Haplopappus Cass. (Astereae) *sensu* Hall:
a polyphyletic conundrum revealed by plastid data

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ABSTRACT

The genus *Haplopappus* Cass. has undergone drastic taxonomic changes since its inception in 1828 by Cassini. Initially based on a single species from Chile, *H. glutinosus* Cass., it was expanded to over 150 species by Hall and others to encompass cushion-like alpine herbs, caulescent perennials, low-elevation subshrubs, and sizeable shrubs, mostly indigenous to North America. *Haplopappus* means simple or single pappus consisting of scabrous capillary bristles, a feature seized upon by Hall, along with homochromous discoid or radiate capitula usually with yellow corollas, for uniting species in the genus. Various explanations were given to exclude other genera similar in this regard such as *Solidago* L. and *Chrysothamnus* Nutt. Hall's treatment formed the basis for numerous subsequent taxonomic treatments and floras for decades. As cytological and other sorts of data emerged, however, its polyphyly became evident, and many researchers sought to define monophyletic lineages within this artificial group. Subsequently, *Haplopappus* sensu Hall has been disassembled into over thirty genera across several subtribes predominantly within a clade known as "North American Astereae". Previously, limited phylogenetic resolution was achieved in this lineage with nuclear ribosomal data via Sanger Sequencing. In this study, high-throughput sequencing allowed the assembly of whole chloroplast genomes for phylogenetic analyses. The results from this work demonstrate that *Haplopappus* as circumscribed by Hall is deeply polyphyletic.

Keywords: Asteraceae, Compositae, North America, Phylogenetics, Taxonomy.

INTRODUCTION

The cosmopolitan tribe Astereae (Asteraceae) includes over 3,000 species in approximately 200 genera and underwent multiple transitions to the Americas largely from Eurasia and Africa (Nesom & Robinson, 2007; Brouillet et al., 2009). One diverse clade, termed "North American Astereae" (Brouillet et al. 2009) migrated north from Central and South America even though few other Astereae colonized the U.S. and Canada. This lineage subsequently underwent notable diversification and in numerous cases migrated back to South America (Brouillet et al., 2009). The North American Astereae includes many widespread, diverse genera and bears a long, complicated taxonomic history – in large part due to the genus *Haplopappus* Cass.

Haplopappus ("*Aplopappus*" as originally spelled) was defined by Cassini on the basis of a single species (*Haplopappus glutinosus* Cass.) from Chile (Cassini, 1828), as small cushion plants with sticky-glandular foliage and solitary, terminal capitula containing yellow corollas in radiate heads. Later authors significantly expanded the genus describing numerous species, (Gray, 1868, 1873, 1880, 1884; Greene, 1885; Blake, 1922, 1932; Hall, 1928; Anderson, 1980, 1983; Dorn, 1977, 1988) but most notably substantially broadening its morphological circumscription. Hall's (1928) treatment of *Haplopappus* included 16 sections and over 150 predominantly North American species. Other mat or cushion-forming plants, such as *H. pygmaeus* (Torrey & A.Gray) A.Gray (≡*Tonestus pygmaeus* Torrey & A.Gray), were included along species with a wide variety of habits and morphological features.

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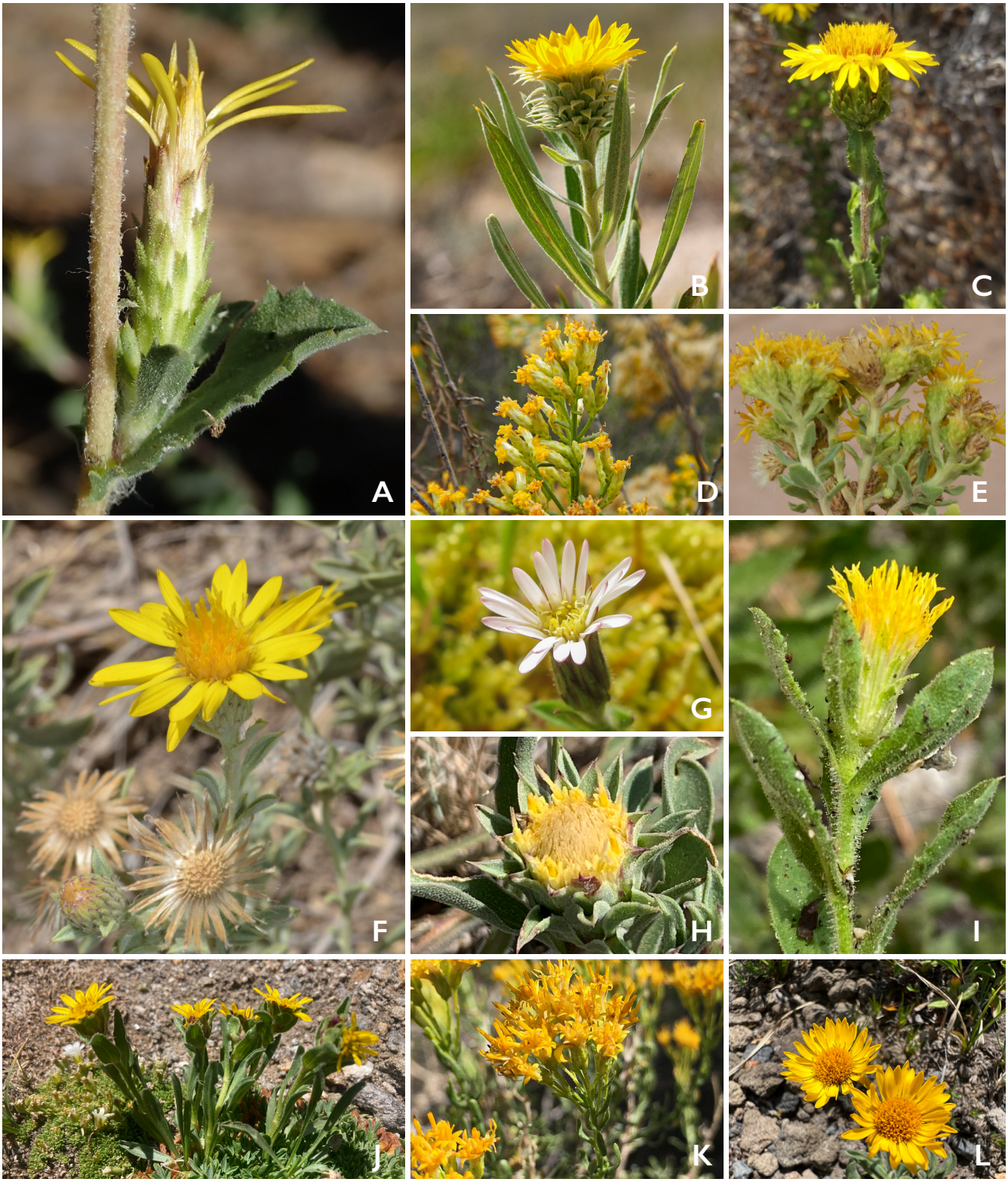

