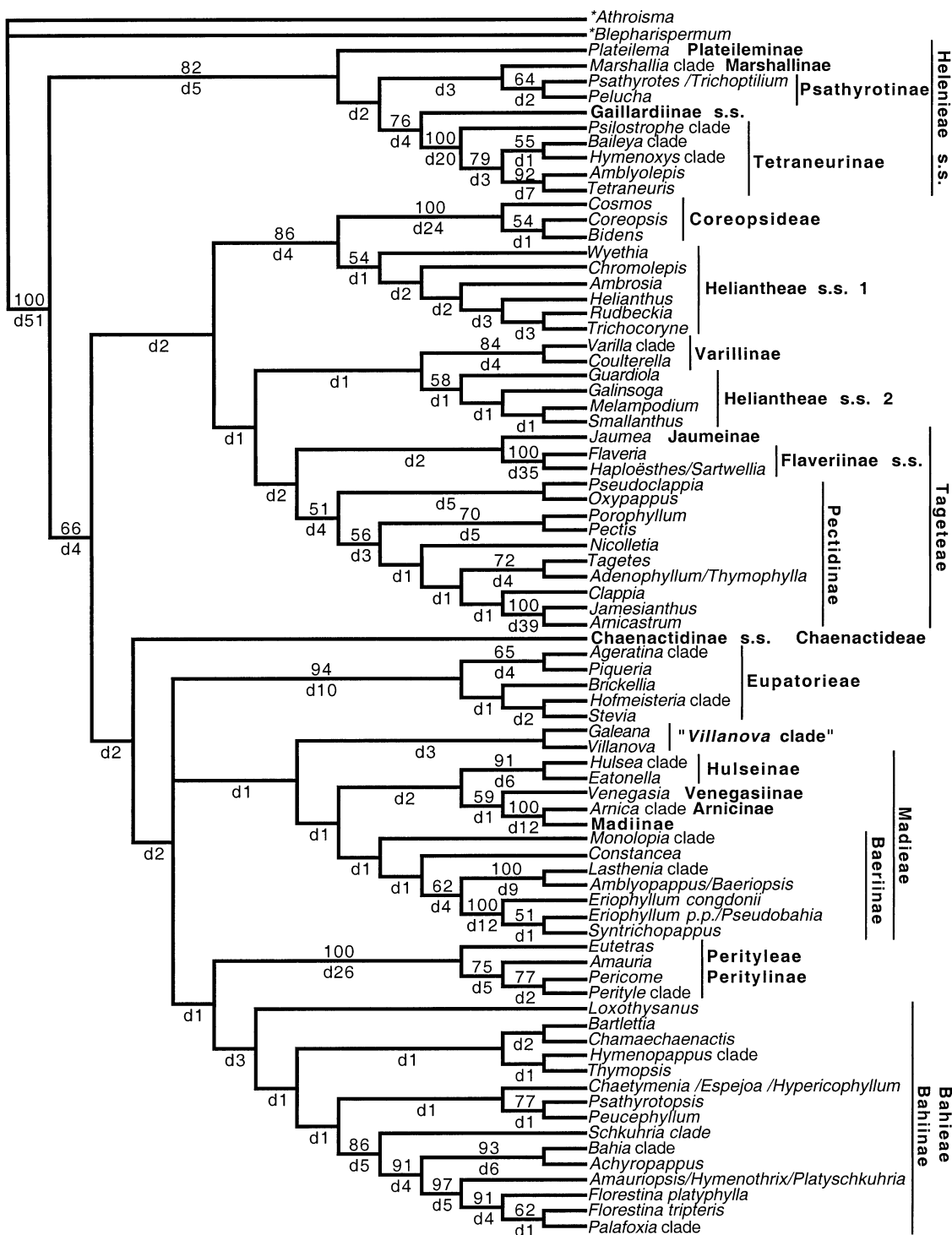


FIG. 2. Strict consensus of two minimum-length trees from parsimony analysis of ITS-region sequences and ITS-region archetypes (i.e., estimated ancestral sequences, including recoded indel mutations; see Materials and Methods) for clades in Fig. 1. Consistency index (excluding uninformative characters) = 0.25. Retention index = 0.44. Tree-length = 3925 steps. Numbers above branches are bootstrap values (above 50%). Decay values are given below branches (preceded by the letter "d"). Asterisks (\*) denote outgroup sequences (from the *Athroisma*—*Blepharispermum* clade). See Table 2 for new taxonomy of helenioid Heliantheae followed here. The two trees differ in resolution of relationships among Bahieae + Perityleae, Eupatorieae, and Madieae + "Villanova clade" [i.e., (1) Madieae/"Villanova clade" + Eupatorieae sister to Bahieae/Perityleae and (2) Madieae/"Villanova clade" + Bahieae/Perityleae sister to Eupatorieae].

original and archetype ITS data sets (Figs. 1, 2). In trees based on parsimony analyses of ITS data for Helenieae s.s. alone, with *Athroisma* and *Blepharispernum* as the outgroup, *Marshallia* is positioned as sister to other taxa of Helenieae s.s. (see Baldwin and Wessa 2000a), but the unrooted topology is congruent with the original and archetype tree topologies (Figs. 1, 2). In trees based on parsimony analyses of ITS data for Madieae alone, *Constancea* is placed outside a clade corresponding to other members of Baeriinae (Baldwin and Wessa 2000b) rather than in a nested position within Baeriinae, as in the archetype ITS trees (Fig. 2).

**Combined-Data Analyses.** Our ITS data and Karis's (1993a, b) morphological data are significantly heterogeneous based on results of a partition homogeneity test ( $P = 0.01$ ), with or without inclusion of *Jaumea*. *Jaumea* was removed from the final analyses because of concerns based on bootstrap results that homoplasy introduced by the taxon (representing the most divergent terminal branch in the trees) was disrupting clade structure. We combined the ITS and morphological data (except for *Jaumea*) considering the possibility that a low signal-to-noise ratio in the morphological data may account for the apparent conflict between data sets. The three maximally parsimonious trees obtained from simultaneous analysis of ITS and morphological data (Fig. 3) are largely congruent with the strict consensus tree from analyses of the original and archetype ITS matrices (Figs. 1, 2). For the genera in common between the two data sets, both the ITS and ITS + morphology trees resolve clades corresponding to (1) Helenieae s.s. (with the same internal structure), (2) the ingroup except Helenieae s.s., (3) Flaveriinae, (4) Pectidinae, including *Clappia*, (5) *Chaenactis* and *Dimeresia*, (6) *Coulterella* and *Varilla*, (7) *Galinsoga*, *Guardiola*, *Melampodium*, and *Smallanthus*, (8) Coreopsidinae + *Ambrosia*, *Helianthus*, and *Rudbeckia*, (9) Bahiinae (with the same internal structure), and (10) *Arnica* and Madiinae. Clades resolved with ITS data alone (for the same reduced set of taxa) that received enhanced bootstrap and decay support with the addition of morphological data include those comprising (1) Helenieae s.s., (2) Helenieae except *Marshallia*, (3) *Gaillardia* and *Helenium*, (4) Flaveriinae, (5) *Chaenactis* and *Dimeresia*, (6) *Coulterella* and *Varilla*, (7) *Melampodium* and *Smallanthus*, (8) Clade 7 + *Galinsoga* and *Guardiola*, (9) *Coreopsis* L. and *Cosmos* Cav., (10) *Helianthus* and *Rudbeckia*, (11) *Lasthenia* and Eupatorieae, (12) Madiinae, and (13) *Arnica* and Madiinae. Topological conflicts with ITS trees involve only weakly supported clades.

A partition homogeneity test yielded evidence of significant heterogeneity between the ITS data and Kim and Jansen's (1995) *ndhF* data ( $P = 0.05$ ). The only evidence of strong incongruence between the two data sets based on separate bootstrap analyses is in place-

ment of Coreopsidinae, which is sister to the ingroup except Helenieae s.s. in the *ndhF* trees and sister to *Ambrosia* and *Helianthus* in the ITS trees (and in the combined ITS + *ndhF* trees). Simultaneous analysis of the two data sets with Coreopsidinae excluded yielded a strict consensus tree that is topologically congruent with the most parsimonious tree obtained with Coreopsidinae included (Fig. 4). In the absence of a disruptive effect on clade structure, we retained Coreopsidinae in subsequent analyses of combined ITS and *ndhF* data. Seven well-supported clades corresponding to the following taxa were resolved in the single most parsimonious tree from simultaneous analysis of the two data sets (Fig. 4): (1) the ingroup, (2) Helenieae s.s., (3) Pectidinae, (4) Bahiinae, (5) Madiinae and *Venegasia* (Madieae), (6) *Coreopsis* and *Cosmos* (Heliantheae s.s.), and (7) *Ambrosia* and *Helianthus* (Heliantheae s.s.). All seven clades were also recovered in analyses of ITS data alone. Six of the seven clades (all but the clade consisting of Madiinae and *Venegasia*) received elevated bootstrap and decay support with the addition of *ndhF* data to the analyses, as did the moderately supported clade uniting members of the ingroup except Helenieae s.s.

Simultaneous analysis of ITS, morphological, and *ndhF* data yielded five maximally parsimonious trees that share seven clades in common (Fig. 5). The strict consensus tree is identical to the strict consensus tree obtained from analysis of ITS data alone for the same set of taxa. The addition of morphological and *ndhF* data to the parsimony analyses increased bootstrap and/or decay support for clades comprising (1) all ingroup taxa except *Marshallia*, the sole representative of Helenieae s.s., (2) Flaveriinae sensu Turner and Powell (1977) and *Jaumea*, (3) all ingroup taxa except Flaveriinae, *Jaumea*, and *Marshallia*, (4) Madiinae and *Palafoxia*, (5) *Coreopsis* and *Cosmos*, and (6) *Ambrosia* and *Helianthus*. Bootstrap and decay support for a clade comprising Heliantheae s.s. (including *Coreopsis* and *Cosmos*) was reduced by adding morphological and *ndhF* data to the analyses.

**Morphological and anatomical character-state evolution.** As noted above, changes in morphological characters, as coded by Karis (1993a), augment support for 13 clades resolved in the simultaneous parsimony analysis of ITS and morphological/anatomical data (Fig. 3). A clade comprising all members of the ingroup except Helenieae s.s. is supported by opposite leaves and ecaudate anthers (with a putative parallel origin of ecaudate anthers in the *Amblyolepis*-*Baileya* clade, within Helenieae s.s.). Morphological and anatomical changes diagnosing Helenieae s.s. (including *Marshallia*) include uniseriate corolla hairs with a rounded to sac-like ultimate cell, disc corolla lobes with continuous veins, pericarp with large crystals or druses, and cypselae with non-carbonized walls. Inclusion of an-

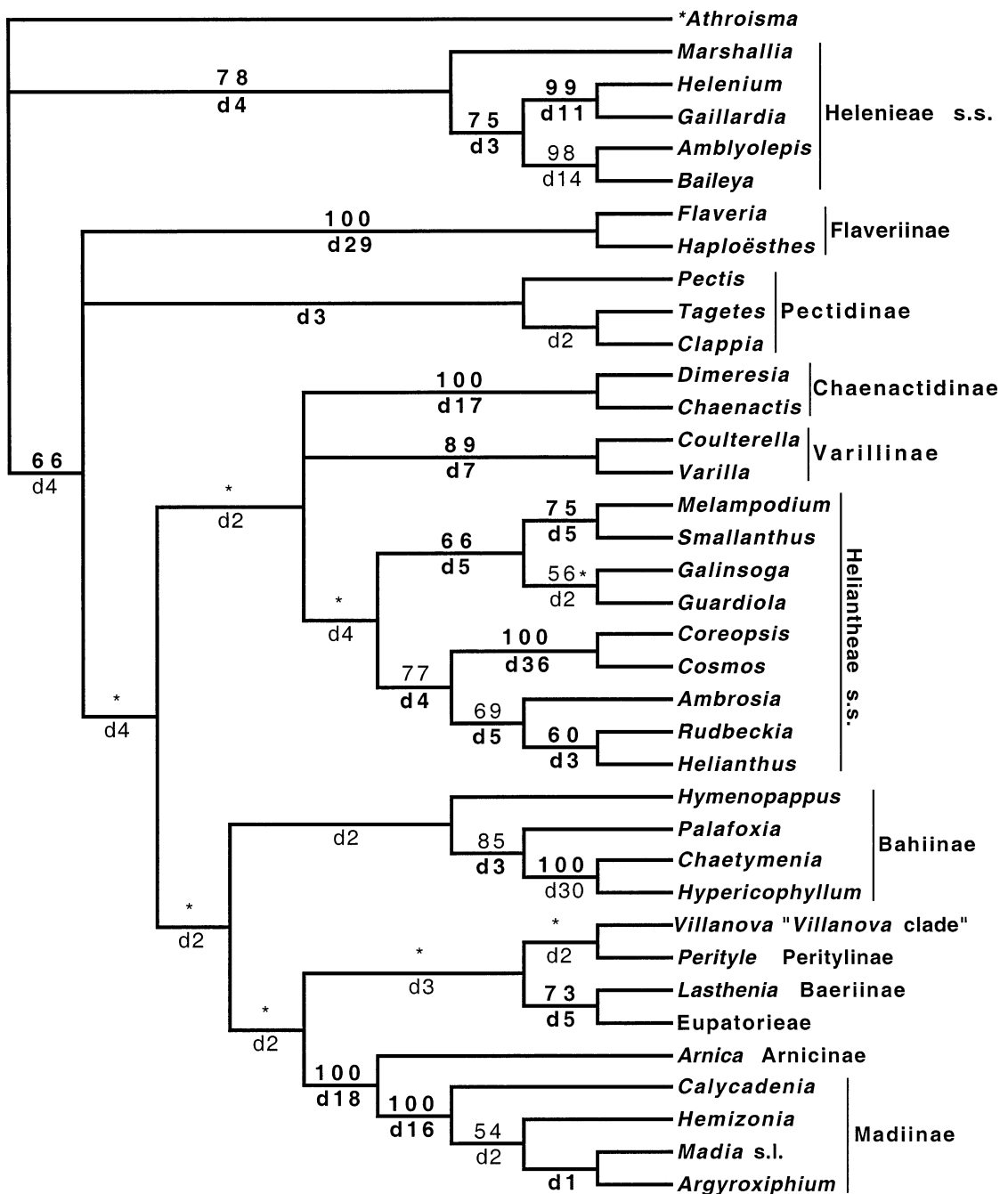


FIG. 3. Strict consensus of three minimum-length trees from parsimony analysis of ITS-region sequences (indels recoded) combined with Karis's (1993a, b) morphological data for taxa of Heliantheae s.l. + Eupatorieae. Consistency index (excluding uninformative characters) = 0.35. Retention index = 0.41. Tree-length = 2554 steps. Bootstrap values (above 50%) are shown above branches; decay values are shown below branches (preceded by the letter "d"). Bootstrap or decay values in bold represent enhanced or identical support compared to values obtained for the same set of taxa with ITS data alone. Asterisks denote clades not resolved in an analysis of ITS data alone for the same set of taxa. Clades without boldface support values or asterisks are resolved with ITS data alone but support is diminished with morphological data included. Archetype ITS-region sequences were used for *Arnica*, *Bailey*, *Chaenactis*, *Eupatorieae*, *Hymenopappus*, *Hypericophyllum*, *Lasthenia*, *Marshallia*, *Palafoxia*, *Perityle* (including *Correllia*), and *Varilla*. *Kyhosia* (*Madia*) *bolanderi* was used for *Madia* s.l., in conformance with Karis's (1993a) interpretation of *Madia* and extensive molecular evidence for both *Kyhosia* and *Madia* s.s. being more closely related to *Argyroxiphium* than to *Calycadenia* or *Hemizonia* (e.g., Fig. 1B; Baldwin 1996). See Table 2 for new taxonomy of helenioid Heliantheae followed here.