Figure 1. Select genera segregated from *Haplopappus s.l.* **A.** *Adeia whitneyi* (A.Gray) G.L.Nesom. **B.** *Oonopsis puebloensis* S. Kelso, Heckmann, J. Lawton & Maentz. **C.** *Hazardia berberidis* (A.Gray) Greene. **D.** *Xylothamia diffusa* (Benth.) G.L.Nesom. **E.** *Isocoma acradenia* (Greene) Greene. **F.** *Heterotheca canescens* (DC.) Shinners. **G.** *Noticastrum marginatum* (Kunth) Cuatrec. **H.** *Pyrrocoma carthamoides* Hook. **I.** *Triniteurybia aberrans* (A.Nelson) Brouillet, Urbatsch & R.P.Roberts. **J.** *Tonestus pygmaeus* A.Nelson **K.** *Ericameria cooperi* (A. Gray) H.M.Hall. **L.** *Erigeron aureus* Greene. *Photos by: A. Keir Morse (iNaturalist observation: 143617355), B. Richard Bunn (93382668), C. Gwen Fish (133668894), D. Oscar Jimenez (35617164), E. Richard Abbott (133835240), F. Richard Abbott (13612158), G. Omar Javier López Gómez (133778200), H. Matt Reala (143148497), I. Matt Berger (87951215), J. Peter Zika (131061374), K. Jim Tietz (121487540), L. James Thomas (130636095)*

Figure 2. Species of *Haplopappus* s.s. from South America. **A.** *H. macrocephalus* (Poepp. ex Less.) DC. **B.** *H. cf. foliosus* DC. **C.** *H. grindelioides* (Less.) DC. **D.** *H. donianus* (Hook. & Arn.) Sch.Bip. ex Reiche. **E.** *H. velutinus* J.Remy. **F.** *H. taeda* Reiche. **G.** *H. foliosus* DC. **H.** *H. glutinosus* Cass. **I.** *H. chrysanthemifolius* DC. *Photos by: A. Eitel Pinto (iNaturalist observation: 120175330), B. Eitel Pinto (120174775), C. Eitel Pinto (105806884), D. Zona Norte de Quilpué (103767807), E. Nodora Moyano 108700701), F. Orlando Montes (69568777), G. Catalina Chappuzeau (108396872), H. Nicolas Olejnik (1187277), I. Charif Tala (100444307)*

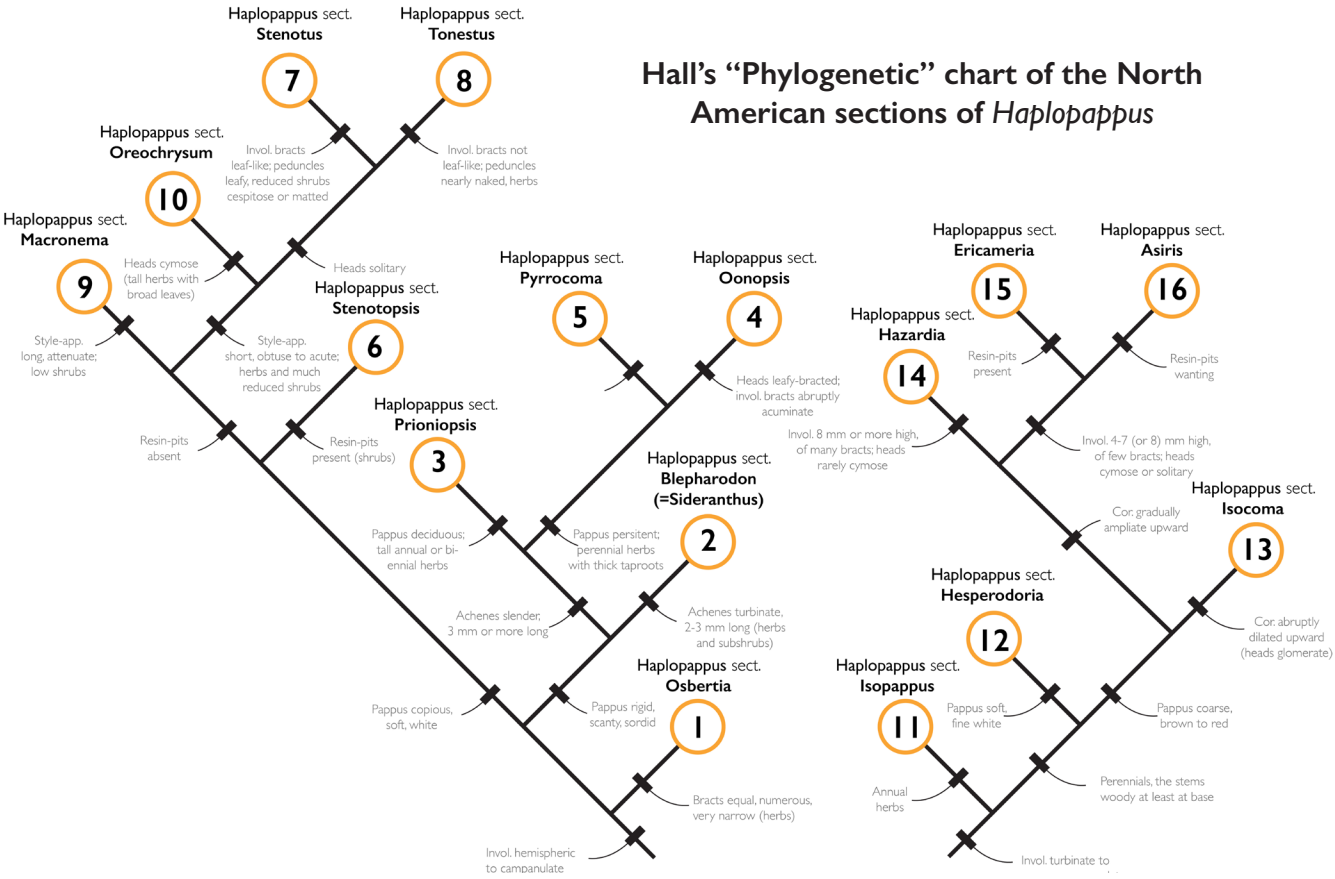

Figure 3. Hall's interpretation of the relationships among his sections of *Haplopappus* with a dichotomous key separating the supposed clades from his 1928 monograph. Key features of proposed importance included the presence or absence of leafy bracts subtending the capitula and overall capitulescence structure. These features, however, would turn out to be homoplaseous within the American Astereae.