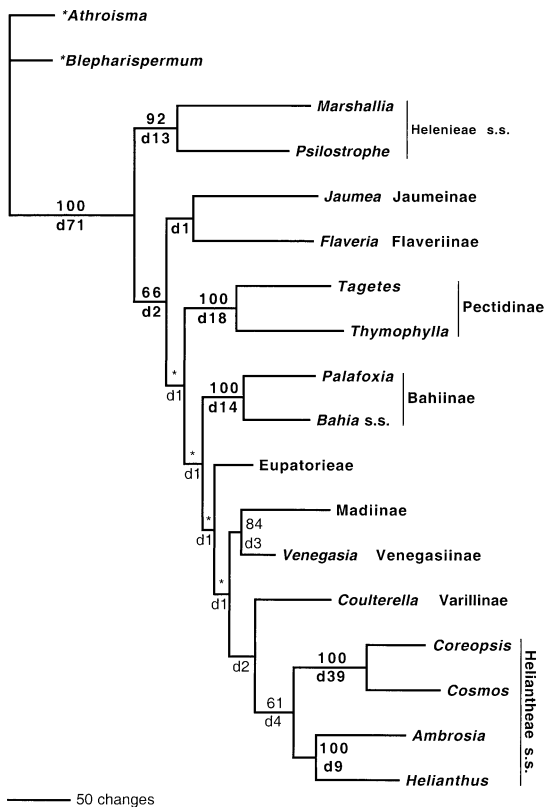


FIG. 4. The single minimum-length tree from parsimony analysis of ITS-region sequences (indels recoded) combined with Kim and Jansen's (1995) *ndhF* sequence data for taxa of Heliantheae s.l. + Eupatorieae. Consistency index (excluding uninformative characters) = 0.51. Retention index = 0.42. Tree-length = 1618 steps. Bootstrap values (above 50%) are shown above branches; decay values are shown below branches (preceded by the letter "d"). Bootstrap or decay values in bold represent enhanced or identical support compared to values obtained for the same set of taxa with ITS data alone. Asterisks denote clades not resolved in an analysis of ITS data alone for the same set of taxa. Clades without boldface support values or asterisks are resolved with ITS data alone but support is diminished or unchanged with *ndhF* data included. Branch lengths correspond to numbers of nucleotide substitutions and indels, optimized under ACCTRAN. Archetype ITS-region sequences were used for *Bahia* s.s., *Blepharisperrum*, *Eupatorieae* (combined with *ndhF* sequence for *Bartlettina sordida*), *Madiinae* (combined with *ndhF* sequence for *Madia elegans*), *Marshallia*, *Palafoxia*, and *Psilostrophe* (see text).

other outgroup taxon (e.g., in Inuleae) that lacks carbonization in the fruit walls, would render equivocal the reversal to non-carbonized cypselae in Helenieae s.s. The *Gaillardia*—*Helenium* clade is diagnosed in part by phyllaries strongly reflexed at anthesis, ray corolla lobes elongate, disc corolla tubes reduced, and pappus elements in more than one series. The *Flaveria*—*Haploësthes* clade is diagnosed by only one unequivocal morphological change: reduced ray floret limbs. *Chaenactis* and *Dimeresia* are united in part by discoid heads,

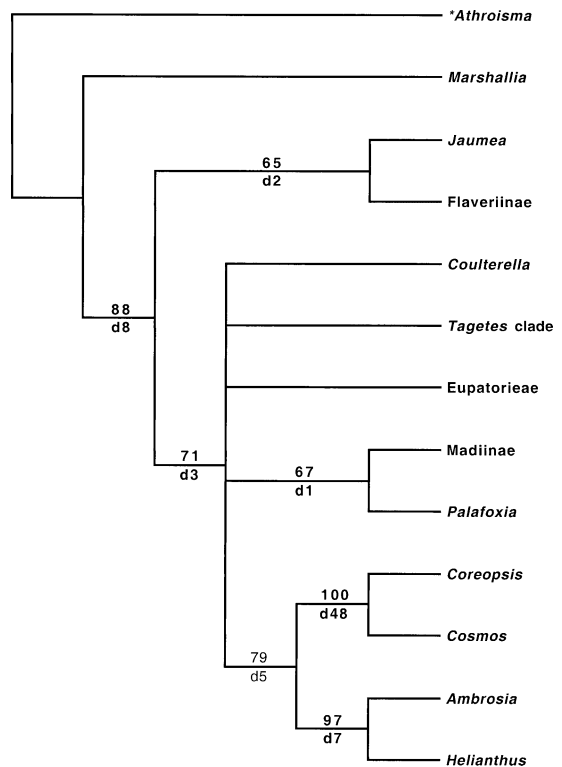


FIG. 5. Strict consensus of five minimum-length trees from simultaneous parsimony analysis of ITS-region sequences (indels recoded), Kim and Jansen's (1995) *ndhF* sequence data, and Karis's (1993a, b) morphological data for taxa of Heliantheae s.l. + Eupatorieae. Consistency index (excluding uninformative characters) = 0.54. Retention index = 0.39. Tree-length = 1388 steps. Bootstrap values (above 50%) are shown above branches; decay values are shown below branches (preceded by the letter "d"). Bootstrap or decay values in bold represent enhanced or identical support compared to values obtained for the same set of taxa with ITS data alone. The clade without boldface support values is resolved with ITS data alone but support is diminished with *ndhF* and morphological data included. Archetype ITS sequences were used for *Eupatorieae*, *Flaveriinae* sensu Turner and Powell (1977), *Madiinae*, *Marshallia*, a clade comprising *Adenophyllum*, *Tagetes*, and *Thymophylla* ("Tagetes clade"), and *Palafoxia* (see text).

veins of the disc floret lobes distant from the lobe margins, narrowly oblong anther endothelial cells, and bulging anther-collar cells. Derived morphological and anatomical characteristics uniting members of *Madiinae* (but not necessarily common to all taxa) include entire and uninerved leaves, extracellular pectic polysaccharides, paleae associated with the outermost disc florets only, and dilation of the throat distal to its base (i.e., distal to insertion of filaments). An additional characteristic uniting members of *Madiinae*—ray cypselae surrounded at least in part by phyllary margins—is obtained after correcting the state assignment for *Calycadenia*. Treatment of reddish and violet anther colors as a common state results in another morpho-

logical characteristic uniting Madiinae, i.e., darkly colored (but not blackened) anthers. Apart from the exceptions noted above for Madiinae, we did not reassess Karis's (1993a) morphological character and character-state codings. Resolution of morphological character evolution and chromosome number evolution in Heliantheae s.l. + Eupatorieae was also obtained by mapping characters onto the archetype ITS trees (Figs. 6–10).

**Biogeographic History.** Most taxa in almost all major ingroup clades sampled occur at least in part in the region of southwestern North America and northern Mexico. Most taxa restricted to other areas are apically positioned in the clade comprising Heliantheae s.l. + Eupatorieae, minus the *Athroisma-Blepharispermum* clade. As expected, parsimony mapping using MacClade 3.1 (Maddison and Maddison 1992) places the ancestor of the clade comprising Heliantheae s.l. + Eupatorieae in southwestern North America/northern Mexico (Fig. 11). Using that approach, most of the major clades of helenioid Heliantheae are placed ancestrally in the same area. A major exception is the clade comprising Baeriinae, Madiinae, and the paraphyletic  $x = 19$  ("arnicoid") group, which is reconstructed as ancestrally occurring in the California Floristic Province, as is each of the major lineages therein, including *Arnica*. The African genus *Hypericophyllum* appears to be of southern Mexican or Central American descent based on its placement in a clade with *Chaetymenia* and *Espejoa* (Bahiinae). Dispersal-vicariance analysis (Ronquist 1997) on pared (49 or fewer taxa) data sets yielded identical biogeographic reconstructions for ancestors of some major clades, e.g., California Floristic Province for Madiinae and southwestern North America for Flaveriinae s.s., Helenieae s.s., Pectidinae s.l., Perityleae, and the clade encompassing Tageteae s.l. + *Galinsoga*, *Guardiola*, *Melampodium*, and *Smallanthus* (results not shown).

#### DISCUSSION

**Major Clades of Helenioid Heliantheae.** Based on ITS sequence data from our sampling of taxa, the following previously recognized subtribes of helenioid Heliantheae (= Helenieae s.l.) consisting of more than one genus appear to be monophyletic: Flaveriinae sensu Turner and Powell (1977) and Robinson (1981), Madiinae sensu Carlquist (1959) and most subsequent authors, and Peritylinae sensu Robinson (1981). Other helenioid subtribes (e.g., Baeriinae, Bahiinae, Chaenactidinae, Hymenopappinae, and Pectidinae) appear to be paraphyletic or polyphyletic groups as previously circumscribed.

**SUBTRIBE BAERIINAE.** A weakly supported ITS clade (Fig. 2) encompasses a group corresponding to a modified Baeriinae, with a circumscription that combines elements of previous treatments. Based on the

ITS trees, Baeriinae sensu Robinson (1981) [= Baeriinae sensu Karis and Ryding (1994a)] is monophyletic if *Eatonella* s.s. (sister to *Hulsea* in ITS trees; Fig. 1B) and *Oxypappus* [close to Pectidinae sensu Robinson (1981) in ITS trees; Figs. 1A, 2] are excluded and *Syntrichopappus* is included. Eriophyllinae (= Baeriinae) sensu Turner and Powell (1977) is monophyletic if *Trichoptilium* (sister to *Psathyrotes* in ITS trees; Fig. 1A) is excluded and *Lembertia* (treated by us as *Monolopia congdonii*; Fig. 2) is included. Phylogenetic distinction between subtribes Baeriinae and Eriophyllinae is not upheld by the ITS results; "core" Eriophyllinae genera [*Eriophyllum* s.l. (including *Constancea*), *Monolopia* (including *Lembertia*), *Pseudobahia*, and *Syntrichopappus*] do not constitute a clade exclusive of "core" Baeriinae genera [*Amblyopappus*, *Baeriopsis*, and *Lasthenia*] in the ITS trees (Figs. 1B, 2). The circumscription adopted here for Baeriinae (Fig. 1B; Table 2) is provisional until questions concerning the positions of *Constancea* (see below) and the *Eatonella* + *Hulsea* clade (Panero, Baldwin, Schilling, and Clevinger, unpubl. data) are fully resolved.

*Constancea*, a monospecific genus for *Eriophyllum nevinii* (see Baldwin 2000), is placed outside the well-supported clade corresponding to *Eriophyllum* s.l., *Pseudobahia*, and *Syntrichopappus* (Figs. 1B, 2). Phylogenetic analyses of ITS data (also see Baldwin and Wessa 2000b) and data from the external transcribed spacer (ETS) of 18S–26S nuclear rDNA (Baldwin and Wessa, unpubl. data) place *C. nevinii* either in Baeriinae, in a basal or near basal position (e.g., in Fig. 2), or sister to a clade encompassing most  $x = 19$  helenioid genera [i.e., *Arnica* (including *Mallotopus* and *Whitneya*), *Eatonella* s.s., *Hulsea*, and *Venegasia*] and Madiinae. The ITS and ETS results and recent chromosome counts for *C. nevinii* of  $2n = 19$  II (Mooring 1997), a chromosome number otherwise unknown in Baeriinae, lead us to accept a refined version of Mooring's (1997) hypothesis that *C. nevinii* is an evolutionary outlier (although probably not ancestral) to other members of *Eriophyllum* sensu Constance (1937). *Constancea* appears to represent a more ancient lineage than earlier suspected and may be a relict in the flora of the Californian Channel Islands, where the taxon is endemic.

The positions of *Lasthenia* and *Syntrichopappus* in the ITS trees (Figs. 1B, 2) affirm a much closer relationship of the two morphologically-unusual genera with *Eriophyllum* s.l. than with Coreopsidinae. *Lasthenia* has been noted as biochemically anomalous among Heliantheae s.l. for possessing anthoclor (alkali-sensitive) pigments (as does *Syntrichopappus*) and polyacetylenes of an unusual structural type (ene-tetrayne-ene, also reported in *Schkuhria*), characteristics that are also found in subtribe Coreopsidinae (see Bohm 1977). Based on the ITS evidence, the striking chemical similarities between *Lasthenia*/*Syntrichopappus* and Cor-

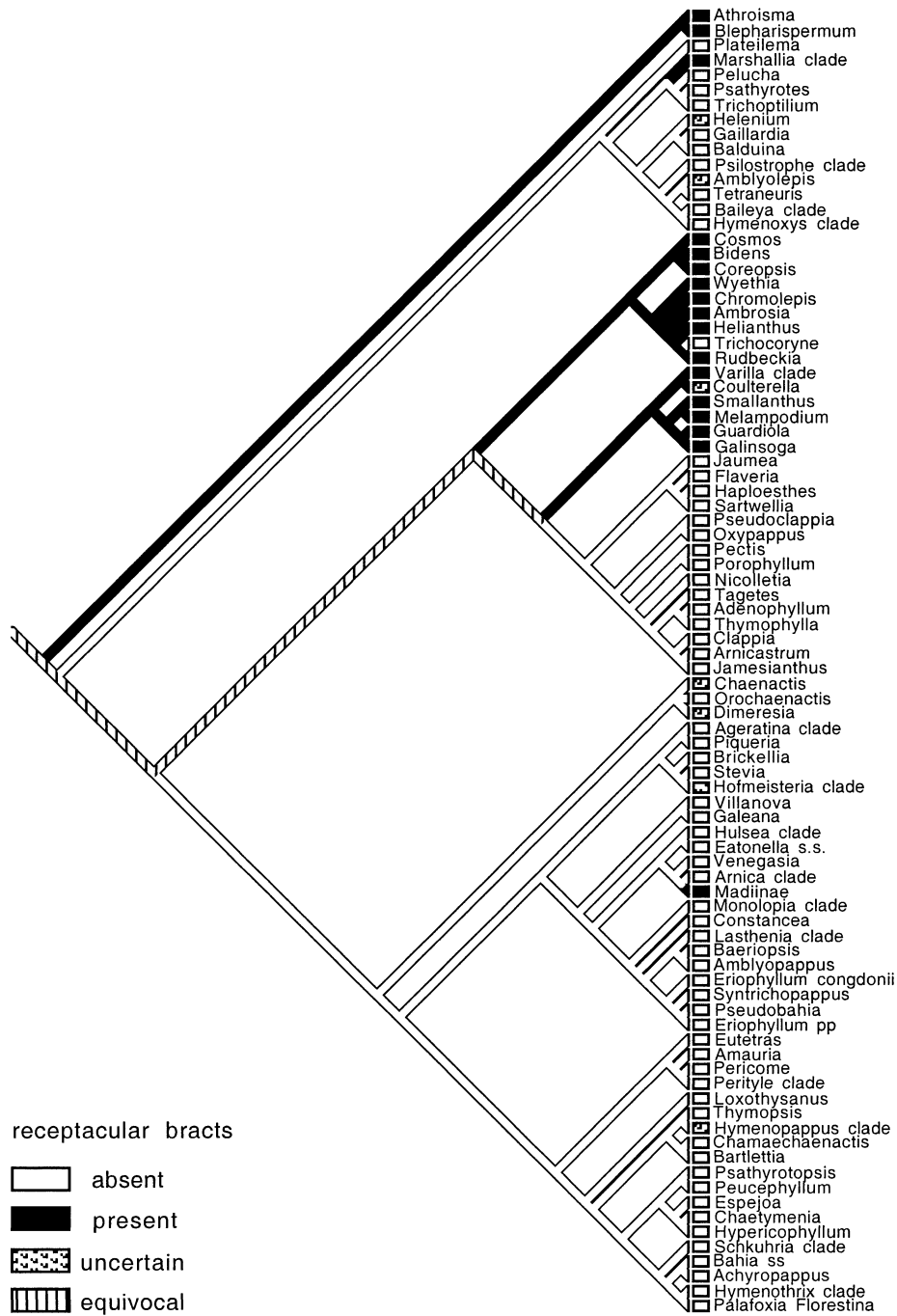


FIG. 6–10. Hypotheses of morphological, ecological, and chromosomal evolution for the clade corresponding to Heliantheae s.l. + Eupatorieae based on parsimony mapping of unordered character states on minimum-length trees. The tree topology shown corresponds to one of two minimum-length ITS archetype trees (see Fig. 2 for strict consensus tree). Character-state changes estimated here are identical to those estimated for the other minimum-length tree unless otherwise stated. *Hymenothrix* clade contains *Amauriopsis*, *Hymenothrix*, and *Platyschkuhria*. Fig. 6. Evolutionary losses and gains of receptacular bract (palea) expression.

TABLE 2. Tribal and subtribal classification of genera of helenioid Heliantheae. See text for comparison of the revised taxonomy with previous treatments.

Tribe Bahieae B. G. Baldwin, here.

Subtribe Bahiinae Rydb., N. Amer. Fl. 34(1): 31. 1914. [“*Bahia* clade” (*Achyropappus* Kunth 1818, *Amauriopsis* Rydb. 1914, *Bahia* Lag. 1816, *Florestina* Cass. 1817, *Hymenothrix* A. Gray 1849, *Palafoxia* Lag. 1816, *Platyschkuhria* Rydb. 1906, *Schkuhria* Roth 1797), “*Chaetymeria* clade” (*Chaetymeria* Hook. & Arn. 1838, *Espejoa* DC. 1836, *Hypericophyllum* Steetz 1864); “*Peucephyllum* clade” (*Peucephyllum* A. Gray 1859, *Psathyrotopsis* Rydb. 1927), *Bartlettia* A. Gray 1855, *Chamaechaenactis* Rydb. 1906, *Hymenopappus* L’Hér. 1788, *Loxothysanus* B. L. Rob. 1907, *Thymopsis* Benth. 1873]

Tribe Chaenactideae B. G. Baldwin, here.

Subtribe Chaenactidinae Rydb., N. Amer. Fl. 34(1): 63. 1914. [*Chaenactis* DC. 1836, *Dimeresia* A. Gray 1886, *Orochaenactis* Coville 1893]

Tribe Helenieae Benth. & Hook., Gen. Pl. 2: 199. 1873. [see Baldwin and Wessa (2000a) for key to subtribes]

Subtribe Gaillardinae Less., Linnaea 6: 516. 1831. [*Balduina* Nutt. 1818, *Gaillardia* Foug. 1786, *Helenium* L. 1753]

Subtribe Marshallinae H. Rob., Phytologia 41: 42. 1978. [*Marshallia* Schreb. 1791]

Subtribe Plateileminae B. G. Baldwin, Syst. Bot. 25: 536. 2000. [*Plateilema* (A. Gray) Cockerell 1904]

Subtribe Psathyrotinae B. G. Baldwin, Syst. Bot. 25: 535. 2000. [*Pelucha* S. Watson 1889, *Psathyrotes* (Nutt.) A. Gray 1853, *Trichoptilium* A. Gray 1859]

Subtribe Tetraneurinae Rydb., N. Amer. Fl. 34(1): 2. 1914. [*Amblyolepis* DC. 1836, *Baileya* Harv. & A. Gray ex Torr. 1849, *Hymenoxys* Cass. 1828 (including *Dugaldia* Cass. 1828 and *Plummera* A. Gray 1882), *Psilostrophe* DC. 1838, *Tetraneuris* Greene 1898]

Tribe Heliantheae Cass., Journ. Phys. 88: 189. 1819. [genus below is the only taxon recently treated as a member of Helenieae s.l. (Karis and Ryding 1994a); see Karis and Ryding (1994b) for other taxa of Heliantheae s.s.]

Incertae Sedis [*Trichocoryne* S. F. Blake 1924, close to Zinniinae; see Urbatsch et al. 2000]

Tribe Madieae Jeps., Fl. West. Middle Calif., 486. 1901.

Subtribe Arnicinae B. G. Baldwin, here. [*Arnica* L. 1753 (including *Mallotopus* Franch. & Sav. 1878 and *Whitneya* A. Gray 1865)]

Subtribe Baeriinae Benth. & Hook., Gen. Pl. 2: 200. 1873. [*Amblyopappus* Hook. & Arn. 1841, *Baeriopsis* J. T. Howell 1942, *Constancea* B. G. Baldwin 1999, *Eriophyllum* Lag. 1816, *Lasthenia* Cass. 1834, *Monolopia* DC. 1837 (including *Lembertia* (A. Gray) Greene 1897), *Pseudobahia* (A. Gray) Rydb. 1915, *Syntrichopappus* A. Gray 1857]

Subtribe Hulseinae B. G. Baldwin, here. [*Eatonella* A. Gray 1883, *Hulsea* Torr. & A. Gray 1858]

Subtribe Madiinae Benth. & Hook., Gen. Pl. 2: 198. 1873. [*Achyraea* Schauer 1838, *Adenothamnus* D. D. Keck 1935, *Anisocarpus* Nutt. 1841 (including *Raillardia* Rydb. 1927 p.p.), *Argyroxiphium* DC. 1836, *Blepharipappus* Hook. 1833, *Blepharizonia* (A. Gray) Greene 1885, *Calycadenia* DC. 1836, *Carlquistia* B. G. Baldwin 1999 (including *Raillardia* Rydb. 1927 p.p.), *Centromadia* Greene 1894, *Deinandra* Greene 1897, *Dubautia* Gaudich. 1830, *Harmonia* B. G. Baldwin 1999, *Hemizonella* A. Gray 1874, *Hemizonia* DC. 1836, *Holocarpa* (DC.) Greene 1897, *Holozonia* Greene 1882, *Jensia* B. G. Baldwin 1999, *Kyhosia* B. G. Baldwin 1999, *Lagophylla* Nutt. 1841, *Layia* Hook. & Arn. ex DC. 1838, *Madia* Molina 1781, *Osmadenia* Nutt. 1841, *Raillardella* (A. Gray) Benth. 1873, *Wilkesia* A. Gray 1852]

Subtribe Venegasinae B. G. Baldwin, here. [*Venegasia* DC. 1838]

Tribe Perityleae B. G. Baldwin, here.