Haplopappus, as conceived by Hall and later authors was morphologically heterogeneous, in habit and plant height, capitulum type, floret number, and pubescence (Figure 1 & Figure 2).

Hall (1928) believed the North and South American species of *Haplopappus* were two discrete clades and greatly increased the number of North American species within the genus. He described and incorporated numerous new taxa, gradually increasing the morphological complexity of the group. Hall created sections defined by similarity and based on various combinations of morphological characters (Figure 3). Before long, the genus existed as a catch-all of sorts that accounted for a substantial portion of mostly species of North American Astereae with yellow corollas bar the "Asters" (including *Eurybia* (Cass.) Cass., *Ionactis* Greene, *Symphyotrichum* Nees), goldenrods (*Chrysoma* Nutt., *Euthamia* (Nutt.) Cass., *Solidago* L.), and snakeweeds (including *Gutierrezia* Lag., *Amphiachyris* (DC.) Nutt.).

Comparative morphological and molecular phylogenetic work (Brouillet et al., 2009; Lane and Hartman, 1996; Suh & Simpson, 1990) resulted in the allocation of over one-hundred North and Central American species of *Haplopappus* s.l. into approximately thirty genera among several subtribes (particularly Chrysopsidinae Nesom, Machaerantherinae Nesom, Pentachaetinae Nesom, and Solidagininae O.Hoffm.; Table 1) as defined by Nesom (2020a) which expanded upon the synopsis presented by Brouillet et al. (2009).

Haplopappus sect. *Blepharodon* DC. was eventually split into several genera (Lane & Hartman 1996), including *Adeia* G.L.Nesom, *Erigeron* L. (*E. aureus* Greene), *Hazardia* Greene, *Rayjacksonia* R.L.Hartm. & M.L.Lane, and *Xanthisma* DC.

Alternatively, genera like *Ericameria* Nutt. in the modern sense include members of several of Hall's

Life in the skies

Tonestus pygmaeus (Torrey & A.Gray) A.Nelson: Morphologically similar to *Nestotus* R.P.Roberts, Urbatsch & Neubig and *Stenotus* Nutt., this alpine or subalpine species was originally described as *Haplopappus pygmaeus* (Torrey & A.Gray) A. Gray. Native to the central and southern Rocky Mountains, this dwarf species is a classic montane "cushion plant:" short stature with deep taproots, densely pubescent foliage, and relatively large flowers/capitula. Dozens of species just within Astereae have converged upon this habitat, including *Heterotheca pumila* (Greene) Semple and *Lorandersonia peirsonii* (D.D.Keck) Urbatsch, R.P.Roberts & Neubig, as it provides protection from frigid and windy conditions throughout short growing seasons.

San Juan mountains in Colorado, USA
Photo by Patrick Alexander

Adapted to the arid

Xanthisma grindelioides (Nutt.) D.R.Morgan & R.L.Hartm., Found throughout much of the low and mid-elevation western U.S., this species exhibits numerous adaptations to drier climates which many other Astereae have converged upon. These subshrubs are coated in dense glands and have lost their ray florets to reduce water loss – similar to many species of *Ericameria* Nutt. and *Isocoma* Nutt. Like many other species in the North American Astereae clade, it has belonged to various genera at different times including *Haplopappus* Cass. and *Machaeranthera* Nees. This species has been previously known as *Ericocarpum grindelioides* Nutt. and *Sideranthus grindelioides* (Nutt.) Britton, but those names would eventually be lumped into *Xanthisma* DC.

Red Canyon of Wyoming, USA
Photo by Patrick Alexander

sections of *Haplopappus*, as *H.* sect. *Asiris* H.M. Hall, *H.* sect. *Ericameria* (Nutt.) A Gray, *H.* sect. *Macronema* (Nutt.) A. Gray, and *H.* sect. *Stenotopis* (Rydb.) H.M.Hall (Roberts, 2002; Urbatsch & Roberts, 2003; Urbatsch et al., 2006).

Additionally, about one-third of the species of *Chrysothamnus* Nutt., a genus largely excluded from *Haplopappus* by Hall (1928), were transferred to *Ericameria* (Nesom & Baird, 1993, 1995; Roberts & Urbatsch, 2003). The sections of *Haplopappus* as defined by Hall were circumscribed according to a combination of several homoplaseous characters, including the loss or reduction of ray florets in several sections (Roberts & Urbatsch, 2003) and shift to annual habit in select members of *Haplopappus* sect. *Blepharodon* DC. (Hartman, 2006) and *H.* sect. *Isopappus* (Torr. & A.Gray) Benth. & Hook.f. (Markos & Strother, 2006; Nesom, 2006). Features such as phyllary, involucre, style, and pappus shape were of principal importance in Hall's (1928) treatment. These morphological features have been interpreted variously to support either lumping or splitting different lineages across numerous genera or sections (Nesom, 1989, 2007, 2018, 2020b; Nesom & Baird, 1993; Nesom et al., 1990), even by the same author with most changes made within the Gutierrezzinae and Solidagininae s.s..

Generic delimitation would not reach a consensus for many groups such as Machaerantherinae (Brouillet & Selliah, 2005; Morgan, 1990, 2003; Morgan et al., 2009; Selliah, 2009; Selliah & Brouillet, 2008) and Solidagininae s.s. (Roberts, 2002; Roberts & Urbatsch, 2003, 2004; Urbatsch et al., 2005) without molecular studies to help identify monophyletic groups.

As speciation within the North American Astereae, many of which were formerly included in *Haplopappus,* the colonization of similar climates by different lineages likely contributed to the rise of many convergences which in turn yielded the rather complex taxonomy of today (Akram et al., 2020; Billing,s 1974; Hughes & Atchison, 2015). Shifts in overall form and habit were likely dictated in large by elevational changes; species approaching or within the alpine zones must grow relatively low to counter the dry air and colder temperatures (Billings, 1974; Billings et al., 1968; Hughes et al., 2015) while those in the lowland deserts faced evolutionary pressure to become either short-lived annuals or (sub)shrubs with deep taproots as drought stress intensified and water availability decreased (Akram et al., 2020; He et al., 2021; Mulroy & Randel, 1977). The colonization and occupation of new niches via speciation occurred repeatedly, making proper classifications difficult at best without the aid of molecular data.