Subtribe Lycapsinae H. Rob., Phytologia 46: 120. 1980. [*Lycapsus* Phil. 1870]

Subtribe Peritylinae Rydb., N. Amer. Fl. 34 (1): 11. 1914. [*Amauria* Benth. 1844, *Eutetras* A. Gray 1879, *Pericome* A. Gray 1853, *Perityle* Benth. 1844 (including *Correllia* A. M. Powell 1973)]

Tribe Tageteae Cass., Journ. Phys. 88: 162. 1819.

Subtribe Flaveriinae Less., Synopsis, 235. 1832. [*Flaveria* Juss. 1789, *Haploësthes* A. Gray 1849, *Sartwellia* A. Gray 1852]

Subtribe Jaumeinae Benth. & Hook., Gen. Pl. 2: 199. 1873. [*Jaumea* Pers. 1807]

Subtribe Pectidinae Less., Linnaea 5: 134. 1830. [*Arnicastrum* Greenm. 1903, *Clappia* A. Gray 1859, *Jamesianthus* S. F. Blake & Sherff 1940, *Oxyappus* Benth. 1845, *Pseudoclappia* Rydb. 1923, plus genera of Tageteae sensu Strother 1977, 1986; i.e., *Adenopappus* Benth. 1840, *Adenophyllum* Pers. 1807, *Boeberastrum* (A. Gray) Rydb. 1916, *Boeberoides* (DC.) Strother 1986, *Chrysactinia* A. Gray 1849, *Comaclinium* Scheidw. & Planch. 1852, *Dysodiopsis* (A. Gray) Rydb. 1915, *Dyssodia* Cav. 1802, *Gymnolaena* (DC.) Rydb. 1915, *Harnackia* Urb. 1925, *Hydrodyssodia* B. L. Turner 1988, *Hydropectis* Rydb. 1916, *Lescaillaea* Griseb. 1866, *Leucactinia* Rydb. 1915, *Nicolletia* A. Gray 1845, *Pectis* L. 1759, *Porophyllum* Adans. 1763, *Schizotrichia* Benth. 1843, *Strotheria* B. L. Turner 1972, *Tagetes* L. 1753, *Thymophylla* Lag. 1816, *Urbinnella* Greenm. 1903, *Vilobia* Strother 1968]

Subtribe Varillinae B. L. Turner & A. M. Powell, Biol. Chem. Compositae, 719. 1977. [*Coulterella* Vasey & Rose 1890, *Varilla* A. Gray 1849]

“*Anisopappus* clade” [*Anisopappus* Hook. & Arn. 1837]

“*Athroisma-Blepharispermum* clade” [*Athroisma* DC. 1833, *Blepharispermum* Wight ex DC. 1834, *Leucoblepharis* Arn. 1838]

Incertae Sedis

*Apostates* Lander 1989

“*Villanova* clade” (*Galeana* La Llave & Lex. 1824, *Villanova* Lag. 1816)

*Welwitschiella* O. Hoffm. 1894



TABLE 3. Alphabetical list of genera of helenioid Heliantheae, with tribal and subtribal placement indicated. An asterisk (\*) indicates a provisional assignment to tribe or subtribe in lieu of additional data on relationships.

<i>Achyrachaena</i> Schauer, Madieae, Madiinae	<i>Hemizonella</i> A. Gray, Madieae, Madiinae
<i>Achyropappus</i> Kunth, Bahieae, Bahiinae ("Bahia clade")	<i>Hemizonia</i> DC., Madieae, Madiinae
<i>Adenopappus</i> Benth., Tageteae, Pectidinae	<i>Holocarpa</i> (DC.) Greene, Madieae, Madiinae
<i>Adenophyllum</i> Pers., Tageteae, Pectidinae	<i>Holozonia</i> Greene, Madieae, Madiinae
<i>Adenothamnus</i> D. D. Keck, Madieae, Madiinae	<i>Hulsea</i> Torr. & A. Gray, Madieae, Hulseinae
<i>Amauria</i> Benth., Perityleae, Peritylinae	<i>Hydrodyssodia</i> B. L. Turner, Tageteae, Pectidinae
<i>Amauriopsis</i> Rydb., Bahieae, Bahiinae ("Bahia clade")	<i>Hydropectis</i> Rydb., Tageteae, Pectidinae
<i>Amblyolepis</i> DC., Helenieae, Tetraneurinae	<i>Hymenopappus</i> L'Hér., Bahieae, Bahiinae
<i>Amblyopappus</i> Hook. & Arn., Madieae, Baeriinae	<i>Hymenothrix</i> A. Gray, Bahieae, Bahiinae ("Bahia clade")
<i>Arnica</i> L., Madieae, Arnicinae	<i>Hymenoxys</i> Cass., Helenieae, Tetraneurinae
<i>Arnicastrum</i> Greenm., *Tageteae, *Pectidinae	<i>Hypericophyllum</i> Steetz, Bahieae, Bahiinae ("Chaetymenia clade")
<i>Anisocarpus</i> Nutt., Madieae, Madiinae	<i>Jamesianthus</i> S. F. Blake & Sherff, *Tageteae, *Pectidinae
<i>Anisopappus</i> Hook. & Arn., "Anisopappus clade"	<i>Jaumea</i> Pers., *Tageteae, Jaumeinae
<i>Apostates</i> Lander, Incertae Sedis	<i>Jensia</i> B. G. Baldwin, Madieae, Madiinae
<i>Argyroxiphium</i> DC., Madieae, Madiinae	<i>Kyhosia</i> B. G. Baldwin, Madieae, Madiinae
<i>Athroisma</i> DC., "Athroisma-Blepharispermum clade"	<i>Lagophylla</i> Nutt., Madieae, Madiinae
<i>Baeriopsis</i> J. T. Howell, Madieae, Baeriinae	<i>Lasthenia</i> Cass., Madieae, Baeriinae
<i>Bahia</i> Lag., Bahieae, Bahiinae ("Bahia clade")	<i>Layia</i> Hook. & Arn. ex DC., Madieae, Madiinae
<i>Baileya</i> Harv. & A. Gray ex Torr., Helenieae, Tetraneurinae	<i>Lembertia</i> (A. Gray) Greene (not recognized; synonym of <i>Monolopia</i> )
<i>Balduina</i> Nutt., Helenieae, Gaillardinae	<i>Lescaillea</i> Griseb., Tageteae, Pectidinae
<i>Bartlettia</i> A. Gray, Bahieae, Bahiinae	<i>Leucactinia</i> Rydb., Tageteae, Pectidinae
<i>Blepharipappus</i> Hook., Madieae, Madiinae	<i>Leucoblepharis</i> Arn., "Athroisma-Blepharispermum clade"
<i>Blepharispermum</i> Wight ex DC., "Athroisma-Blepharispermum clade"	<i>Loxothysanus</i> B. L. Rob., *Bahieae, *Bahiinae
<i>Blepharizonia</i> (A. Gray) Greene, Madieae, Madiinae	<i>Lycapsus</i> Phil., *Perityleae, *Lycapsinae
<i>Boeberastrum</i> (A. Gray) Rydb., Tageteae, Pectidinae	<i>Madia</i> Molina, Madieae, Madiinae
<i>Boeberoides</i> (DC.) Strother, Tageteae, Pectidinae	<i>Mallotopus</i> Franch. & Sav. (not recognized; synonym of <i>Arnica</i> )
<i>Calycadenia</i> DC., Madieae, Madiinae	<i>Marshallia</i> Schreb., Helenieae, Marshalliinae
<i>Carlquistia</i> B. G. Baldwin, Madieae, Madiinae	<i>Monolopia</i> DC., Madieae, Baeriinae
<i>Centromadia</i> Greene, Madieae, Madiinae	<i>Nicolletia</i> A. Gray, Tageteae, Pectidinae
<i>Chaenactis</i> DC., Chaenactideae, Chaenactidinae	<i>Orochaenactis</i> Coville, Chaenactideae, Chaenactidinae
<i>Chaetymenia</i> Hook. & Arn., Bahieae, Bahiinae ("Chaetymenia clade")	<i>Osmadenia</i> Nutt., Madieae, Madiinae
<i>Chamaechaenactis</i> Rydb., Bahieae, Bahiinae	<i>Oxypappus</i> Benth., *Tageteae, *Pectidinae
<i>Chrysactinia</i> A. Gray, Tageteae, Pectidinae	<i>Palafoxia</i> Lag., Bahieae, Bahiinae ("Bahia clade")
<i>Clappia</i> A. Gray, Tageteae, *Pectidinae	<i>Pectis</i> L., Tageteae, Pectidinae
<i>Comaclinium</i> Scheidw. & Planch., Tageteae, Pectidinae	<i>Pelucha</i> S. Watson, Helenieae, Psathyrotinae
<i>Constancea</i> B. G. Baldwin, Madieae, *Baeriinae	<i>Pericome</i> A. Gray, Perityleae, Peritylinae
<i>Correllia</i> A. M. Powell (not recognized; synonym of <i>Perityle</i> )	<i>Perityle</i> Benth., Perityleae, Peritylinae
<i>Coulterella</i> Vasey & Rose, *Tageteae, Varillinae	<i>Peucephyllum</i> A. Gray, Bahieae, Bahiinae ("Peucephyllum clade")
<i>Deinandra</i> Greene, Madieae, Madiinae	<i>Plateilema</i> (A. Gray) Cockerell, Helenieae, Plateileminae
<i>Dimeresia</i> A. Gray, Chaenactideae, Chaenactidinae	<i>Platyschkuhria</i> Rydb., Bahieae, Bahiinae ("Bahia clade")
<i>Dubautia</i> Gaudich., Madieae, Madiinae	<i>Porophyllum</i> Adans., Tageteae, Pectidinae
<i>Dugaldia</i> Cass. (not recognized; synonym of <i>Hymenoxys</i> )	<i>Psathyrotes</i> (Nutt.) A. Gray, Helenieae, Psathyrotinae
<i>Dysodiopsis</i> (A. Gray) Rydb., Tageteae, Pectidinae	<i>Psathyrotopsis</i> Rydb., Bahieae, Bahiinae ("Peucephyllum clade")
<i>Dyssodia</i> Cav., Tageteae, Pectidinae	<i>Pseudobahia</i> (A. Gray) Rydb., Madieae, Baeriinae
<i>Eatonella</i> A. Gray, Madieae, Hulseinae	<i>Pseudoclappia</i> Rydb., Tageteae, *Pectidinae
<i>Eriophyllum</i> Lag., Madieae, Baeriinae	<i>Psilostrophe</i> DC., Helenieae, Tetraneurinae
<i>Espejoa</i> DC., Bahieae, Bahiinae ("Chaetymenia clade")	<i>Raillardella</i> (A. Gray) Benth., Madieae, Madiinae
<i>Eutetras</i> A. Gray, Perityleae, Peritylinae	<i>Raillardiopsis</i> Rydb. (not recognized; synonym of <i>Anisocarpus</i> )
<i>Flaveria</i> Juss., Tageteae, Flaveriinae	<i>Sartwellia</i> A. Gray, Tageteae, Flaveriinae
<i>Florestina</i> Cass., Bahieae, Bahiinae ("Bahia clade")	<i>Schizotrichia</i> Benth., Tageteae, Pectidinae
<i>Gaillardia</i> Foug., Helenieae, Gaillardinae	<i>Schkuhria</i> Roth, Bahieae, Bahiinae ("Bahia clade")
<i>Galeana</i> La Llave & Lex., Incertae Sedis ("Villanova clade")	<i>Strotheria</i> B. L. Turner, Tageteae, Pectidinae
<i>Gymnolaena</i> (DC.) Rydb. Tageteae, Pectidinae	<i>Syntrichopappus</i> A. Gray, Madieae, Baeriinae
<i>Haploësthes</i> A. Gray, Tageteae, Flaveriinae	<i>Tagetes</i> L., Tageteae, Pectidinae
<i>Harmonia</i> B. G. Baldwin, Madieae, Madiinae	<i>Tetraneuris</i> Greene, Helenieae, Tetraneurinae
<i>Harnackia</i> Urb., Tageteae, Pectidinae	<i>Thymophylla</i> Lag., Tageteae, Pectidinae
<i>Helenium</i> L., Helenieae, Gaillardinae	<i>Thymopsis</i> Benth., *Bahieae, *Bahiinae

TABLE 3. Continued.

<i>Trichocoryne</i> S. F. Blake, Heliantheae, Incertae Sedis	<i>Villanova</i> Lag., Incertae Sedis ("Villanova clade")
<i>Trichoptilium</i> A. Gray, Helenieae, Psathyrotinae	<i>Vilobia</i> Strother, Tageteae, Pectidinae
<i>Urbinnella</i> Greenm., Tageteae, Pectidinae	<i>Welwitschiella</i> O. Hoffm., Incertae Sedis
<i>Varilla</i> A. Gray, *Tageteae, Varillinae	<i>Whitneya</i> A. Gray (not recognized; synonym of <i>Arnica</i> )
<i>Venegasia</i> DC., Madieae, Venegasiinae	<i>Wilkesia</i> A. Gray, Madieae, Madiinae

eopsidinae appear to be the result of homoplasy, as suggested by Robinson (1981), and do not diagnose a close relationship between the two groups.

Howell's (1942) hypothesis on relationships of *Baeriopsis*, a monotype endemic to Guadalupe Island, Mexico (also see Moran 1996), is upheld by ITS evidence (Figs. 1B, 2) for lineages comprising (1) *Amblyopappus* and *Baeriopsis*, (2) Clade 1 plus *Lasthenia*, and, in archetype trees (Fig. 2), (3) Clade 2 plus *Eriophyllum* s.l. (minus *Constancea*), *Pseudobahia*, and *Syntrichopappus*. In his description of *Baeriopsis*, Howell (1942) indicated that capitular characteristics "seem to relate the plant to *Amblyopappus*" and that from "*Baeria* (= *Lasthenia*), our plant seems further removed . . . and yet further from . . . *Eriophyllum*," in complete agreement with the ITS results. *Amblyopappus*, a monospecific genus of diminutive annuals, and *Baeriopsis*, a subshrub, are both indigenous to Guadalupe Island; *Amblyopappus* also occurs in coastal habitats in California, Baja California, Peru, and Chile. *Amblyopappus* and *Baeriopsis* share a common chromosome number ( $2n = 8$  II) with some members of *Lasthenia*. The ITS clade corresponding to the three genera affirms Raven and Kyhos's (1961) suggestion that  $x = 8$  may be the base chromosome number of a group comprising *Amblyopappus*, *Baeriopsis*, and *Lasthenia* and upholds Ornduff's (1966) conclusion that  $x = 8$  is the probable base chromosome number in *Lasthenia*, a genus noted for dysploidy and polyploidy (Fig. 11).

ITS evidence of relationships in the clade comprising *Eriophyllum* s.l., *Pseudobahia*, and *Syntrichopappus* (Figs. 1B, 2; Baldwin and Wessa, unpubl.) leads us to conclude that perennial members of *Eriophyllum* (excluding *Constancea*) are more closely related to *Pseudobahia* (an annual, epappose group) than to annuals traditionally included in *Eriophyllum* (and *Syntrichopappus*). The convoluted taxonomic history of members of *Pseudobahia* (reviewed by Carlquist 1956), once placed in *Eriophyllum* and *Monolopia*, is indicative of confusion surrounding their relationships. Based on the taxon sampling to date, a base chromosome number of  $x = 8$  appears most likely for the clade encompassing *Eriophyllum* s.s. (i.e., the perennial members of *Eriophyllum* minus *Constancea*) and *Pseudobahia* (Fig. 11); *P. peirsonii* and the diploid perennials in *Eriophyllum* s.s. have  $2n = 8$  II. The chromosome numbers  $2n = 3$  II (in *P. heermanni*) and  $2n = 4$  II (in *P. bahiifolia*) probably reflect dysploid changes from  $x = 8$ .

Robust placement of the monospecific *Lembertia* (here treated as *Monolopia congdonii*) with *Monolopia*, and of *Eatonella* s.s. with *Hulsea* (see below), in the ITS trees (Figs. 1B, 2) adds strength to Johnson's (1978) argument for dissociation of *Eatonella* s.l. [i.e., *E. (Monolopia) congdonii* and *E. nivea*]. *Eatonella* s.l. is anomalous from a chromosomal perspective, with  $2n = 19$  II in *E. nivea* and  $2n = 10$  II or  $11$  II in *E. (Monolopia) congdonii*. Positions of the two species in the ITS trees are consistent with chromosome numbers (Fig. 11): *Hulsea*, like *Eatonella* s.s. (i.e., *E. nivea*), has  $2n = 19$  II; *Monolopia* in the old sense, with  $2n = 10$  II,  $12$  II, and  $13$  II, encompasses the chromosome numbers reported from *M. congdonii*. *Eatonella nivea* and *M. congdonii* are both diminutive annuals with woolly foliage and strikingly similar fruit and pappus morphology. Vestiture, fruit, and pappus characteristics of *Hulsea* are also highly similar to those of *Eatonella* s.s. *Monolopia congdonii* and other members of *Monolopia* share a suite of unusual morphological characteristics, including an appendage of tissue opposite the ray-corolla lamina, as noted by Johnson (1978; see also Baldwin 1999a). Ecologically, the two pairs of genera are distinct. *Monolopia congdonii* and other monolopias are all vernal ephemerals that occur at low elevations, mostly in summer-dry grassland, chaparral, or woodland habitats of the California Floristic Province; *Eatonella* s.s. and *Hulsea* are mostly summer-flowering taxa of mid- to high-elevation habitats in western North America. Based on the data presented here and additional evidence (Baldwin 1999a), *Monolopia* is paraphyletic without inclusion of *Monolopia congdonii*.