`Through innumerable chromosome counts and molecular phylogenetic data (Brouillet et al., 2009; Morgan, 2003; Morgan et al., 2009; Roberts, 2002; Urbatsch et al., 2003, 2005), it became apparent that *Haplopappus* as originally described constituted numerous independent lineages. Sanger Sequencing helped produce the backbone phylogeny for Astereae that could not be reasonably inferred with morphology alone, and cytological work confirmed the existence of many groups therein often defined by the number of chromosomes present. Gradually, work by several authors (Brown & Keil, 1992; Clark, 1979; Cronquist, 1947; Hartman, 1976; Kartesz, 1994; Kartesz & Gandhi, 1991a, 1991b; Lane, 1993; Mayes, 1976; Nesom, 1991a, 1991b, 1991c; Nesom & Morgan, 1990; Smith, 1981; Turner & Hartman, 1976) established monophyly for the appropriate species into new or existing genera. The last genus to be established out of Hall's definition of *Haplopappus* in North America was *Rayjacksonia* R.L. Hartm. and M.A. Lane of the Machaerantherinae (Lane & Hartman, 1996). With a revised classification of the "North American Astereae" clade (Brouillet et al., 2009), the production of revised keys and an ameliorated understanding of the numerous new clades could begin.

As molecular phylogenetic tools have become far more available and affordable in the past decades, a phylogeny based on whole chloroplast genome data is presented here to highlight the discrepancies between initial treatments of *Haplopappus* and modern taxonomic treatments. Modern molecular data, along with an account of the gradual disarticulation of North American *Haplopappus,* further provides a prime example of how convergent adaptations to various extreme conditions can confound initial treatments. The objective of this paper is to reveal the polyphyletic nature of Hall's *Haplopappus* treatment using whole chloroplast genome sequence data.

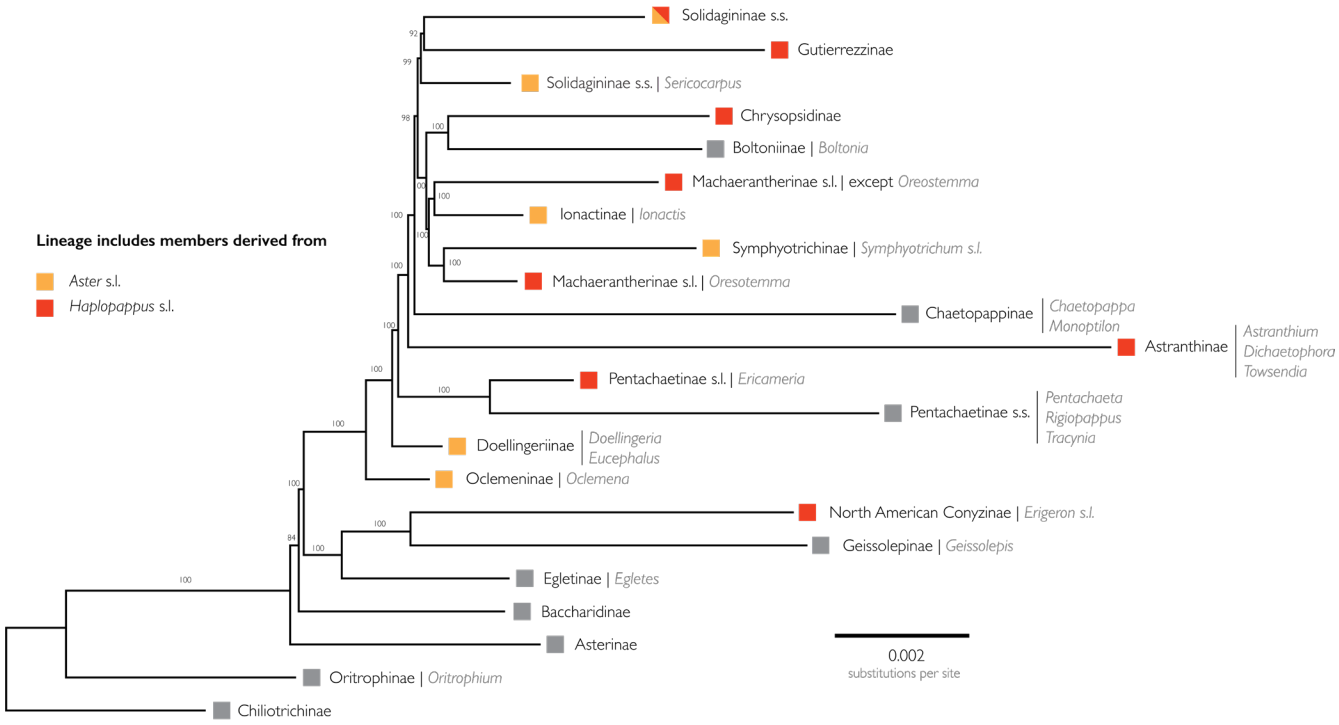

Figure 4. Subtribal relationships within North American Astereae. Lineages in red have members which have been segregated from "*Haplopappus* s.l." while those in orange were segregated from "*Aster* s.l."; lineages with members derived from both are in purple. While both of these previously large genera were once classified as monophyletic, they have since been split into numerous genera spread across various subtribes following the advent of molecular phylogenetic data and additional morphological studies. This topology represents the maximum likelihood tree of the partitioned chloroplast genome dataset generated in IQ-TREE, viewed in FigTree, and edited in Adobe Illustrator.

MATERIALS & METHODS

Taxa were selected to include representatives from each of the subtribes of North American Astereae postulated by Nesom (2020a). Species belonging to *Ericameria, Euthamia,* and species from the Solidagininae *s.s.* and Gutierrezzinae, collectively forming the Solidagininae *s.l.,* were further included as parts of other projects investigating the relationships among and within those lineages. Species of the South American *Haplopappus* s.s., along with many other genera from Machaerantherinae, were also included to help elucidate the origin of this genus from within the North American Astereae clade identified by Brouillet et al. (2009).

Leaf tissues for phylogenetic studies were gathered either through fresh collections, predominantly by Lowell Urbatsch, and various herbarium specimens. Several herbaria generously permitted the sampling of leaf tissues from specimens, including ACAD, ARIZ, ASC, ASU, AUA, BALT, BRY, COLO, DES, ECS, FLAS, LL, LSU, MICH, MISS, MO, NCU, NLU, NO, NY, OBI, RM, SDS, SIU, STAR, UAL, UCR, UNA, USAM, US, UTC, UWAL, TEX, and TROY (acronyms according to Thiers, 2023); LSU, LL, and TEX warrant particular recognition for providing the majority of samples used here. Genetic or DNA material was extracted from herbarium specimen leaves using a modified CTAB protocol with silica columns (Doyle & Doyle, 1987; Neubig et al., 2014). Samples were then quantified using a QuBit v. 3.0 Fluorometer and evaluated for degradation on an agarose gel. High and medium quality DNA extractions at suitable concentrations were then sent to Rapid Genomics LLC (Gainesville, FL, USA) for library preparation and paired-end

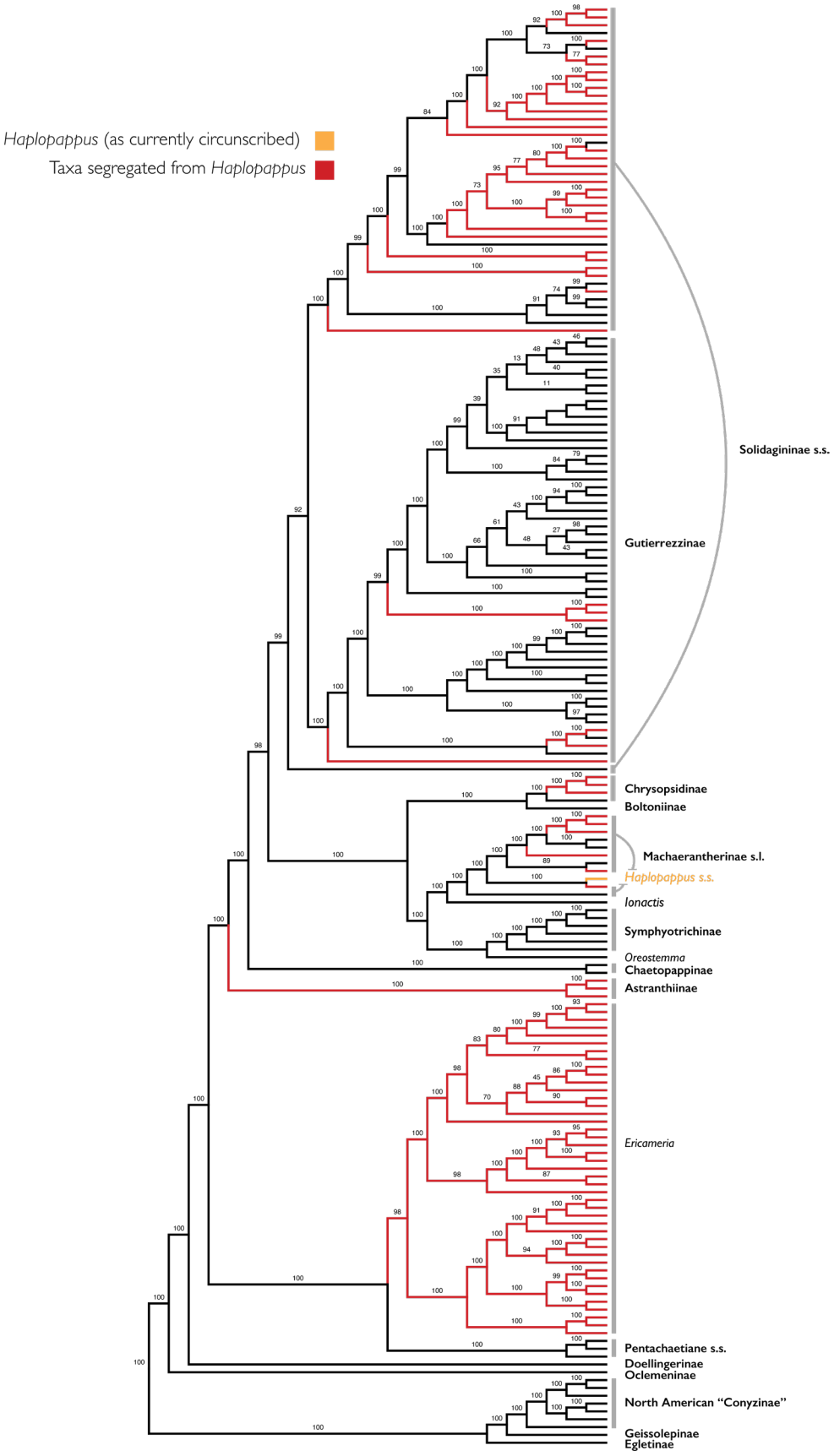

Figure 5. Chloroplast cladogram showing taxa segregated from *Haplopappus* in red with reference to the modern definition of Haplopappus in orange. These data indicate that *Haplopappus*, as Hall defined it, is deeply polyphyletic within the Americas. This partitioned chloroplast cladogram is identical to that to the phylogram in Figure 4 but without any collapsed nodes for various subtribes or genera.

Table 1. Species segregated from *Haplopappus* have been split into the following genera among seven subtribes. Generic circumscription within Solidagininae s.s. may change noticeably with additional data.

Genus	Subtribe
Townsendia Hook., Fl. Bor.-Amer. (Hooker) 2(7): 16. t. 119 (1834).	**Astranthinae**
Croptilon Raf., Fl. Tellur. 2: 47 (1837).	**Chrysopsidinae**
Heterotheca Cass., Bull. Sci. Soc. Philom. Paris 1817: 137 (1817)	
Noticastrum DC., Prodr. (DC.) 5: 279 (1836).	
Osbertia Greene, Erythea 3: 14 (1895).	
Pityopsis Nutt., Trans. Amer. Philos. Soc. ser. 2, 7: 317 (1841).	
Tomentaurum G.L.Nesom, Phytologia 71: 129 (1991).	
Erigeron L., Species Plantarum. Pl. 2.: 863 (1753).	**Conyzinae**
Gundlachia A.Gray, Proc. Amer. Acad. Arts 16: 100 (1880).	**Gutierrezzinae**
Medranoa Urbatsch & R.P.Roberts, Sida 21(1): 254 (2004).	
Adeia G.L.Nesom, Phytoneuron 39: 1 (2021).	**Machaerantherinae s.l.**
Benitoa D.D.Keck, Leafl. W. Bot. 8: 26 (1957).	
Grindelia Willd., Mag. Neuesten Entdeck. Gesammten Naturk. Ges. Naturf. Freunde Berlin 1: 259 (1807).	
Hazardia Greene, Pittonia 1: 28 (1887).	
Isocoma Nutt., Trans. Amer. Philos. Soc. ser. 2, 7: 320 (1841).	
Machaeranthera Nees, Gen. Sp. Aster.: 224 (1832).	
Oonopsis (Nutt.) Greene, Pittonia 3: 45 (1898).	
Oreostemma Greene, Pittonia 4: 224 (1899).	
Pyrrocoma Hook., Fl. Bor.-Amer. (Hooker) 1: 306 (1833).	
Rayjacksonia R.L.Hartm. & M.L.Lane, Amer. J. Bot. 83: 368 (1996).	
Xanthisma DC., Prodr. (DC.) 5: 94 (1836).	
Xylorhiza Nutt., Trans. Amer. Philos. Soc. ser. 2, 7: 297 (1841).	
Ericameria Nutt., Trans. Amer. Philos. Soc. ser. 2, 7: 318 (1841).	**Pentachaetinae s.l.**
Acamptopappus A.Gray, Proc. Amer. Acad. Arts 8: 634 (1873).	**Solidagininae s.s.**
Chrysothamnus Nutt., Trans. Amer. Philos. Soc. ser. 2, 7: 323 (1841).	
Columbiadoria G.L.Nesom, Phytologia 71: 249 (1991).	
Lorandersonia Urbatsch, R.P.Roberts & Neubig, Sida 21(3): 1619 (2005).	
Nestotus R.P.Roberts, Urbatsch & Neubig, Sida 21(3): 1650 (2005).	
Oreochrysum Rydb., Bull. Torrey Bot. Club 33: 152 (1906).	
Stenotus Nutt., Trans. Amer. Philos. Soc. ser. 2, 7: 334 (1841).	
Toiyabea R.P.Roberts, Urbatsch & Neubig, Sida 21(3): 1652 (2005).	
Tonestus A.Nelson, Bot. Gaz. 37: 262 (1904).	