**SUBTRIBE CHAENACTIDINAE.** Members of Chaenactidinae sensu Robinson (1981) fall into three paraphyletic groups and one monophyletic group in the ITS trees.

**Chaenactidinae Group 1.** The paraphyletic ITS group comprising *Arnica* (including *Mallotopus* and *Whitneya*), *Eatonella* s.s. (i.e., *E. nivea*), *Hulsea*, and *Venegasia* (Fig. 2) does not conform closely with a previously recognized taxon, but is united by a shared base chromosome number ( $x = 19$ ; also see Baldwin and Wessa 2000b). The group constitutes a clade with inclusion of the tarweeds and silverswords (Madiinae), none of which has a reported chromosome number of  $n = 19$  or multiples thereof. The close relationship between *Arnica* and *Whitneya* (here treated as *Arnica dealbata*) was suggested by Ornduff et al. (1967) and sub-

sequent authors (Turner and Powell 1977; Nordenstam 1977). Ornduff et al. (1967) also suggested a close relationship between *Arnica* and *Hulsea* based on a shared base chromosome number and other, unstated similarities. The monospecific genus *Venegasia* has been of uncertain relationship within Compositae (see Turner and Zippin 1992); Robinson (1981) associated the genus with the same subtribe as *Arnica*, *Hulsea*, and *Whitneya* and noted it as "singularly distinctive" for having stalked glands on the staminal filaments. The previously unproposed relationship between *Eatonella* s.s. and *Hulsea* is discussed above under Baeriinae.

Chaenactidinae Group 2. The largest clade of taxa referable to Chaenactidinae sensu Robinson (1981) corresponds to an expanded Bahiinae that combines elements of the circumscriptions of Bahiinae sensu Stuessy (1977) and Chaenactidinae sensu Robinson (1981) (Figs. 1A, 2). *Achyropappus*, *Amauriopsis*, *Bahia*, *Florestina*, *Hymenothrix*, *Palafoxia*, *Platyschukhria*, and *Schukhria* constitute one well-supported subclade [note: deep phylogenetic separation of two lineages of *Bahia* sensu Ellison (1964) in the ITS tree warrants provisional resurrection of *Amauriopsis* for *B. dissecta* until more detailed study of the *Bahia* alliance (also including *Achyropappus*, *Florestina*, *Hymenothrix*, *Palafoxia*, and *Platyschukhria*) is completed]. Also included in the Bahiinae clade are genera regarded as part of the same natural (but informal) group by Robinson (1981): *Espejoa* and *Hypericophyllum*. *Psathyrotopsis* and the monospecific genera *Bartlettia*, *Chamaechaenactis*, and *Peucephyllum* have been of uncertain relationship to other members of Chaenactidinae sensu Robinson (1981); the four genera appear to belong to the Bahiinae lineage, along with *Chaetymenia* and *Hymenopappus* (Figs. 1A, 2). In the ITS trees, the eastern Mexican genus *Loxothysanus* appears to be a basally divergent element of Bahiinae, but with only minimal support.

Robinson's (1981) dissociation of *Psathyrotopsis* from *Psathyrotes* s.s. and placement of *Psathyrotes* in Gaillardinae (= Helenieae s.s. here), with other Heliantheae s.l. having uncarbonized cypselae (except *Marshallia*), is affirmed by the ITS trees. A clade comprising members of *Psathyrotes* s.s. and *Trichoptilium* is placed with "core" Helenieae s.s. (see below and Figs. 1A, 2) and is apparently only distantly related to *Psathyrotopsis*. Striking pappus similarities between *Psathyrotes* s.s. and *Psathyrotopsis* appear to be homoplastic rather than indicative of a close relationship between Helenieae s.s. and Chaenactidinae (see Robinson 1981).

The anomalous *Peucephyllum*, here placed sister to *Psathyrotopsis* in Bahiinae (Heliantheae s.l.), also has been associated with tribes Astereae and Senecioneae (see Strother and Pilz 1975). *Peucephyllum* ( $x = 20$ ) and *Psathyrotopsis* ( $x = 19$ ) are similar in chromosomal, floral, and fruit characteristics and have been treated as congeners, in *Psathyrotes* s.l. (see Strother and Pilz

1975). Carlquist's (1962a) conclusion that the shrubby *Peucephyllum* possesses specialized wood conforms with the nested position of the taxon in the predominantly herbaceous Bahiinae; woodiness in *Peucephyllum* appears to have been derived from an herbaceous ancestral condition (Fig. 9).

The robust clade corresponding to *Chaetymenia*, *Espejoa*, and *Hypericophyllum* (Fig. 1A) unites taxa that were treated by Benthams (1873) as members of *Jaumea*. Robinson's (1981) narrow circumscription of Jaumeinae and placement of *Espejoa* and *Hypericophyllum* (*Chaetymenia* not treated) in one of his two informal groups within Chaenactidinae conforms with our ITS results; we conclude that a group encompassing *Jaumea* s.s. ( $x = 19$ ) and the robust,  $x = 9$  clade corresponding to *Chaetymenia*, *Espejoa*, and *Hypericophyllum* would be polyphyletic. The nested phylogenetic position of a member of *Hypericophyllum*, a tropical African genus, in the paraphyletic group comprising the Mexican/Central American genera *Chaetymenia* and *Espejoa* leads us to conclude that *Hypericophyllum* descended from an ancestor dispersed to Africa from subtropical or tropical North America. A vicariant relationship between the African and American plants is untenable given the evident youth of Compositae (Graham 1996) and the highly nested phylogenetic position of Heliantheae s.l. in the family (Kim and Jansen 1995).

Chaenactidinae Group 3. The position of *Dimeresia howellii* in a strongly-supported western North American clade with other discoid, herbaceous species in *Chaenactis* and *Orochaenactis* (Figs. 1B) appears to settle the long-standing uncertainty about relationships of the monospecific *Dimeresia*, a diminutive annual that is endemic to volcanic ash deposits of the northwestern Great Basin of California, Idaho, Nevada, and Oregon. *Dimeresia* has highly reduced heads of typically two florets and two phyllaries each, and a deciduous pappus of basally connate, plumose, subulate scales. The genus has been variously classified as a member of Inuleae, Senecioneae, and Heliantheae s.l. *Dimeresia* has been treated as a monospecific subtribe (Dimeresiinae H. Rob.) of Heliantheae and as one of six genera of uncertain subtribal position in Helenieae (Karis and Ryding 1994a). Karis's (1993a) morphology-based phylogeny of Heliantheae s.l. is congruent with the ITS tree in placement of *Dimeresia* as sister to *Chaenactis* (*Orochaenactis* was not sampled by Karis), as reflected by reinforced support for the *Dimeresia* + *Chaenactis* clade in trees based on combined ITS and morphological data (Fig. 3).

*Orochaenactis* has been of uncertain position in helenioid Heliantheae, but is strongly placed with *Chaenactis* and *Dimeresia* in the ITS trees (Fig. 1A). The only species, *O. thysanocarpa*, was originally described as a member of *Chaenactis*. *Orochaenactis* shares with *Dimeresia* the unusual characteristic of basally connate

pappus elements that are deciduous as a unit, a possible homology for pappi of the two genera. *Orochaenactis* is ecologically unusual and narrowly endemic—an annual confined to high-elevation habitats in the southern Sierra Nevada, California.

Dysploidy in the clade encompassing *Chaenactis*, *Dimeresia*, and *Orochaenactis* has been somewhat more extensive than in *Chaenactis* alone (Kyhos 1965, pers. comm.); the chromosome number of *Dimeresia* ( $2n = 7$  II) falls within the range of diploid numbers reported for *Chaenactis* ( $2n = 5, 6, 7$ , and  $8$  II), but *Orochaenactis* has a unique chromosome number in the group,  $2n = 9$  II. The monospecific *Chamaechaenactis* ( $2n = 16$  II), previously (and understandably) considered a good candidate for closest (polyploid) relative of *Chaenactis* (see Preece and Turner 1953), appears instead to be part of the Bahiinae clade (Figs. 1B, 2), in keeping with the strong medial thickening of the pappus scales.

Chaenactidinae Group 4. *Arnicastrum* and *Jamesianthus* are highly divergent in ITS sequences from other taxa in Chaenactidinae sensu Robinson (1981), including *Arnica*, but constitute a well-supported clade (Figs. 1A, 2). The resolved close relationship between the two genera corroborates a biogeographic connection between taxa of the southeastern United States (i.e., *Jamesianthus*, a monospecific genus) and the mountains of western and southern Mexico [Sierra Madre Occidental (*Arnicastrum glandulosum* Greenm., not sampled here) and Sierra Madre del Sur (*A. guerrerense*)] proposed by Sherff (1940) and seconded by Turner and Powell (1977). The *Arnicastrum*—*Jamesianthus* clade appears to be closely related to members of Pectidinae sensu Robinson (1981) and *Clappia* (Figs. 1A, 2).

The insertion mutations in ITS-1 of *Arnicastrum* and, to a lesser extent, *Jamesianthus* are exceptionally large for angiosperms in general. At 410 bp, ITS-1 in *Arnicastrum guerrerense* is, to our knowledge, the longest internal transcribed spacer reported in angiosperms.

SUBTRIBE GAILLARDIINAE S.L. (HELENIEAE S.S.). As noted above, a close relationship between Gaillardiiinae s.l. (hereafter, Helenieae s.s.) and members of Chaenactidinae sensu Robinson (1981) is not supported by the ITS trees (Figs. 1, 2). Chemical (sesquiterpene lactone) similarities between *Arnica* and Helenieae s.s. (see Bohlmann 1990) and morphological similarities between *Psathyrotes* and *Psathyrotopsis* (see Robinson 1981) are interpreted as homoplasious based on our results.

The position of *Marshallia*, *Psathyrotes* s.s., and *Trichoptilium* in the same ITS clade as members of “core” Helenieae s.s. (Figs. 1A, 2) upholds Karis and Ryding’s (1994a) circumscription of Gaillardiiinae (= Helenieae s.s. minus *Pelucha* here) to comprise all taxa of Heliantheae s.l. with uncarbonized cypselae [also see discussion above on Group II of Chaenactidinae sensu Robinson (1981)] and approximates Robinson’s (1981) ear-

lier placement of all Heliantheae taxa with uncarbonized fruits in two adjacent subtribes, Gaillardiiinae and Marshalliinae (together constituting Helenieae s.s. here—with the addition of *Pelucha*). Our results also echo robust placement of *Marshallia* with representatives of Helenieae s.s. in cpDNA trees (Watson et al. 1991; Kim and Jansen 1995; Jansen and Kim 1996) and in morphological cladograms (Karis 1993a, b, 1996; Karis and Ryding 1994a). *Marshallia* is of uncertain placement within Helenieae s.s. in the ITS trees (Figs. 1A, 2), a consequence, in part, of unstable root placement in Helenieae s.s.

The well-supported ITS clade comprising representatives of the discoid herbaceous genera *Psathyrotes* and *Trichoptilium* (Fig. 1A) affirms Gray’s (1855) original placement of *Trichoptilium*, a monospecific genus, in *Psathyrotes* and Bentham’s (1873) and Robinson’s (1981) placements of the two genera together, despite noted pappus differences and disparate chromosome numbers (*Psathyrotes* s.s.,  $2n = 17$  II; *Trichoptilium*,  $2n = 13$  II). Relationships of the two genera have been uncertain, as has been the circumscription of *Psathyrotes*, in part because of pappus similarities between *Psathyrotes* s.s. and *Psathyrotopsis* and between *Psathyrotes* s.l. and Senecioneae (see Strother and Pilz 1975; Robinson 1981). Placement of the shrubby *Pelucha* with the herbaceous *Psathyrotes* and *Trichoptilium* in the ITS trees conforms with vegetative and floral characteristics of the three genera and a common distribution in the deserts of southwestern North America (see Baldwin and Wessa 2000a). *Pelucha* was treated as a member of Inuleae s.l. or Plucheeae until Baldwin and Wessa (2000a) recognized the relationship of *Pelucha* with *Psathyrotes*, *Trichoptilium*, and other members of Helenieae s.s.

The well-supported clade comprising representatives of *Balduina*, *Gaillardia*, and *Helenium* s.s. (Fig. 1A) supports Bierner’s (1989) hypothesis from morphological, cytological, and chemical data that the three genera form a natural group to the exclusion of other genera of Helenieae s.s. Sesquiterpene lactone and flavonoid similarities among *Balduina*, *Gaillardia*, and *Helenium* led Parker and Jones (1975) to conclude similarly that the three genera are closely related. The ITS sister-group relationship between members of *Balduina* and *Gaillardia* upholds Rock’s (1957) placement of the two genera together in his synopsis of *Helenium* and related genera. We interpret the deeply-pitted receptacle with subulate projections seen in *Balduina* and *Gaillardia* as synapomorphic.

Our ITS results (Figs. 1A, 2) corroborate Bierner and Jansen’s (1998) conclusion from cpDNA restriction site data that *Hymenoxys* s.s. is more closely related to *Dugaldia* (= *Hymenoxys hoopesii*) and *Plummera* (= *Hymenoxys ambigens*) than to *Tetrameuris* (often included in *Hymenoxys*). The ITS evidence adds additional support to Bierner’s (1994) taxonomic transfers of *Dugaldia* and



*Plummera* to *Hymenoxys* based on morphological, chemical, and cytological evidence. The ITS trees also provide support for Bierner and Jansen's (1998) hypothesis that *Psilostrophe* is more closely related to *Hymenoxys* sensu Bierner and *Tetranneuris* than earlier suspected.

The ITS trees affirm that *Baileya* and *Psilostrophe*, once placed in a distinct subtribe, Riddelliinae A. Gray (with *Whitneya* = *Arnica dealbata*), are members of Gailardiinae s.l. (= Helenieae s.s. here), as concluded by Stuessy (1977) and Robinson (1981). Turner (1993) concluded that *Baileya* and *Psilostrophe* are probably sister-taxa based on shared chromosome number ( $2n = 16$  II) and chemical and ecological similarities. Bierner and Jansen's (1998) cpDNA analyses placed *Tetranneuris* closer to *Psilostrophe* than to *Hymenoxys* sensu Bierner (1994), with high (88%) bootstrap support (*Baileya* was not sampled). Similarly, the ITS trees (Figs. 1A, 2) place *Baileya* and *Psilostrophe* in a well-supported clade with *Hymenoxys* sensu Bierner and *Tetranneuris* [and *Amblyolepis*—not included in Bierner and Jansen's (1998) trees]. Papery, persistent ray corollas, although not uniformly present, may be synapomorphic for the clade encompassing *Amblyolepis*, *Baileya*, *Hymenoxys* sensu Bierner, *Psilostrophe*, and *Tetranneuris*. Turner's (1993) hypothesis of relationships within *Baileya* is upheld by the ITS results (Fig. 1A), with the small-headed *B. pauciflora* sister to the two larger-headed species, *B. multiradiata* and *B. pleniradiata*.

Relationships of the monospecific *Amblyolepis* have been confusing because of its unusual morphology and chemistry, but now appear to be resolved. Bierner (1990) suggested a possible close relationship between *Amblyolepis* and *Hymenoxys* based on chemical similarities and cpDNA results. The well-supported position of *Amblyolepis* as sister-group to a representative of *Tetranneuris* in the ITS trees (Fig. 1A) closely approximates Bierner's (1990) hypothesis on relationships of *Amblyolepis* and adds additional weight to the decision by Bierner (1994) and Bierner and Jansen (1998) to recognize *Tetranneuris* as a genus distinct from *Hymenoxys*, as hinted at by Strother (1966).

**SUBTRIBE HYMENOPAPPINAE.** The positions of *Hymenopappus* and (weakly) *Loxothysanus* as basally divergent lineages within an ITS clade corresponding to an expanded Bahiinae (Figs. 1A, 2) corroborate Stuessy's (1977) subtribal placement of the genera. *Hymenopappus* and the eastern Mexican genus *Loxothysanus* have been placed in a distinct subtribe, Hymenopappinae (Robinson 1981; Karis and Ryding 1994a), on the basis of fruit wall characters, but share pappus characteristics with Bahiinae. Representatives of the epappose, herbaceous genera *Galeana* and *Villanova*, from Mexico, Central America, and (in *Villanova*) South America, also treated as members of either Bahiinae (Stuessy 1977) or Hymenopappinae (Robinson 1981; Karis and

Ryding 1994a) constitute a (weak) clade of unstable placement in the ITS trees (Figs. 1B, 2).

Based on the ITS trees (Figs. 1A, 2), the monospecific *Trichocoryne*, tentatively placed in Hymenopappinae by Robinson (1981), appears to be part of Heliantheae s.s., consistent with black anthers in both groups. Although our sampling of Heliantheae s.s. was too limited to allow precise determination of the relationships of *Trichocoryne*, we conclude that the genus is an unusual example of an epaleate lineage that descended from paleate ancestors. An analysis of the position of *Trichocoryne* within an expanded sample of taxa in Heliantheae s.s. has led Urbatsch et al. (2000) to conclude that the genus is closely related to members of Zinninae.

**SUBTRIBE MADIINAE.** Madiinae sensu Carlquist (1959) is resolved as a well-supported monophyletic group in the ITS trees (Figs. 1B, 2; also see Baldwin and Wessa 2000b). As in trees from previous analyses (e.g., Baldwin et al. 1991; Baldwin and Robichaux 1995; Baldwin 1996), the monophyletic Hawaiian silversword alliance appears to have descended from the primarily-Californian tarweeds and belongs to the "Madiia lineage" (Baldwin 1996), i.e., *Madiia* and closely related genera (e.g., *Anisocarpus*, *Carlquistia*, *Hemizonella*, and *Kyhosia*; see Baldwin 1999b for revised taxonomy). In general, clades within Madiinae were poorly supported, a result we attribute in part to insufficient taxon sampling in the analyses presented here (Baldwin and Wessa, unpubl. data).

**SUBTRIBE PERITYLINAE.** Monophyly of a group corresponding to Peritylinae sensu Robinson (1981) and recognized informally by Powell (1968a, b) is well-supported by the ITS trees (Figs. 1B, 2). Within Peritylinae, we interpret the unusual "Perityle-type" layer of cypselar carbonization reported for all genera except *Eutetras* (Robinson 1981) as a likely synapomorphic state for a clade resolved here uniting *Amauria*, *Pericome*, and *Perityle* (Figs. 1B, 2). At a finer scale, the ITS data provide support for Powell's (1968a, 1973) hypotheses that (1) the relationship between *Perityle* and *Laphamia* A. Gray [treated here in *Perityle*, following Powell (1968a)] is closer than the relationship between either group and *Pericome*, (2) *Correllia*, *Laphamia*, and *Perityle* constitute a natural group, and (3) *Pericome* is more closely related to *Perityle* (including *Laphamia*) and, by extension, *Correllia* than to other members of Peritylinae.

Monophyly of *Perityle* without inclusion of the monospecific, annual genus *Correllia* is not supported; the clade comprising the sampled members of *Perityle* and *Correllia* is well supported from bootstrap analysis. The following new combination is made:

***Perityle montana*** (A. M. Powell) B. G. Baldwin, comb. Nov.—*Correllia montana* A. M. Powell, Brittonia 25: 116. 1973.—TYPE: MEXICO. Chihuahua: "in mats

on boulders, on summit of Sierra Mohinora," 16–17 Oct 1959, D. S. Correll & H. S. Gentry 23185 (holotype: TEX).

Within *Perityle*, two well-supported clades are resolved—one uniting the two sampled members of *Perityle* sect. *Laphamia* (A. Gray) A. M. Powell (*P. cochisensis* and *P. megacephala*) and the other uniting the two sampled members of Powell's (1974) "white-flowered series" of *P.* sect. *Perityle* (*P. emoryi* and *P. incana*). The large, shrubby, Guadalupe Island endemic *P. incana* has been treated in a monotypic genus, *Nesothamnus* (A. Gray) Rydb., and was regarded by Powell (1974) as morphologically anomalous in *Perityle*. Our data corroborate Powell's (1974) conclusion that *P. incana* belongs in *P.* sect. *Perityle*.

SUBTRIBES CLAPPIINAE, FLAVERIINAE, JAUMEINAE, AND PECTIDINAE SENSU ROBINSON. A well-supported ITS clade comprising representatives of *Flaveria*, *Haploësthes*, and *Sartwellia* corresponds to Flaveriinae sensu Turner and Powell (1977), Powell (1978), and Robinson (1981) (Figs. 1A, 2). A broader circumscription of Flaveriinae to include *Clappia*, *Coulterella*, *Jaumea*, *Pseudoclappia*, and *Varilla* (Bremer 1987) is not a monophyletic group based on the ITS trees. The weakly-supported sister-group relationship between representatives of Flaveriinae sensu Turner and Powell (1977) and *Jaumea carnos*a (Jaumeinae) in trees based on ITS, ITS + *ndhF* and ITS + *ndhF* + morphology (Figs. 1A, 2) comes closest to reflecting previous treatments. *Clappia* and *Pseudoclappia* (Clappiinae H. Rob.) do not constitute a clade in the ITS trees, even if areas of equivocal sequence alignment are resolved to favor their union.

Sampled genera of Pectidinae sensu Robinson (1981) do not constitute a clade in the ITS trees (Figs. 1A, 2); a weakly-supported clade consisting of *Clappia* and *Arnicastrum* + *Jamesianthus* is nested within the group. In the ITS + morphology trees (Fig. 3), *Clappia* is also weakly nested within Pectidinae (*Arnicastrum* and *Jamesianthus* were not included in the ITS + morphology analyses). Although *Clappia* has been considered a member of Pectidinae (Smith and Turner 1975), all recent taxonomic treatments of subfamily Asteroideae have placed *Clappia* (and *Arnicastrum* and *Jamesianthus*) in other subtribes. Relationships in Pectidinae sensu Robinson (1981) based on ITS, cpDNA, and morphological data were addressed by Loockerman (1996), whose results from a much broader sampling of genera in the group are consistent with the ITS topologies (Figs. 1A, 2) if *Arnicastrum*, *Clappia*, and *Jamesianthus* (not sampled by Loockerman) are removed from consideration. Additional data are needed to discern whether Pectidinae sensu Robinson (1981) is truly monophyletic.

The weakly-supported ITS clade uniting *Clappia* with *Arnicastrum* and *Jamesianthus* warrants further

consideration as an hypothesis of relationship. *Clappia*, *Arnicastrum*, and *Jamesianthus* were placed together in Rydberg's (1914) Jaumeinae based on their graduated, multiseriate involucre of broad, rounded phyllaries. The three genera also share similar pappi of bristles and long-pedunculate, large, and usually solitary capitulae. *Clappia* and *Jamesianthus* share  $n = 16$  (chromosome counts have not been reported for *Arnicastrum*), a possibly synapomorphic chromosome number not otherwise known from Flaveriinae sensu Bremer (1987) [= Flaveriinae sensu Turner and Powell (1977) + *Clappia*, *Coulterella*, *Jaumea*, *Pseudoclappia*, and *Varilla*] and rare in Pectidinae sensu Robinson (1981).

A weakly-supported clade including Flaveriinae sensu Turner and Powell (1977), *Arnicastrum*, *Clappia*, *Jamesianthus*, *Jaumea*, *Oxypappus*, *Pseudoclappia*, and Pectidinae sensu Robinson (1981) (Figs. 1, 2) corroborates cpDNA and morphological evidence (shared corolla and anther characteristics) for a close relationship between Flaveriinae s.l. and Pectidinae sensu Robinson (1981) (Kim et al. 1992; Karis and Ryding 1994a). *Oxypappus*, a monospecific genus (see Turner 1966), has been variously treated within helenioid Heliantheae (e.g., in Baeriinae or Peritylinae) and represents a highly-divergent lineage in the ITS trees. The sole species, *Oxypappus scaber*, has been treated as a member of *Pectis*, *P. seemannii* Sch. Bip. (and as a member of the *Astereae* genera *Chrysopsis* (Nutt.) Nutt. & Elliott and *Pentachaeta* Nutt.). *Varilla*, a member of Flaveriinae s.l., is placed with *Coulterella* in our trees, not with members of Flaveriinae sensu Turner and Powell (1977), *Arnicastrum*, *Clappia*, *Jamesianthus*, *Jaumea*, Pectidinae sensu Robinson (1981), *Oxypappus*, and *Pseudoclappia* (Figs. 1A, 2).

SUBTRIBES COULTERELLINAE AND VARILLINAE. *Coulterella*, a monospecific genus of succulent-leaved shrubs with discoid, often single-flowered heads, appears to be the sister-group of *Varilla* based on a moderately robust clade in the archetype ITS trees (Fig. 2) and ITS + morphology trees (Fig. 3). Taxonomically, *Coulterella* has been problematical: Robinson (1981) erected a monospecific subtribe for the genus and Karis and Ryding (1994a) placed *Coulterella* in their list of (six) genera of uncertain subtribal placement in Heleniinae s.l. Like *Coulterella*, *Varilla* is a genus of shrubs with discoid heads (see Turner 1990) and a chromosome number of  $2n = 18$  II. One of the two species of *Varilla* (*V. texana*) is succulent-leaved, as is *Coulterella*. The two genera occur on opposite sides of the Gulf of California at similar latitudes (*Coulterella* near La Paz, Baja California, and on nearby islands; *Varilla* from interior mainland Mexico, to southern Texas), and both occur at least in part on saline soils. Divergence of the two groups is conceivably the result of vicariance following opening of the Gulf of California, ca. 4.5 Ma

(Atwater 1970) and subsequent geological and climatic change.

**Higher-Level Relationships Within *Heliantheae* s.l. + *Eupatorieae*.** HELENIEAE S.S. SISTER TO OTHER IN-GROUP TAXA. The sister-group relationship between Helenieae s.s. (i.e., Gaillardiiinae s.l., including *Marshallia* and *Pelucha*) and the rest of the ingroup taxa resolved in the ITS trees (Figs. 1, 2) and combined data trees (Figs. 3–5) corroborates the placement of representatives of Helenieae s.s. in Kim and Jansen's (1995) *ndhF* trees and Kim et al.'s unpubl. cpDNA restriction site trees (see Jansen and Kim 1996). Addition of morphological or *ndhF* data (Figs. 3–5) enhanced support for a basally divergent Helenieae s.s. compared to results of analyses of ITS data alone for the same sets of taxa.

MADIINAE,  $x = 19$  ("ARNICOID") TAXA, AND BAERIINAE. Robust support for a sister-group relationship between *Arnica* (including *Mallotopus* and *Whitneya*) and Madiinae was obtained from all analyses that included both groups (Figs. 1B, 2, and 3; also see Baldwin and Wessa 2000b). Analyses of the original and archetype ITS matrices resolved a larger, weakly-supported clade comprising Madiinae and the  $x = 19$  genera *Arnica*, *Eatonella*, *Hulsea*, and *Venegasia* (Figs. 1B, 2). The relationships of *Arnica* have been controversial (see Nordenstam 1977; Turner and Powell 1977; Robinson 1981), in part because of morphological (e.g., pappus) similarities to *Doronicum* L. and other members of Senecioneae, and chemical (sesquiterpene lactone) similarities with Helenieae s.s. Robinson's (1981) placement of *Arnica* in Heliantheae s.l.—in closer taxonomic association with *Hulsea* and *Venegasia* (all in his subtribe Chaenactidinae) than with Helenieae s.s.—comes close to matching our results. The nested position of Madiinae within a helenioid lineage, rather than with other paleate Heliantheae, confirms Carlquist's (1958) earlier suggestion about possible relationships of the tarweeds (see Baldwin and Wessa 2000b).

Most analyses of subsets of taxa (results not shown) provided considerable support (>70% bootstrap) for a still larger group comprising Baeriinae, Madiinae, and the  $x = 19$  genera *Arnica*, *Eatonella*, *Hulsea*, and *Venegasia*, a clade also resolved in analyses of the archetype ITS matrix (Fig. 2). Morphologically, *Constancea* (*Eriophyllum*) *nevini* conforms rather closely with Baeriinae, where traditionally placed, but chromosomally (and to some extent morphologically) fits well with the other  $x = 19$  genera (see above discussion of subtribe Baeriinae; Baldwin 2000). Geographically, the clade corresponding to Baeriinae, Madiinae, and the  $x = 19$  taxa is cohesive—most members are found in far western North America, especially in the California Floristic Province (CFP), except the Hawaiian silversword alliance (*Argyroxiphium*, *Dubautia*, *Wilkesia*; Madiinae).

Based on phylogenetic and cytogenetic data, the silversword alliance evidently descended from an ancestral tarweed species of the "*Madia*" lineage (Baldwin 1996) dispersed from western North America to the Hawaiian archipelago (Fig. 1B; see Baldwin et al. 1991; Baldwin 1992; Carr et al. 1996; Baldwin and Sanderson 1998; Barrier et al. 1999).

FLAVERIINAE S.L. AND PECTIDINAE. As noted above, members of Pectidinae sensu Robinson (1981) are resolved in ITS trees as part of a clade including *Clappia*, *Arnicastrum*, and *Jamesianthus* (Figs. 1A, 2). A larger clade including the above taxa, most members of Flaveriinae s.l., and *Oxypappus* was evident in results from analyses of the original ITS matrix (Fig. 1A) and the archetype ITS matrix (Fig. 2). Combined analysis of ITS and morphological data yielded a congruent (but not fully resolved) strict consensus tree (Fig. 3), with *Flaveria* and *Haploësthes* sister to Pectidinae sensu Robinson (1981) + *Clappia* in only a subset of trees. Simultaneous analyses of ITS and *ndhF* data and all three data sets combined do not yield trees with Flaveriinae and Pectidinae resolved as sister groups, a possible artifact of insufficient taxon sampling—analyses of ITS data alone with the same small sets of highly-divergent taxa also fail to resolve a Flaveriinae + Pectidinae clade. *Coulterella* and *Varilla*, each constituting a subtribe in Robinson's (1981) treatment of Heliantheae and included in Flaveriinae by Bremer (1987), are, as noted above, sister groups in ITS trees and ITS + morphology trees. *Coulterella* and *Varilla* are placed outside the clade(s) including other taxa of Flaveriinae s.l. and Pectidinae in the ITS trees (Figs. 1A, 2), but appear to be closely related to Flaveriinae s.l. and Pectidinae on the basis of floral and cypselae characteristics (see Robinson 1981) and cpDNA evidence (Panero, Baldwin, Schilling, and Clevinger, unpubl. data).

EUPATORIEAE. Our analyses corroborate previous molecular evidence for descent of the highly-diverse tribe Eupatorieae (ca. 2,400 species; Bremer et al. 1994) from within the lineage encompassing Heliantheae s.l. (see Jansen and Kim 1996). A clade corresponding to Eupatorieae is nested among lineages of helenioid Heliantheae in the ITS trees (Figs. 1B, 2) and the combined-data trees (Figs. 3–5). In trees based on the original ITS matrix, Eupatorieae is part of a weakly-supported clade that also encompasses Baeriinae, Madiinae, and the  $x = 19$  "arnicoid" taxa (Fig. 1B). Following compartmentalization, ITS analyses placed Eupatorieae in a larger clade including Bahiinae, Peritylinae, and the "*Villanova* clade," in addition to Baeriinae, Madiinae, and the  $x = 19$  "arnicoid" taxa (Fig. 2).

We explored the possibility that subanalyses of the ITS sequence data might allow us to make more robust (albeit more limited) hypotheses about the relationships of Eupatorieae than are possible from analyses



that include representatives of all lineages sampled in Figs. 1 and 2. Parsimony analyses of small data sets comprising multiple taxa representative of various well-supported groups in the taxon-comprehensive analyses (Figs. 1, 2) yielded results congruent with placement of Eupatorieae in Figs. 1B, 2, i.e., the Eupatorieae clade was usually placed sister to (1) a clade comprising Baeriinae, Madiinae, and the  $x = 19$  "arnicoid" taxa or (2) Peritylinae (results not shown). A close relationship of Eupatorieae ( $x = \text{ca. } 17$ ; Watanabe et al. 1995; Schilling et al. 1999; Ito et al. 2000) to either of the two groups is easily reconciled with putative base chromosome numbers estimated here of  $x = 19$  for the clade corresponding to Baeriinae, Madiinae, and the  $x = 19$  "arnicoid" taxa, i.e., Madiaceae (also see Baldwin and Wessa 2000b), and of  $x = 18$  for Peritylinae [in agreement with Robinson et al. (1981)].

Studies based on cpDNA sequencing are underway to test further whether Eupatorieae is indeed most closely related to relatively depauperate, epaleate lineages and may have undergone accelerated diversification (Panero, Baldwin, Schilling, and Clevinger, unpubl. data).

**Broad-scale Evolutionary and Biogeographic Hypotheses.** Parsimony mapping of character states on the ITS trees (Figs. 6–10) provides new perspectives, presented below, on evolution of paleae, pappus, life-form, and chromosome numbers in the clade corresponding to Heliantheae s.l. + Eupatorieae.

**EVOLUTION OF PALEAE.** Based on our sampling of taxa, paleae (receptacular bracts) originated separately in the ancestors of Heliantheae s.s., Madiinae, and *Marshallia* [Fig. 6; see Robinson (1981), Stuessy and Spooner (1988), and Karis and Ryding (1994a) for occurrence of paleae in helenioid Heliantheae]. If *Lycapsus* (not sampled) belongs with Peritylinae (Robinson 1981; Karis 1993a), then an additional origin of paleae must be hypothesized, as for *Chaenactis carphoclinia* A. Gray, *Hymenopappus newberryi* I. M. Johnst. (Turner 1956), some members of *Amblyolepis* and *Helenium* (Karis and Ryding 1994a), and various Eupatorieae (King and Robinson 1987). In Madiinae, paleae among the inner disc florets appear to have originated repeatedly (e.g., in *Blepharipappus*, *Dubautia*, *Hemizonia*, and *Layia*; not shown in Fig. 6). In Heliantheae s.l., we conclude that loss of paleae has occurred in *Trichocoryne* (Fig. 6) and probably in various other, unsampled members of Heliantheae s.s. (Robinson 1981). In summary, we interpret absence of paleae in the vast majority of taxa of Heliantheae s.l. and Eupatorieae as plesiomorphic; loss of paleae appears to have occurred rarely. Whether losses or gains of paleae represent merely changes at the level of gene expression or more fundamental homoplasy remains in question.

**PAPPUS EVOLUTION.** Our results lead us to suggest that pappus evolution in Heliantheae s.l. has been

highly dynamic, with repeated evolution of bristles or bristle-like subulate elements from a putatively plesiomorphic state of free scales (Fig. 7). We concur with Robinson (1981) that the great importance given to pappus type in assigning taxa to tribes or subtribes in some earlier classifications appears to have been in part misguided. Bristles, in particular, have been generally regarded to be too conservative evolutionarily. Examples of helenioid taxa that have been misplaced at the tribal or subtribal level based in part on possession of pappi of bristles or bristle-like subulate scales include *Arnica*, *Arnicastrum*, *Bartlettia*, *Dimeresia*, *Haploësthes*, *Jamesianthus*, *Pelucha*, *Peucephyllum*, *Psathyrotes*, *Psathyrotopsis*, *Pseudoclappia*, *Raillardella*, and *Syntrichopappus*.

**LIFE-FORM EVOLUTION.** Based on the ITS trees, the annual habit in lineages of helenioid Heliantheae appears to have usually evolved from an ancestral perennial condition (Fig. 8). Evolution of perennials from an ancestral annual state also appears to have occurred in helenioid Heliantheae, e.g., in Baeriinae (*Baeriopsis* and *Eriophyllum* s.s.), though less frequently than the shift from perennial to annual habit (Fig. 8).

We conclude that evolution of above-ground woodiness has occurred repeatedly in helenioid Heliantheae, mostly from an ancestral perennial herbaceous state (Fig. 9). Examples include *Chaetymenia* (Bahiinae), *Constancea* (*Eriophyllum*) *nevinii* (Baeriinae), *Peucephyllum* (Bahiinae), and *Venegasia* (Venegasiinae). The putative shift to a woody growth form is associated with island endemism in the Hawaiian silversword alliance (*Argyroxiphium*, *Dubautia*, *Wilkesia*) (not shown in Fig. 9; see Fig. 1B), *Baeriopsis*, and *Constancea* (*Eriophyllum*) *nevinii*. Origin of woodiness in insular Compositae is well-documented from phylogenetic studies (see Baldwin et al. 1998; Panero et al. 1999a). Our results provide additional examples consistent with Carlquist's (1962b, 1995) conclusion that evolution of woodiness on islands is a widespread phenomenon.