sequenced on an Illumina MiSeq before processing the data files in Geneious Prime R10.

Sequences were assembled using a mixture of reference and *de novo* assemblies in Geneious to a reference sequence of *Baccharis genistelloides* (Lam.) Pers. (GenBank accession KX063864); the sequences were then aligned on the CIPRES supercomputer cluster (Miller et al., 2015) using MAFFT v. v7.427 (Katoh et al., 2018). Annotations were generated using the 'Annotate from' function in Geneious using *Baccharis genistelloides* (NCBI GenBank accession number: KX063864) at 80% similarity. Truncated annotations were permitted, and annotations which overlapped with the best match by 75% were excluded to avoid annotating the same sequence portion multiple times. The index length was limited to 10 nucleotides, and only 'gene' type sequences were annotated. Sequences were partition based on their type: coding sequence exons and introns, tRNA exons and introns, rRNAs, and intergenic spacers. Each sequence type was evaluated for the optimal substitution model in IQ-TREE v. 1.6.8 using the automatic Model Finder function (Chernomer et al., 2016; Hoang et al., 2018; Nguyen et al., 2015); IQ-TREE further generated maximum likelihood phylogenies for the entire concatenated dataset. The output consensus tree was then viewed in FigTree v. 1.4.4 (Rambaut, 2018) and edited in Adobe Illustrator. The sequences used in this study are available upon request and will be made available through NCBI GenBank in the BioProject SUB12953760 entitled "North American Astereae Genome Skimming project."

RESULTS & DISCUSSION

The chloroplast phylogeny (Figure 4 & Figure 5) obtained from the analysis of a combination of previously unpublished chloroplast genomes and data from NCBI GenBank, confirmed the monophyly of the North American Astereae *sensu* Brouillet et al. (2009) with most relationships being well-supported (>80% bootstrap support). Only two subtribes, Solidagininae s.s. and Machaerantherinae *s.l.,* are polyphyletic due to the placement of *Sericocarpus* Nees and *Oresotemma* Greene of the 'Eurybioid grade', respectively (Figure 4). The lineages which contain former *Haplopappus* species did not form a clade but rather indicated that these species had multiple origins, especially for the Machaerantherinae and Solidagininae. Collectively, the species once treated within *Haplopappus* are deeply polyphyletic, having several origins throughout the North American Astereae clade (Fig. 5). These results highlight the strong polyphyletic nature of *Haplopappus* as circumscribed by Hall (1928) whose species have since been segregated into several genera scattered among several subtribes. These trees collectively indicate that previous classifications have been artificial and imply that the characters previously seen as phylogenetically informative among taxa were instead homoplaseous.

The phylogenetic hypothesis presented here can be compared with previously described biogeographic patterns. For example, despite most taxa occurring within the Canada and the U.S., numerous southern migrations have occurred repeatedly. Phylogenetic data (Brouillet et al., 2009) have indicated that multiple dispersal events to Central and South America from North America have occurred within the Chrysopsidinae, Machaerantherinae *s.l.*, Solidagininae *s.l.,* and Conyzinae. *Haplopappus* s.s. of the Machaerantherinae *s.l.* represents the most diverse group whose ancestors migrated south from North America after the group first moved northwards. Other genera (*Erigeron, Eurybia,* and *Solidago*) have migrated even further back to Eurasia or even various Pacific Islands (Brouillet et al., 2009). Further, not all Astereae native to North America fall within the North American clade: *Aster* s.s. and *Baccharis* have dispersed from Eurasia and Central/South America, respectively, into various parts of North America.

CONCLUSIONS

While great strides have been made to better understand the taxonomy of New World Astereae, there remains much to do. Uncovering the circumscription and biogeographic origin of *Haplopappus* in its modern sense based on molecular phylogenetic data represents considerable progress from treatments published a century ago. Resolving taxonomic issues could not have been done properly without dozens of researchers carefully measuring morphological traits, counting chromosomes, and

sequencing genetic material, all to understand how the Astereae have evolved. Efforts to elucidate monophyletic lineages and establish an appropriate taxonomic classification, particularly in Solidagininae *s.s.* and Machaerantherinae *s.l.,* will continue to require thorough work which has been increasingly guided by high-throughput sequence data.

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APPENDIX

North American Astereae samples, including outgroups from NCBI GenBank, that were used to generate chloroplast genome assemblies. The South American Astereae data were largely taken from Vargas et al. 2017. Multiple specimens used here have not been given formal herbaria accession numbers or digitized yet. GenBank Accession numbers will be deposited in the NCBI GenBank within Bio Project SUB12953760.

Species	Voucher
Acamptopappus shockleyi A.Gray	Lane 3072 (COLO01182724)
Acamptopappus sphaerocephalus A.Gray	Beck s.n. (ASC00063004)
Almutaster pauciflorus (Nutt.) Á.Löve & D.Löve	Sundberg 2568 (Unknown)
Amphiachyris amoena (Shinners) Solbrig	Nesom 7742 (TEX00211062)
Amphipappus fremontii Torr. & A.Gray	Gierisch 4221 (ASC00047356)
Ampelaster carolinianus (Walter) G.L.Nesom	Sundberg 2294 (Unknown)
Aquilula riskindii (B.L.Turner & G.E.Langford) G.L.Nesom	Nesom 7697 (TEX00139365)
Archibaccharis asperifolia S.F.Blake	Olazo 1192 (TEX449024)
Aster alpinus var. vierhapperi (Onno) Cronquist	Weber 18495 (COLO00046375)
Astranthium ciliatum (Raf.) G.L.Nesom	Rosen 3607 (TEX00442205)
Aztecaster matudae (Rzed.) G.L.Nesom	Hinton 29102 (TEX452243)
Baccharis genistelloides (Lam.) Pers.	Vargas 358 (HUSA s.n.)
Baccharis halimifolia L.	Urbatsch 10186 (LSU00133981)
Baccharis tricuneata Pers.	Vargas 356 (HUSA s.n.)
Bigelowia nudata (Michx.) DC.	Abbott 23624 (FLAS227170)
Blakiella bartsiifolia (S.F.Blake) Cuatrec.	Cuatrecasas 28129 (TEX s.n.)
Boltonia asteroides var. recognita (Fernald & Griscom) Cronquist	Swayne 110 (Unknown)
Brintonia discoidea (Elliott) Greene	Urbatsch 11540 (LSU00179297)
Canadanthus modestus (Lindl.) G.L.Nesom	Semple 10290 (LSU00134614)
Chaetopappa ericoides (Torr.) G.L.Nesom	Carr 30166 (MO s.n.)
Chihuahuana purpusii (Brandegee) Urbatsch & R.P.Roberts	Johnson 12105 (LSU s.n.)
Chrysoma pauciflosculosa Greene	Urbatsch 8015 (LSU00061087)
Chrysopsis linearifolia subsp. linearifolia Semple	Abbott 23545 (FLAS227171)
Chrysothamnus depressus Nutt.	Urbatsch 7916 (LSU00179306)
Chrysothamnus eremobius L.C.Anderson	Smith 3745 (UTC00227344)
Chrysothamnus greenei Greene	Urbatsch 7965 (LSU00076515)
Chrysothamnus humilis Greene	Tiehm 9309 (DES00028726)
Chrysothamnus molestus (S.F.Blake) L.C.Anderson	Urbatsch 7963 (LSU s.n.)
Chrysothamnus scopulorum (M.E.Jones) Urbatsch, R.P.Roberts & Neubig	Welsh 24648 (NY2905944)
Chrysothamnus stylosus (Eastw.) Urbatsch, R.P.Roberts & Neubig	Urbatsch 7627 (LSU00063484)
Chrysothamnus vaseyi Greene	Urbatsch 7914 (LSU00179296)
Chrysothamnus viscidiflorus Nutt.	Urbatsch 11062 (LSU00137506)
Chrysothamnus viscidiflorus Nutt.	Urbatsch 11064 (LSU00137508)
Columbiadoria hallii (A.Gray) G.L.Nesom	Urbatsch 7692 (LSU00061150)
Cuniculotinus gramineus (H.M.Hall) Urbatsch, R.P.Roberts & Neubig	Urbatsch 7941 (LSU00177491)
Dichaetophora campestris A.Gray	Lievens 2 (LSU00061061)
Diplostephium barclayanum Cuatrec.	Vargas 477 (QCA s.n.)
Diplostephium callilepis S.F.Blake	Vargas 376 (HUSA s.n.)
Diplostephium crypteriophyllum Cuatrec.	Vargas 467 (QCA s.n.)
Diplostephium ericoides (Lam.) Cabrera	Vargas 489 (QCA s.n.)
Diplostephium foliosissimum S.F.Blake	Sagastegui 16804 (F s.n.)
Diplostephium gnidioides S.F.Blake	Vargas 430 (HUSA s.n.)
Diplostephium gynoxyoides Cuatrec.	Vargas 395 (HUSA s.n.)
Diplostephium hartwegii Hieron.	Vargas 456 (QCA s.n.)
Diplostephium jelskii Hieron.	Cano 14716 (USM s.n.)
Diplostephium lechleri Wedd.	Vargas 381 (HUSA s.n.)
Diplostephium oblanceolatum S.F.Blake	Vargas 465 (QCA s.n.)
Diplostephium pulchrum S.F.Blake	Vargas 404 (HUSA s.n.)
Diplostephium serratifolium Cuatrec.	Sagastegui 16159a (F s.n.)
Doellingeria sericocarpoides Small	Urbatsch 7774 (LSU00032463)
Eastwoodia elegans Brandegee	Urbatsch 12124 (LSU00181276)
Egletes viscosa dissecta Shinners	Roberts 10170 (Unknown)

APPENDIX (CONT.)