**CHROMOSOME NUMBER EVOLUTION.** Based on our estimate of chromosome number evolution (Fig. 10), the ancestral base chromosome number in the clade comprising Heliantheae s.l. + Eupatorieae (exclusive of the *Athroisma*—*Blepharispermum* clade and *Anisopappus*—not sampled here; see Eldenäs et al. 1999) is  $x = 18$ , within the range of  $x = 17$ – $19$  hypothesized earlier by Smith (1975) and Robinson et al. (1981) for Heliantheae s.l. and by Watanabe et al. (1995), Schilling et al. (1999), and Ito et al. (2000) for Eupatorieae. Estimated base chromosome numbers for helenioid tribes recognized here include  $x = 19$  for Madiaceae;  $x = 18$  for Helenieae s.s., Perityleae, and Tageteae; and  $x = 17$  for Bahieae. Evidence for extensive gene duplications in some taxa with high and low base chromosome numbers in Heliantheae s.l. and Eupatorieae [e.g., *Helianthus* ( $x = 17$ ); Berry et al. (1995); Gentzbittel et al.



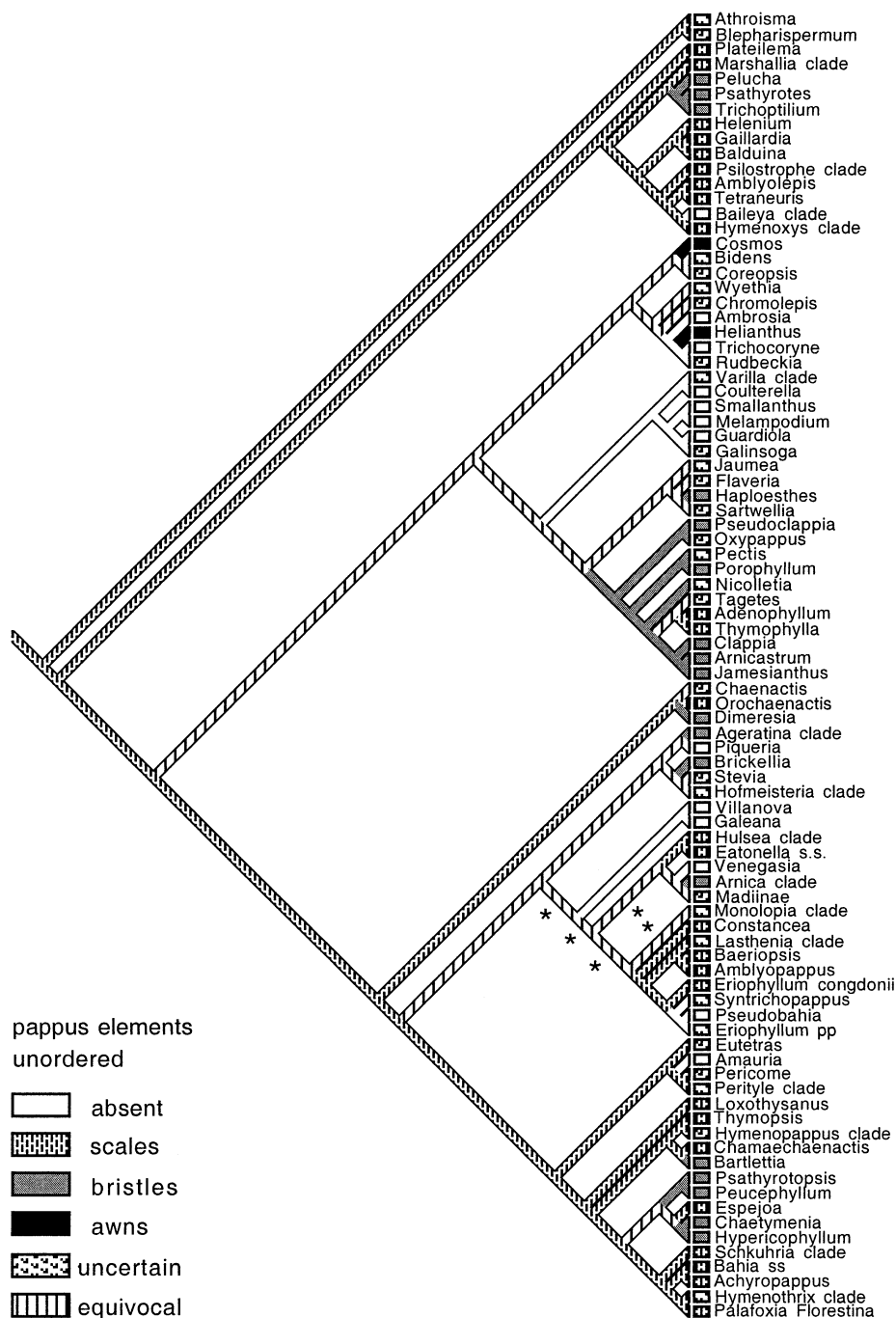


FIG. 7. Pappus evolution. For simplicity of mapping character states, bristles, as scored here, include bristle-like subulate scales (often treated as bristles by synantherologists). In the other minimum-length tree, the branches indicated by asterisks are estimated as unequivocal for scales.

(1995); *Eupatorium* ( $x = 10$ ); Yahara et al. (1989)] may conceivably reflect a paleopolyploid basis for  $x = 18$  in the clade encompassing Heliantheae s.l. + Eupatorieae. Relatively low base chromosome numbers in the closest relatives of Heliantheae s.l. + Eupatorieae, i.e.,

the *Athroisma-Blepharispermum* clade ( $x = 10$ ) and *Anisopappus* ( $x = 7$ ), are consistent with a hypothesis of polyploidy arising at the base of the Heliantheae s.l. + Eupatorieae clade following divergence of the lineage from common ancestors with *Athroisma-Blepharisper-*

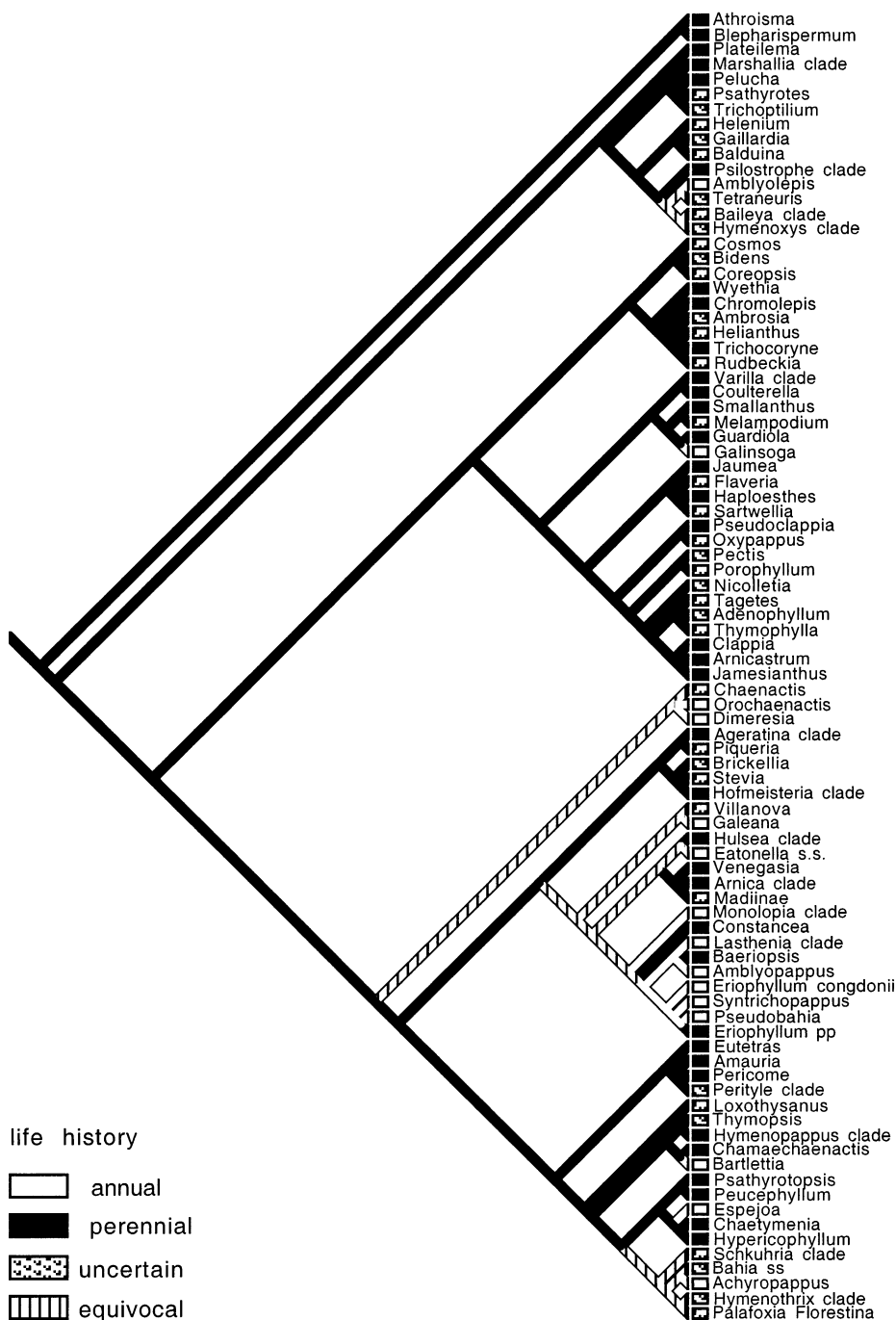


FIG. 8. Life-history evolution. The perennial state includes herbaceous and woody perennials. Biennial life history is not shown; none of the terminal taxa is exclusively biennial.

*mum* and *Anisopappus*. We note, however, that minor changes in topology of the ITS tree can result in an equivocal reconstruction of base chromosome number in Heliantheae s.l. + Eupatorieae, at either  $x = 9$  or 18 [a result that, in part, reflects the low base chromosome number of  $x = 9$  in *Marshallia* (Helenieae s.s.)].

Dysploid reduction in chromosome number from the putatively high base number in Heliantheae s.l. + Eupatorieae to typical diploid levels appears to have occurred repeatedly in different sublineages, especially in groups rich in annuals, e.g., Baeriinae, Chaenactidinae s.s., and Madiinae, as suggested by Robinson

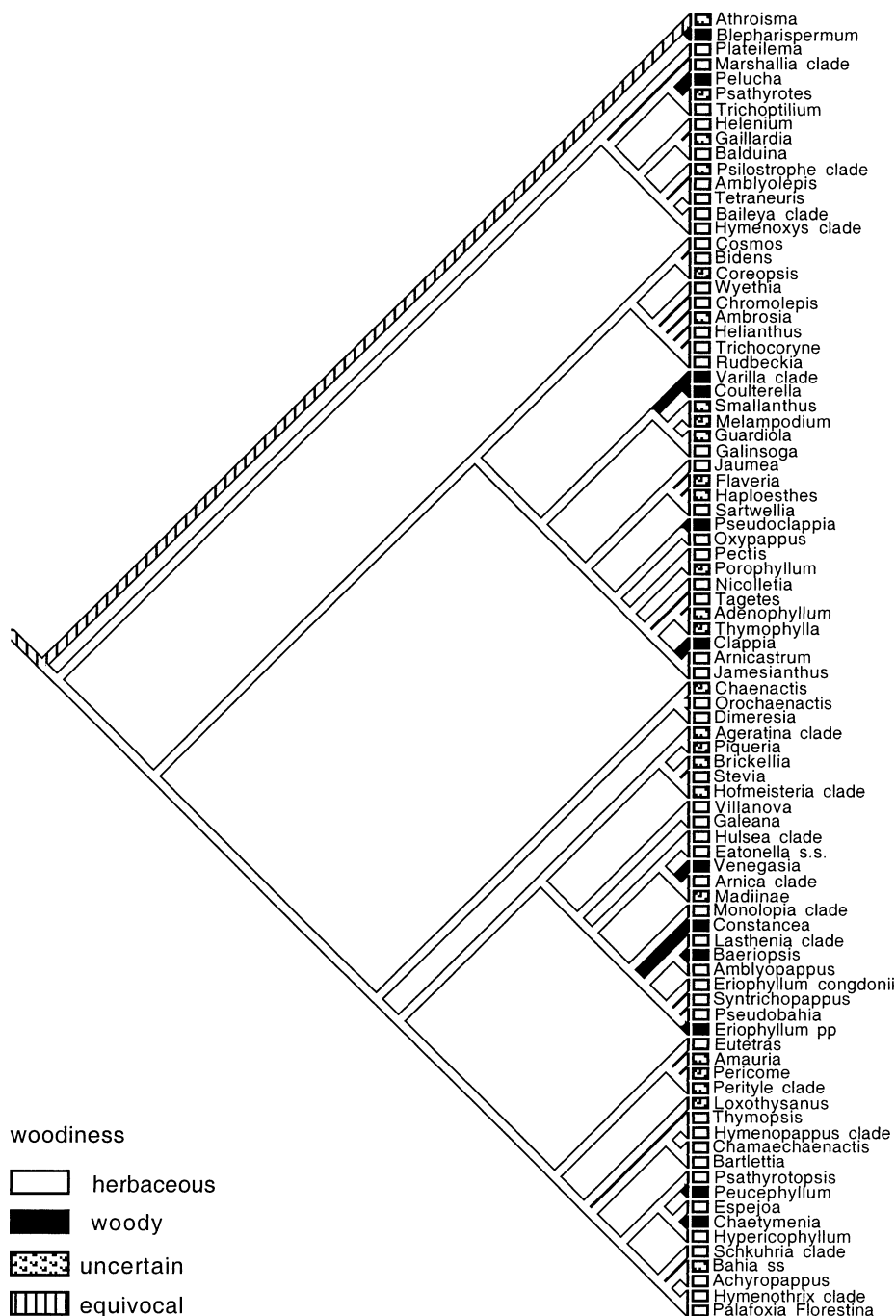


FIG. 9. Evolution of above-ground woodiness.

et al. (1981) for Heliantheae s.l. and by Stebbins (1950) for annuals in general. Subsequent polyploidy has secondarily elevated chromosome numbers in groups wherein low base numbers apparently resulted from ancestral dysploidy (e.g., in *Chaenactis*, *Eriophyllum* s.s., *Layia*, *Madia*, and the Hawaiian silversword alliance).

Parsimony mapping of habit and chromosome number change on the ITS trees reveals an association between polyploidy and a shift in life-history from herbaceous to woody habit (results not shown) in the ancestors of the silversword alliance (*Argyroxiphium*, *Dubautia*, and *Wilkesia*) and of *Eriophyllum* s.s. (*E. lanatum* and *E. stae-*

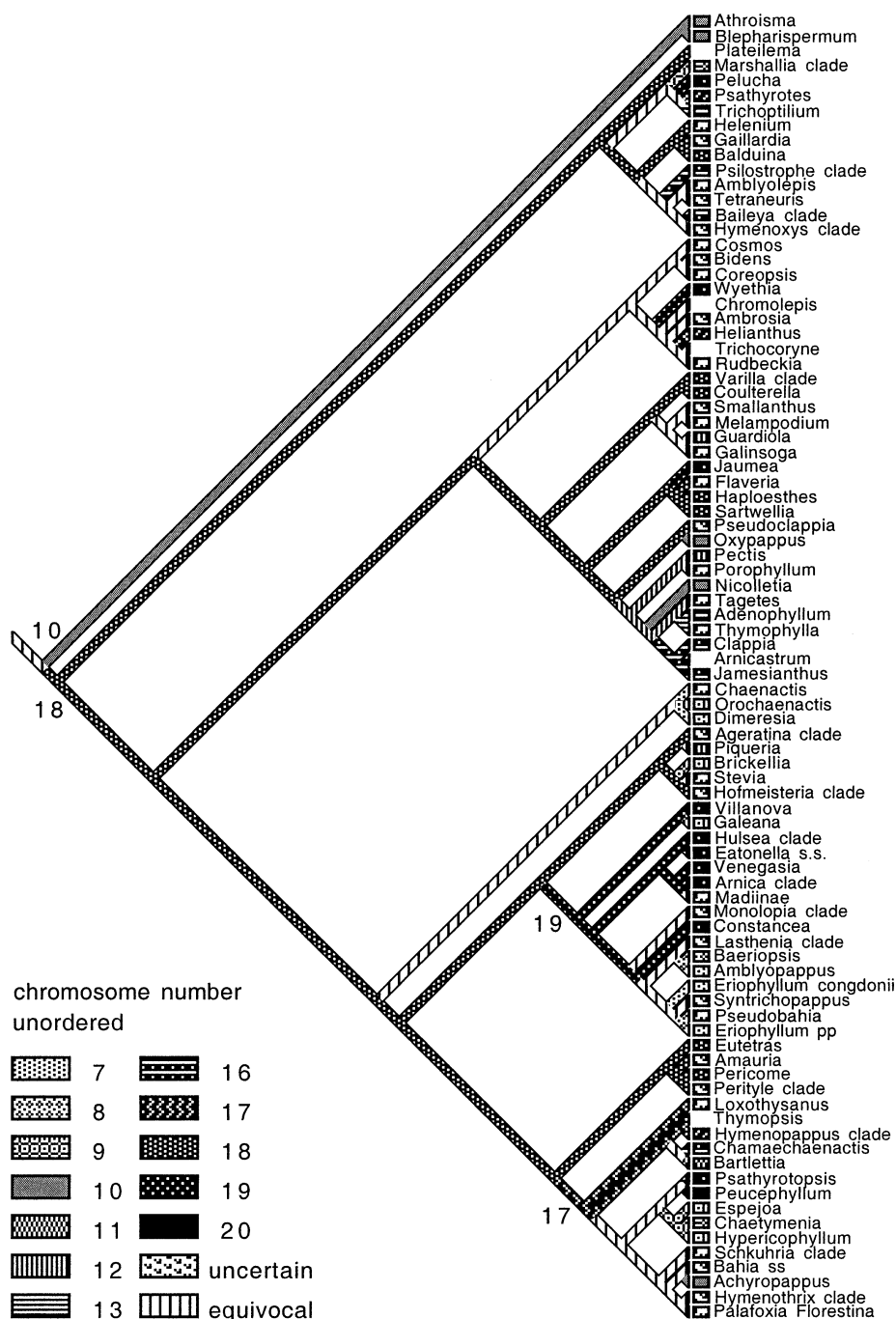


FIG. 10. Chromosome-number evolution (numbers used are from published reports, mostly of meiotic counts, and equate to gametophytic chromosome numbers). For clarity of presentation, the legend includes only those chromosome numbers that are estimated as unequivocal for at least one branch of the tree. Chromosome numbers indicated alongside branches highlight major lineages discussed in the text. Chromosome numbers are unavailable for *Arnicastrum*, *Chromolepis*, *Plateilema*, *Thymopsis*, and *Trichocoryne*.



*chadifolium* sampled here). In *Eriophyllum* s.s., polyploidy must postdate the origin of woodiness (both diploid and polyploid populations are documented for woody species of *Eriophyllum* s.s.; see Mooring 1997).

Descent of all members of Heliantheae s.l. + Eupatorieae (excluding the *Athroisma-Blepharispermum* clade and *Anisopappus*), i.e., ca. 25% of species in Compositae (ca. 2.5% of angiosperms), from a putatively polyploid ancestor underscores the potential importance of polyploids in founding major radiations in angiosperms (also see Soltis and Soltis 2000). Examples presented here of extreme descending dysploidy followed by polyploidy extend evidence presented earlier (Baldwin and Wessa 2000b) for wide evolutionary oscillations in chromosome number that confuse identification of diploids and polyploids in helenioid Heliantheae.

**HISTORICAL BIOGEOGRAPHY.** Rzedowski's (1972) hypothesis of a northwestern Mexican origin of Helenieae s.l. corresponds closely with the historical biogeographic interpretation of our phylogenetic results shown in Fig. 11. Based on our interpretation of the trees presented herein, the most recent common ancestor of taxa referable to Helenieae s.l. (and to Heliantheae s.l. + Eupatorieae), exclusive of the basally divergent *Athroisma-Blepharispermum* clade and *Anisopappus*, probably occurred in southwestern North America (including northern Mexico). Old World endemism of the *Athroisma-Blepharispermum* clade, *Anisopappus*, and most members of the putative sister-group to the clade encompassing Heliantheae s.l. + Eupatorieae, *Athroisma-Blepharispermum*, and *Anisopappus*, i.e., Inuleae + Plucheae (Kim and Jansen 1995), may reflect ancient Old World to New World dispersal in the ancestry of the Heliantheae s.l. + Eupatorieae clade.

The high diversity of helenioid Heliantheae endemic to the California Floristic Province is mostly confined to one nested clade corresponding to Baeriinae, Madiinae, and the  $x = 19$  "arnicoid" taxa (Fig. 11). *Arnica*, a circumboreal taxon noted for polyploid apomicts (see Wolf 1987), was previously hypothesized to be of arctic or subarctic origin (Maguire 1943). The high concentration of sexual diploid species of *Arnica* in northern California (Wolf 1987) may reflect a Californian ancestry for the genus, in keeping with our phylogenetic results (Fig. 11; also see Baldwin and Wessa 2000b).

The ITS data reinforce the hypothesis of dispersal of the silversword alliance ancestor from the California Floristic Province to the Hawaiian Islands (Baldwin et al. 1991) and lead us to conclude that the ancestor of *Hypericophyllum* was dispersed from Mexico or Central America to Africa (Fig. 11). Putative examples of amphi-tropical dispersal of helenioid Heliantheae from North America to South America, e.g., *Lasthenia kunthii* Hook. & Arn., *Madia sativa*, and *Perityle emoryi* (see Ornduff 1963; Raven 1963), and one putative example

of dispersal to Australia, *Flaveria australasica* Hook. (see Powell 1978; Kopriva et al. 1996), are consistent with our results but, except for *Madia*, are not addressed directly here.

#### TAXONOMIC TREATMENT

**Tribal classification of Heliantheae s.l. + Eupatorieae.** Previous studies based on cpDNA restriction sites and gene sequences demonstrate that Eupatorieae is nested within Heliantheae s.l. (see Jansen and Kim 1996), a result corroborated here. Adherence to a criterion of taxon monophyly within our rank-based system of botanical nomenclature makes continued recognition of tribe Eupatorieae untenable without partitioning of Heliantheae s.l. into tribes coordinate with Eupatorieae.

A system of tribes is proposed here by Baldwin (see Table 2) that retains the circumscription of Eupatorieae sensu King and Robinson (1987) and a slightly modified circumscription of Heliantheae sensu Karis and Ryding (1994b), i.e., with the addition of *Trichocoryne*. Coreopsidinae is provisionally retained in Heliantheae s.s., but may be best treated as a separate tribe, Coreopsidae (Panero, Baldwin, Schilling, and Clevinger, unpubl. data). Helenieae already has been redefined to comprise only the members of Gaillardinae sensu Karis and Ryding (1994a) + *Pelucha* (see Baldwin and Wessa 2000a). Tageteae here includes Pectidinae sensu Robinson (1981) [= Tageteae sensu Strother (1977, 1986)], Clappiinae sensu Robinson (1981), Flaveriinae sensu Turner and Powell (1977), and, provisionally, Jaumeinae sensu Robinson (1981), *Arnicastrum*, *Jamesianthus*, and *Oxyppappus*. *Coulterella* and *Varilla* (Varillinae) are also included in Tageteae on the basis of morphological similarities to other members of Flaveriinae s.l. (see Robinson 1981; Karis and Ryding 1994a) and cpDNA findings (Panero, Baldwin, Schilling, and Clevinger, unpubl. data). Madiinae includes Madiinae sensu Carlquist (1959) plus *Arnica* (including *Mallotopus* and *Whitneya*), *Eatonella* s.s., *Hulsea*, *Venegasia*, and a slightly modified Baeriinae sensu Robinson (1981), i.e., including *Syntrichopappus* and excluding *Eatonella* and *Oxyppappus*. Exclusion of *Eatonella* (and *Hulsea*) from Baeriinae is provisional, pending further analysis of their relationships (Panero, Baldwin, Schilling, and Clevinger, unpubl. data; Baldwin and Wessa, unpubl. data). *Galeana* and *Villanova* are left as an informal group (the "Villanova clade") pending further analysis of their relationships to other lineages (Panero, Baldwin, Schilling, and Clevinger, unpubl. data).

Three tribes are erected for the remaining members of Heliantheae s.l. (excluding the *Athroisma-Blepharispermum* clade and *Anisopappus*). Bahieae encompasses the first series of genera in Chaenactidinae sensu Robinson (1981)—Robinson's informal Bahiinae—plus five

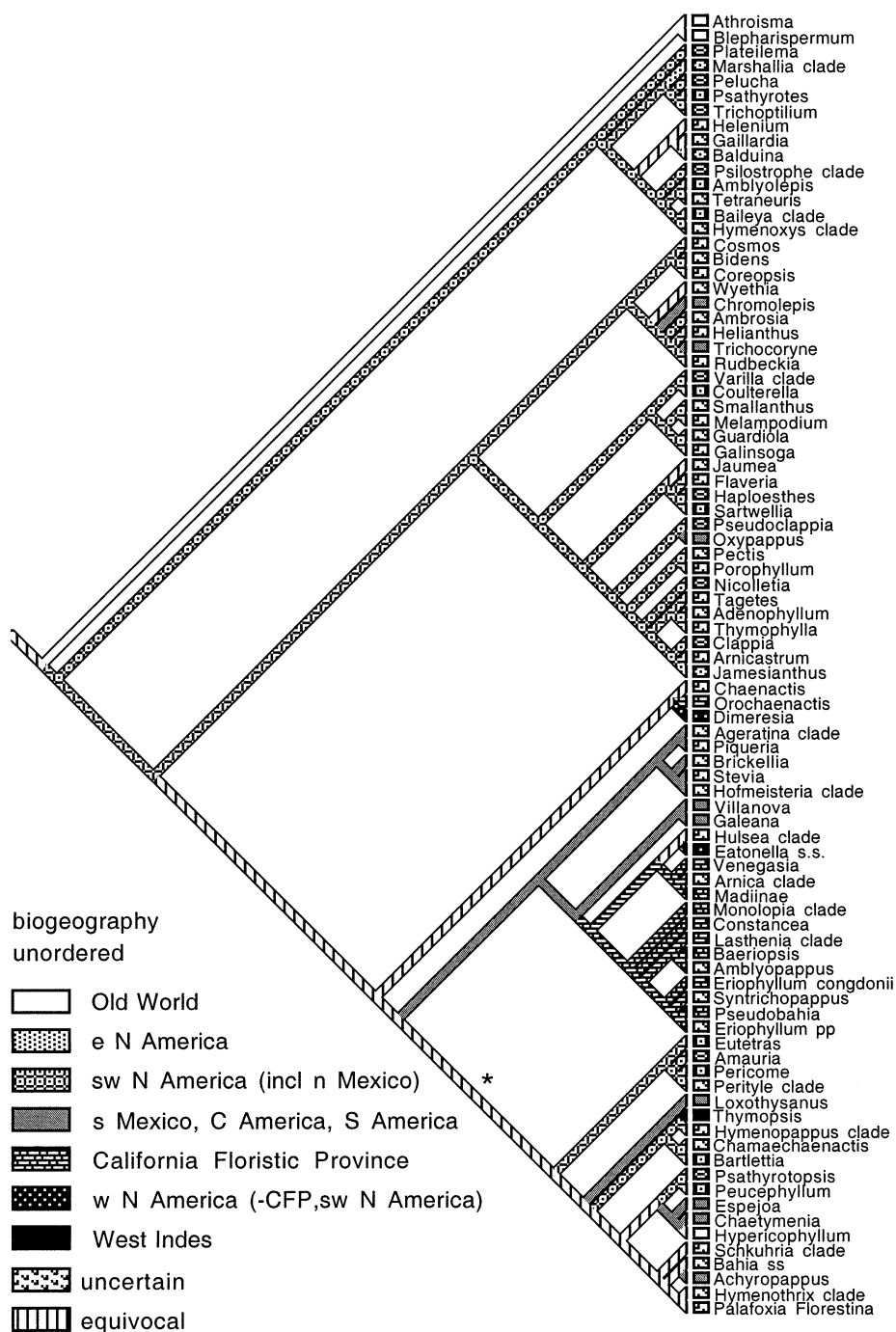


FIG. 11. A hypothesis of historical biogeography in the clade corresponding to Heliantheae s.l. + Eupatorieae based on parsimony mapping of areas on the tree topology shown. The tree corresponds to one of two minimum-length ITS archetype trees (see Fig. 2 for strict consensus tree). Character-state changes for the other minimum-length tree are identical except for the branch marked by an asterisk and all other "equivocal" branches in that clade, which are estimated as unequivocal for southern Mexico, Central America, and/or South America in the other minimum-length tree. *Hymenothrix* clade contains *Amauriopsis*, *Hymenothrix*, and *Platyschkuhria*. Abbreviations: C = Central; e = eastern (including southeastern); incl = including; sw = southwestern; N = North; S = South; (-CFP, sw) = minus the California Floristic Province (western California and southwestern Oregon in the USA and northwestern Baja California in Mexico) and southwestern North America.

other genera in Chaenactidinae sensu Robinson (i.e., *Bartlettia*, *Chamaechaenactis*, *Peucephyllum*, *Psathyrotopsis*, and, provisionally, *Thymopsis*) and two genera of Hymenopappinae sensu Robinson (1981), i.e., *Hymenopappus* and, provisionally, *Loxothysanus*. Chaenactideae comprises *Chaenactis*, *Dimeresia*, and *Orochaenactis*. Perityleae comprises Peritylinae sensu Robinson (1981) plus, provisionally, *Lycapsus* (see Robinson 1981; Karis and Ryding 1994a).

The ITS data do not bear directly on the phylogenetic placement of the *Athroisma*—*Blepharispermum* clade (i.e., *Athroisma*, *Blepharispermum*, and *Leucoblepharis*) or *Anisopappus*, but, based on results of earlier studies (Eriksson 1991; Kim and Jansen 1995; Eldenäs et al. 1999), the three genera should constitute one or two additional tribe(s) (not described here).

*Apostates* and *Welwitschiella* (neither sampled) are not assigned here to any tribe.

KEY TO TRIBES CORRESPONDING TO HELIANTHEAE S.L. + EUPATORIEAE (exclusive of the *Athroisma*—*Blepharispermum* clade and *Anisopappus*)

1. Cypselae walls not carbonized, with raphides in epidermal cells; leaves alternate, often in basal rosettes . . . . . Helenieae s.s.
1. Cypselae walls carbonized, without raphides in epidermal cells; leaves alternate or opposite, usually cauline.
  2. Style-branch appendages usually longer than stigmatic lines; heads discoid; corollas variously colored but not bright yellow; pappi usually of bristles, sometimes of scales or absent . . . . . Eupatorieae
  2. Style-branch appendages usually shorter than stigmatic lines; heads radiate or discoid; corollas variously colored, often bright yellow; pappi of awns and/or bristles and/or scales, sometimes absent.
  3. Receptacles usually paleate throughout, seldom epaleate (in ca. 15 of ca. 200 genera); phyllaries rarely each clasping a ray ovary; anthers usually blackened, sometimes pale; disc corollas 5- (rarely 4-) lobed . . . . . Heliantheae s.s.
  3. Receptacles usually epaleate or with paleae restricted to a ring between ray and disc florets, rarely paleate throughout head (then phyllaries usually each clasping a ray ovary, disc corollas 4-lobed, or cypselae strongly 9–15 ribbed); anthers usually pale or reddish, not blackened (sometimes appearing black from dark purplish pigment in Madiinae); disc corollas 4–5-lobed.
  4. Leaves and/or phyllaries often with secretory cavities or dark resin lines [if cavities and/or lines absent, then cypselae strongly 9–15-ribbed, except for *Arnicastrum* and *Jamesianthus* (perennial herbs with 3-seriate involucre; broad, herbaceous outer phyllaries; cypselae with apical, annular collars; and pappi of unequal, barbellate bristles), *Coulterella* (succulent shrubs with fleshy leaves; 1–2 flowered heads; and fused, fleshy involucre), and *Oxypappus* (Mexican herbs with uniseriate involucre; phyllaries narrow, navicular; and pappi of 2–5 subulate scales)]; all or proximal leaves usually opposite, sometimes alternate; receptacles usually epaleate (paleate in *Varilla*; sometimes paleate in *Chrysactinia*; with stiff, subulate projections in *Clappia*); disc corollas usually 5-lobed; pappi often of bristles and/or bristle-tipped scales, rarely absent or of scales without bristles at tips . . . . . Tageteae
  4. Leaves and phyllaries without secretory cavities or dark resin lines; cypselae not strongly 9–15-ribbed (but often striate); leaves opposite or alternate; receptacles epaleate or paleate; disc corollas 4–5-lobed; pappi usually of scales without apical bristles, sometimes of bristles or of scales and bristles, rarely absent.
  5. Disc corollas usually 4-lobed; cypselae usually strongly compressed [rarely obcompressed (*Perityle montana*) or prismatic (*Lycapsus*)], with thick, usually ciliate margins; phyllaries usually navicular . . . . . Perityleae
  5. Disc corollas usually 5-lobed; cypselae rarely compressed or obcompressed with thick, ciliate margins; phyllaries flat to concave, navicular, or each enfolding a ray ovary.
  6. Pappi usually of medially or basally thickened scales, sometimes of brownish, golden, or orange-reddish, sometimes fasciculate or hooked, awns or bristles, rarely of  $\pm$  uniformly thick scales [then disc corollas 4-lobed] or absent; leaves usually petiolate [if sessile, then phyllaries rounded and in 3+ series (*Chaetymenia*, *Espejoa*, and *Hypericophyllum*), or plants shrubby and leaves needle-like (*Peucephyllum*), or disc cypselae trigonous (*Villanova*)]; receptacles epaleate (except for *Hymenopappus newberryi*, which has medially thickened pappus scales); disc cypselae striate or not, rarely obcompressed (in *Bartlettia*).
  7. Heads radiate; all or proximal leaves opposite; cypselae not striate; pappi absent; plants herbaceous; phyllaries in 1 series . . . . . "Villanova clade"
  7. Heads radiate or discoid; leaves basal and/or alternate or opposite; cypselae striate or rarely not striate [then heads discoid and/or leaves basal and/or alternate]; pappi usually present; plants herbaceous or woody; phyllaries usually in 2+ series . . . . . Bahiinae
  6. Pappi often of  $\pm$  uniformly thick scales (not medially or basally thickened), or sometimes absent or of white, tawny, or, rarely, reddish or purplish, non-fasciculate, straight-tipped, awns or bristles; leaves usually sessile, sometimes the proximal petiolate, rarely petiolate throughout [then heads discoid and pappi, if present, of ovate to subulate scales (*Chaenactis* and *Dimeresia*)], or plants robust or rhizomatous perennials with pappi absent (*Venegasia*) or pappi of bristles (*Arnica*) or scales (*Constancea*); receptacles paleate or epaleate; disc cypselae striate, not obcompressed.
  8. Heads discoid; corollas usually white, pink, or reddish, rarely yellow, those of peripheral florets often somewhat enlarged and  $\pm$  zygomorphic, throats cylindrical to narrowly funnelliform; pappi usually present, persistent, rarely absent or not persistent (shed as a unit in *Dimeresia* and *Orochaenactis*); leaves usually petiolate, often pinnately divided or dissected, sometimes entire . . . . . Chaenactideae
  8. Heads usually radiate, rarely discoid; corollas yellow or orange if heads discoid, those of peripheral disc florets not enlarged or zygomorphic, throats usually narrowly to broadly funnelliform or campanulate; pappi present and persistent if heads discoid; leaves usually sessile, entire or pinnately lobed if heads discoid . . . . . Madieae

**Bahieae** B. G. Baldwin, tribus nov.—Type: *Bahia* Lag.

A Asteroideae ceteris, differt characteribus conjuncte: habitu herbaceo vel fruticoso; foliis plerumque petiolatis, laminis integris vel pinnatim divisis vel dissectis, sine cavitatibus secretoriis; phyllariis 2–3-seriatis; receptaculis epaleatis (praeter *Hymenopappum newberryi* I. M. Johnst.—squamis papporum in mediis longistrorsum incrassatis); capitulis radiatis vel discoideis; flosculis radiorum pistillatis; flosculis discorum bisexualibus vel fungenter staminatis, corollis actinomorpha vel zygomorpha, lobis 5, saepe elongatis; antheris ecaudatis, non denigratis; ramis stylo- rum subtruncatis vel appendicibus lineis stigmaticis multo brevioribus; cypselae  $\pm$  teretibus, trigonis, quadrangularibus, vel obcompressis, parietibus interne denigratis (“carbonized”), striatis vel non striatis; pappis absentibus, vel squamis basaliter vel in mediis longistrorsum incrassatis, vel aristis, vel setis brunneolis, aureis, vel rufis, interdum fasciculatis vel uncinatis;  $2n = 8-12, 15-21, 24, 34, 36$  II.

Annuals, perennial herbs, or shrubs. Leaves basal and/or cauline, alternate or opposite, usually petiolate, blades usually pinnately divided or dissected, sometimes entire or lobed, without secretory cavities. Capitulescences loosely to tightly corymbiform or paniculiform, or heads borne singly. Involucres obconic to campanulate or hemispheric. Phyllaries in ca. 2–3 equal or unequal series, erect, herbaceous, scarious, or scarious-margined, linear, elliptic, lanceolate, oblanceolate, spatulate, or, rarely, orbicular. Receptacles  $\pm$  flat, epaleate (except for *Hymenopappus newberryi* I. M. Johnst.—with medially thickened pappus scales). Heads radiate or discoid. Ray florets pistillate, corollas often white or yellow, sometimes orange, reddish, or purplish. Disc florets bisexual or, rarely, functionally staminate, corollas yellow, white, orange, reddish, or purplish, usually actinomorphic, sometimes zygomorphic, often glandular, throats cylindrical to broadly funnelform, lobes 5 (lobes 4 in *Thymopsis*), often elongate. Anthers pale, reddish, or purplish (not blackened), ecaudate. Style branches subtruncate or with appendages much shorter than the stigmatic lines. Cypselae  $\pm$  terete, trigonous, quadrangular, or, rarely, obcompressed, the walls carbonized, striate or not. Pappi absent or of medially and/or basally thickened scales (pappi of  $\pm$  uniformly thickened scales in *Thymopsis*), or of awns, or of brownish, golden, or reddish, sometimes fasciculate or hooked, bristles.  $2n = 8-12, 15-21, 24, 34, 36$  II.

**Chaenactideae** B. G. Baldwin, tribus nov.—Type: *Chaenactis* DC.

A Asteroideae ceteris, differt characteribus conjuncte: habitu herbaceo vel subfruticoso; foliis plerumque basalibus vel basalibus et caulinis, alternis, plerumque

petiolatis, laminis integris vel lobatis, plerumque pinnatim divisis vel dissectis, sine cavitatibus secretoriis; phyllariis 1–2(–4)-seriatis,  $\pm$  equalibus, angustis, herbaceis; receptaculis epaleatis (praeter *Chaenactidem carphocliniam*—paleatis); capitulis discoideis; corollis plerumque albis, roseis, vel rubellis, interdum flavis, corollis flosculorum peripheralium saepe amplificatis, zygomorpha, faucibus cylindraceis vel anguste infundibuliformibus, lobis 5, saepe brevis et patulis; antheris ecaudatis (raro sagittatis), non denigratis; ramis stylo- rum subtruncatis vel appendicibus lineis stigmaticis multo brevioribus; cypselis  $\pm$  teretibus, parietibus interne denigratis (“carbonized”), striatis; pappis plerumque presentibus, interdum absentibus vel vestigialibus, plerumque squamis 1–2+—seriatis,  $\pm$  libris et persistentibus vel basaliter connatis et deciduis  $\pm$  conjuncte, cuneiformibus, spatulatis, ovatis, vel lanceolatis, aequalibus vel inaequalibus, aequae  $\pm$  scariosis vel hyalinis (non basaliter vel in mediis longistrorsum incrassatis), marginis et apicis saepe laciniatis vel erosis (praeter *Dimeresiam*—squamis 1-seriatis, basaliter connatis et deciduis conjuncte, subulatis, plumosis;  $2n = 5-9, 12-15, 18$  II,  $2n = 18$ ).

Annuals, perennial herbs, or, rarely, subshrubs. Leaves basal and/or cauline, alternate or, rarely, the proximal opposite, usually petiolate, sometimes sessile, blades usually pinnately divided or dissected, sometimes lobed or entire, without secretory cavities. Capitulescences loosely corymbiform to glomerate or heads borne singly. Involucres obconic to campanulate or hemispheric. Phyllaries in 1–2(–4)  $\pm$  equal series, sometimes reflexed or spreading, herbaceous, usually linear, lanceolate, or oblanceolate. Receptacles flat to convex, often alveolate, epaleate. Heads discoid. Corollas white, pinkish, red, or, less commonly, yellow, those of the peripheral florets often enlarged and zygomorphic, all usually glandular, throats cylindrical to narrowly funnelform, lobes 5, often short and spreading. Anthers pale (not blackened), ecaudate (rarely sagittate). Style branches subtruncate or with appendages much shorter than the paired stigmatic lines. Cypselae usually terete, often appressed-hairy, the walls carbonized, striate. Pappi usually present, usually persistent (shed as a unit in *Dimeresia* and *Orochaenactis*), of  $\pm$  uniformly thick (not medially or basally thickened), erose scales in 1+ series or of subulate, plumose scales in 1 connate series (in *Dimeresia*).  $2n = 5-9, 12-15, 18$  II,  $2n = 18$  (triploid).

**Perityleae** B. G. Baldwin, tribus nov.—Type: *Perityle* Benth.

A Asteroideae ceteris, differt characteribus conjuncte: habitu herbaceo vel fruticoso; foliis omnibus vel proximaliter oppositis, plerumque petiolatis; phyllariis 1–2-seriatis, herbaceis, plerumque navicularibus; receptaculis epaleatis (praeter *Lycapsium*—paleatis); cap-



itulis radiatis vel discoideis; flosculis radorum pistillatis; flosculis discorum bisexualibus, corollis 4(–5)-lobatis; antheris ecaudatis, non denigratis; cypselis plerumque compressis, 2- vel 4-angularibus, parietibus interne denigratis ("carbonized"), marginibus  $\pm$  incrassatis, saepe ciliatis; pappis presentibus vel absentibus, plerumque squamis, vel setis, vel squamis et setis, squamis crassitiebus  $\pm$  uniformibus, erosis, pappis saepe redactis, coroniformibus;  $2n = 11$ – $13$ ,  $16$ – $19$ , ca.  $54$  II,  $2n = 102$ .

Annuals, perennial herbs, or shrubs. Leaves usually opposite proximally or throughout, sometimes alternate distally, usually petiolate, blades entire or lobed or, rarely, dissected, without secretory cavities. Capitulescences loosely to tightly paniculiform or corymbiform. Involucres obconic to campanulate or hemispheric. Phyllaries in 1–2 series, erect, herbaceous, usually narrowly navicular. Receptacles flat or convex, epaleate or, rarely, paleate (in *Lycapsus*). Heads radiate or discoid. Ray florets pistillate, corollas white, reddish, or yellow. Disc florets bisexual, corollas usually yellow, sometimes reddish or whitish, actinomorphic, usually glandular, throats cylindrical to broadly funnelform, lobes 4(–5). Anthers not blackened, ecaudate. Style branch appendages shorter than the stigmatic lines. Cypselae usually compressed (obcompressed in *Perityle montana*; prismatic in *Lycapsus*), 2- or 4-angled,  $\pm$  thick-margined, carbonized, usually not striate, often ciliate. Pappi present or absent, of erose, non-cositate scales and/or bristles, often reduced to a crown.  $2n = 11$ – $13$ ,  $16$ – $19$ , ca.  $54$  II,  $2n = 102$ .

**Subtribal Classification of Helenioid Heliantheae.** BAHIEAE. Only one subtribe, Bahiinae, is recognized for members of Bahieae. Informal recognition is given to three distinctive clades, i.e., the "*Bahia* clade", the "*Chaetymenia* clade", and the "*Peucephyllum* clade" (see Table 2). Recognition of the three groups as subtribes would leave five genera of uncertain relationship unassigned to subtribe.

CHAENACTIDEAE. Only one subtribe, Chaenactidiinae, is recognized for Chaenactideae (Table 2).

HELENIEAE. Five distinctive subtribes (Gaillardinae, Marshalliinae, Plateileminae, Psathyrotinae, and Riddelliinae) are recognized for Helenieae (Table 2; see Baldwin and Wessa 2000a for key to subtribes).

MADIEAE. To assign genera to subtribes that correspond to putative monophyletic groups and to maintain subtribal status for Madiinae sensu Carlquist (1959) and Baeriinae, three new subtribes in Madieae are recognized for *Arnica* (including *Mallotopus* and *Whitneya*), *Eatonella* + *Hulsea*, and *Venegasia* (see Table 2). *Constancea* is provisionally retained in Baeriinae pending results of ongoing molecular phylogenetic studies (Baldwin and Wessa, unpubl. data; Panero, Baldwin, Schilling, and Clevinger, unpubl. data). *Eatonella* and *Hulsea* may belong in Baeriinae (Panero, Baldwin, Schilling, and Clevinger, unpubl. data), but morphological, chromosomal, and ecological considerations (in addition to ITS and ETS results; Figs. 1 and 2; Baldwin and Wessa, unpubl. data) warrant provisional recognition of a separate subtribe for the two genera, pending further analysis of their relationships.

#### KEY TO SUBTRIBES OF MADIEAE

1. Receptacles wholly or partially paleate (paleae indistinguishable from phyllaries in discoid taxa); if heads discoid, plants annuals or rhizomatous perennials with pappi of plumose, subulate or lanceolate scales (*Layia discoidea*, *Carlquistia*, and *Raillardella*) or plants of woody life-forms (*Dubautia* and *Wilkesia*) . . . . . Madiinae
1. Receptacles epaleate; if heads discoid, plants annuals or rhizomatous perennials with pappi of bristles (sometimes plumose) or non-plumose scales.
  2. Leaves opposite (at least proximally); pappi of persistent bristles or, if absent, disc florets functionally staminate and ray corollas persistent . . . . . Arnicinae
  2. Leaves opposite or alternate, sometimes in basal rosettes; pappi of awns, scales, or deciduous bristles, or, if absent, disc florets bisexual and ray corollas deciduous.
    3. Subshrubs or shrubs; leaves distinctly petiolate, blades entire or coarsely toothed; phyllaries 3–4+ seriate, the outer 1(–2) often reflexed; pappi absent . . . . . Venegasiinae
    3. Herbs or, less commonly, subshrubs or shrubs; leaves usually sessile or winged-petiolate (distinctly petiolate in *Constancea*—with blades dissected), blades entire, toothed, lobed, or dissected; phyllaries 1–3-seriate, usually erect, sometimes the outer 1 reflexed (in *Hulsea*); pappi present or absent.
      4. Phyllaries 1(–2)-seriate; cypselae usually not compressed and ciliate . . . . . Baeriinae
      4. Phyllaries 2–3-seriate; cypselae compressed, densely ciliate along edges . . . . . Hulseinae

**Arnicinae** B. G. Baldwin, subtribus nov.—Type: *Arnica* L.

A Madieae ceteris, differt characteribus conjuncte: habitu perenni, herbaceo, plerumque rhizomatoso; foliis omnibus vel maximam partem oppositis; phyllariis (1)–2-seriatis, phyllariis exteriorum cum flosculis ra-

diorum consociatis; receptaculis epaleatis tomentosis vel villosis; capitulis radiatis vel discoideis; flosculis discorum bisexualibus (praeter *Arnica* *dealbatam*—fungenter staminatis); cypselis cylindratis vel clavatis vel obovoideis, linitur vel valde angularibus, raro compressis, striatis; pappi radorum et discorum pler-

umque praesentibus et persistentibus (praeter *Arnica dealbatam*—absentibus), setis papporum albis vel fulvis, barbellatis vel plumosis;  $x = 19$ .

Perennial herbs, usually rhizomatous. Leaves all or mostly opposite, sessile or short-petiolate, blades entire or shallowly lobed, glabrous or sparsely to densely tomentose, sometimes glandular. Capitulescences loosely corymbiform or paniculiform or heads borne singly. Involucres narrowly obconic to, often, campanulate or hemispheric. Phyllaries in (1–)2 series, erect, the outer each associated with a ray floret, usually herbaceous, usually narrow, the inner, if present, membranous. Receptacles convex, epaleate, tomentose. Heads radiate or discoid. Ray florets pistillate, corollas yellow to yellowish-orange (cream-colored in *Arnica viscosa*). Disc florets bisexual (functionally staminate in *Arnica dealbata*), corollas yellow to yellowish-orange, 5-lobed. Anthers yellow or, rarely, purple (not blackened). Style-branch appendages much shorter than the stigmatic lines. Cypselae cylindrical or narrowly clavate to obovoid or obpyramidal, weakly to strongly angled, glabrous or hairy, the walls carbonized, striate. Pappi usually present, persistent (absent in *Arnica dealbata*), of white to tawny, barbellate to plumose bristles.  $x = 19$ .

**Hulseinae** B. G. Baldwin, subtribus nov.—Type: *Hulsea* Torr. & A. Gray ex A. Gray

A Madieae ceteris, differt characteribus conjuncte: habitu annuo, bienni, vel perenni; foliis basalibus vel basalibus et caulinis, alternis, laminis integris, dentatis, vel lobatis, basibus omnium vel proximalium foliorum attenuatis, superficiebus glanduliferis et/vel lanatis; involucris cylindraceis, campanulatis, vel hemisphericis; phyllariis 2–3-seriatis, angustis, glanduliferis et/vel lanatis; receptaculis epaleatis, glabris; capitulis radiatis; corollis radorum flavis, rubris, vel purpurascensibus, laminis  $\pm$  linearis vel late ovatis (praeter *Eatonella*— $\pm$  inconspicuis); corollis discorum flavis vel aurantiacis; cypselis compressis, 2-marginatis, superficiebus nitidis-glabris vel sparsim vel dense pubescentibus, marginibus  $\pm$  incrassatis, dense ciliatis; pappis persistentibus, squamis 1 vel 2 paribus oppositis, libris, acuminatis vel truncatis, crassitiebus  $\pm$  uniformibus, apicibus  $\pm$  erosis;  $2n = 19$  II.

Biennial or perennial herbs or, rarely, annuals (*Eatonella*). Leaves cauline and/or in basal rosettes, alternate, sessile or winged-petiolate, blades entire or dentate or, rarely, lobed, glandular and/or woolly. Capitulescences loosely corymbiform, racemiform, or paniculiform or, often, heads borne singly. Involucres usually hemispheric, sometimes cylindrical to campanulate. Phyllaries in 2–3 series, erect or the outer 1 reflexed, herbaceous, narrow. Receptacles flat, epaleate, glabrous. Heads radiate. Ray florets pistillate, corollas yellow, orange, red, or purplish (laminae  $\pm$  inconspic-

uous in *Eatonella*). Disc florets bisexual, corollas yellow or orange, 5-lobed. Anthers pale (not blackened). Style-branch appendages much shorter than the paired stigmatic lines. Cypselae  $\pm$  cylindrical to clavate,  $\pm$  compressed, 2-edged,  $\pm$  thick-margined, the walls carbonized, margins densely ciliate, faces shiny-glabrous or sparsely to densely hairy. Pappi present, persistent, of 1 or 2 opposite pairs of free, acuminate to truncate, non-costate,  $\pm$  uniformly thick, apically erose, scales.  $2n = 19$  II.

**Venegasiinae** B. G. Baldwin, subtribus nov.—Type: *Venegasia* DC.

A Madieae ceteris, differt characteribus conjuncte: habitu subfruticoso vel fruticoso; foliis alternis, petiolatis, laminis deltatis-ovatis vel cordatis, integris vel dentatis, fere glabris; involucris hemisphericis; phyllariis 3–4-seriatis, phyllariis serierum mediarum et intimarum saepe rotundis; receptaculis epaleatis; capitulis radiatis; flosculis discorum bisexualibus, corollis flavis, tubis dense glanduliferis-pubescentibus; antheris flavis; cypselis valde striatis, saepe arcuatis, glabris vel sparsim scabris; pappis absentibus;  $2n = 19$  II.

Perennial herbs, subshrubs, or shrubs. Leaves mostly alternate, proximally opposite, all petiolate, blades rounded-deltate to cordate, subentire or toothed, abaxially minutely resin-dotted, adaxially glabrous. Capitulescences loosely corymbiform or heads borne singly. Involucres hemispheric to globose. Phyllaries in 3–4+ series, the outer 1(–2) often reflexed, herbaceous, the inner 2(–3) erect, membranous or scarious. Receptacles flat or convex, epaleate, sparsely tomentose. Heads radiate. Ray florets pistillate, corollas yellow. Disc florets bisexual, corollas yellow, tubes densely glandular-pubescent. Anthers yellow. Style-branch appendages  $\pm$  deltate, shorter than the paired stigmatic lines. Cypselae strongly striate, often curved, carbonized, glabrous or sparsely scabrous. Pappi absent.  $2n = 19$  II.

**PERITYLEAE.** In Perityleae, Peritylinae sensu Robinson (1981) is retained; Lycapsinae sensu Robinson (1981) is provisionally recognized as a distinct group diagnosed by paleate, rather than epaleate, receptacles (Robinson 1981).

**TAGETEAE.** Provisionally, four subtribes [Flaveriinae sensu Turner and Powell (1977), Jaumeinae sensu Robinson (1981), Pectidinae, and Varillinae] are recognized for Tageteae (Table 2). The circumscriptions of Flaveriinae and Jaumeinae are conventional. Pectidinae is redelimited (with reservations) to include five monospecific or dispecific genera without secretory cavities, i.e., *Arnicastrum*, *Clappia*, *Jamesianthus*, *Oxyppappus*, and *Pseudoclappia*. Varillinae is redelimited to include *Coulterella* and *Varilla*.

## KEY TO SUBTRIBES OF TAGETEAE

1. Receptacles distinctly paleate or bracts of head fused into fleshy, 3–4 winged cup and disc florets 1(–2) . . . . . Varillinae
1. Receptacles epaleate (with subulate projections in *Clappia*); bracts of head not fused into winged cup; disc florets usually  $\geq 10$ .
  2. Cypselae walls usually striate, cypselae mostly 4–5-angled [if strongly 9–15-ribbed, then leaves alternate] . . . . . Pectidinae
  2. Cypselae walls not striate, cypselae strongly 9–15-ribbed; leaves opposite, pairs often connate-perfoliate.
    3. Heads in corymbiform or glomerate capitulescences; herbs, shrubs, or trees . . . . . Flaveriinae
    3. Heads borne singly; stoloniferous herbs . . . . . Jaumeinae

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