Species	Voucher
Ericameria arborescens (A.Gray)Greene	Keil 35389 (OBI s.n.)
Ericameria albida (M.E.Jones ex A.Gray) L.C.Anderson	Urbatsch 7670 (LSU00076170)
Ericameria arizonica R.P.Roberts, Urbatsch & J.Anderson	Crawford 576 (ASC00111045)
Ericameria bloomeri J.F.Macbr.	Urbatsch 7719 (LSU00072800)
Ericameria brachylepis H.M.Hall	Urbatsch 1402 (LSU00209223)
Ericameria brachylepis H.M.Hall	Urbatsch 7090 (LSU00061455)
Ericameria cervina Rydb.	Atwood 13509 (BRYV0250964)
Ericameria cervina Rydb.	Urbatsch 7662 (LSU00179274)
Ericameria compacta (H.M.Hall) G.L.Nesom	Urbatsch 7940 (LSU00076490)
Ericameria cooperi H.M.Hall	Keil 2404 (LSU00061281)
Ericameria cooperi H.M.Hall	Urbatsch 12140 (LSU00181259)
Ericameria cuneata McClatchie	Urbatsch 7092 (LSU00078980)
Ericameria cuneata McClatchie	Urbatsch 7957 (LSU00076491)
Ericameria discoidea (Nutt.) G.L.Nesom	Urbatsch 7654 (LSU00072798)
Ericameria ericoides (Less.) Nutt. ex Jeps.	Keil 10983 (Unknown)
Ericameria fasciculata J.F.Macbr.	Griffin 3963 (Unknown)
Ericameria gilmanii (S.F.Blake) G.L.Nesom	Urbatsch 7948 (LSU00076493)
Ericameria juarezensis (Moran) Urbatsch	Moran 22986 (ASU0017213)
Ericameria laricifolia (A.Gray) Shinners	Urbatsch 1120 (LSU00061374)
Ericameria linearifolia (DC.) Urbatsch & Wussow	Moran 21245 (LSU00179250)
Ericameria martirensis Wiggins	Anderson 4695 (LSU00179260)
Ericameria nana Nutt.	Urbatsch 11073 (LSU00137633)
Ericameria nauseosa (Pursh) G.L.Nesom & G.I.Baird	Urbatsch 10368 (LSU00131738)
Ericameria nauseosa (Pursh) G.L.Nesom & G.I.Baird	Urbatsch 11061 (LSU00137505)
Ericameria nauseosa (Pursh) G.L.Nesom & G.I.Baird	Urbatsch 7722 (LSU00179266)
Ericameria nauseosa var. graveolens (Nutt.) Reveal & Schuyler	Urbatsch 11168 (LSU00137620)
Ericameria obovata (Rydb.) G.L.Nesom	Jones s.n. (NY2076226)
Ericameria obovata (Rydb.) G.L.Nesom	Urbatsch 11079 (LSU00137522)
Ericameria palmeri H.M.Hall	Urbatsch 1105 (LSU00061436)
Ericameria palmeri H.M.Hall	Urbatsch 1106 (LSU00061438)
Ericameria paniculata A.Gray ex Rydb.	Scott 894 (ASC00052925)
Ericameria parishii H.M.Hall	Urbatsch 7082 (LSU00072950)
Ericameria parryi (A.Gray) G.L.Nesom & G.I.Baird	Urbatsch 7931 (LSU00179304)
Ericameria pinifolia H.M.Hall	Urbatsch 7084 (LSU00072951)
Ericameria resinosa Nutt.	Urbatsch 7690 (LSU00076500)
Ericameria sp.	Goorich 28687 (LSU00179347)
Ericameria sp.	Urbatsch 11162 (LSU00137614)
Ericameria suffruticosa (Nutt.) G.L.Nesom	Anderson 4887 (BRYV0251717)
Ericameria teretifolia Jeps.	Urbatsch 7955 (LSU00076501)
Ericameria watsonii (A.Gray) G.L.Nesom	Semple s.n. (LSU00061461)
Ericameria watsonii (A.Gray) G.L.Nesom	Urbatsch 7661 (LSU00179267)
Ericameria winwardii (Dorn & Delmatier) R.P.Roberts & Urbatsch	Windward s.n. (BRYV0048789)
Ericameria zionis (L.C.Anderson) G.L.Nesom,	Urbatsch 7922 (LSU00076504)
Erigeron annuus (L.) Pers.	Unknown (Unknown)
Erigeron bonariensis L.	Unknown (Unknown)
Erigeron breviscapus (Vaniot) Hand.-Mazz.	Unknown (Unknown)
Erigeron breviscapus (Vaniot) Hand.-Mazz.	Unknown (Unknown)
Erigeron canadensis L.	Unknown (Unknown)
Erigeron multiradiatus (Lindl. ex DC.) Benth. & Hook.f.	Unknown (Unknown)
Erigeron vernus (L.) Torr. & A.Gray	Abbott 22381 (Unknown)
Euthamia caroliniana (L.) Greene ex Porter & Britton	Singhurst 15467 (TEX s.n.)
Euthamia caroliniana (L.) Greene ex Porter & Britton	Urbatsch 10780 (LSU00132487)
Euthamia caroliniana (L.) Greene ex Porter & Britton	Urbatsch 11263 (LSU00176929)
Euthamia galetorum Greene	Peck s.n. (ECS029490)
Euthamia galetorum Greene	Smith 7079 (ACAD25860)
Euthamia graminifolia (L.) Nutt.	Szubryt 748 (SIU s.n.)
Euthamia graminifolia (L.) Nutt.	Urbatsch 11019 (LSU00135092)

APPENDIX (CONT.)

Species	Voucher
Euthamia graminifolia (L.) Nutt.	Urbatsch 11220 (LSU00137682)
Euthamia graminifolia (L.) Nutt.	Urbatsch 12167 (LSU s.n.)
Euthamia graminifolia var. tricostata	Brinkman 2529 (US s.n.)
Euthamia gymnospermoides Greene	Reznicek 11027 (MICH1217633)
Euthamia gymnospermoides Greene	Szubryt 52 (SIU s.n.)
Euthamia gymnospermoides Greene	Urbatsch 10809 (LSU00179333)
Euthamia gymnospermoides Greene	Urbatsch 10818 (LSU00134804)
Euthamia gymnospermoides Greene	Urbatsch 12111 (LSU00132485)
Euthamia hirtipes (Fernald) Sieren	Abbott 23380 (FLAS s.n.)
Euthamia hirtipes (Fernald) Sieren	Bell 5291 (NCU00101509)
Euthamia hirtipes (Fernald) Sieren	Szubryt 1 (LSU00179178)
Euthamia leptocephala (Torr. & A.Gray) Greene ex Porter & Britton	Szubrt 630 (LSU00181294)
Euthamia leptocephala (Torr. & A.Gray) Greene ex Porter & Britton	Urbatsch 10790 (LSU00132500)
Euthamia leptocephala (Torr. & A.Gray) Greene ex Porter & Britton	Urbatsch 11212 (LSU00137674)
Euthamia occidentalis Nutt.	Nickrent s.n. (SIU s.n.)
Euthamia occidentalis Nutt.	Urbatsch 7724 (LSU90061862)
Euthamia pulverulenta Greene	Reid 9000 (LSU00139903)
Euthamia scabra Greene	Szubryt 809 (LSU00218467)
Euthamia scabra Greene	Szubryt 98 (SIU s.n.)
Euthamia scabra Greene	Urbatsch 10738 (LSU132431)
Euthamia scabra Greene	Urbatsch 10781 (LSU00132488)
Euthamia scabra Greene	Urbatsch 10784 (LSU00132490)
Euthamia scabra Greene	Urbatsch 10799 (LSU00132516)
Euthamia sp.	Urbatsch 11231 (LSU00176941)
Euthamia sp.	Urbatsch 11236 (LSU00176966)
Euthamia remota Greene	Penskar 1272 (MICH1477521)
Euthamia remota Greene	Urbatsch 11129 (LSU00137581)
Exostigma notobellidiastrum (Griseb.) G.Sancho	Tressens 6388 (TEX s.n.)
Geissolepis suaedifolia B.L.Rob.	Nesom 6634 (ASU0018083)
Grindelia squarrosa (Pursh) Dunal	Szubryt 347 (SIU s.n.)
Gundlachia corymbosa (Urb.) Britton ex Bold.	Keil 16562 (OBI168747)
Gundlachia diffusa (Benth.) Urbatsch & R.P.Roberts	Nash 19640 (LSU00179281)
Gundlachia triantha (S.F.Blake) Urbatsch & R.P.Roberts	Cole 3942 (Unknown)
Gundlachia truncata (G.L.Nesom) Urbatsch & R.P.Roberts	Nesom 5254 (TEX00373677)
Gutierrezia alamanii A.Gray	Bye 8236 (SDS104171)
Gutierrezia californica (DC.) Torr. & A.Gray	Rebman 3037 (SDS139343)
Gutierrezia microcephala (DC.) A.Gray	Murray 1003 (LSU00062063)
Gutierrezia pomariensis (S.L.Welsh) S.L.Welsh	Urbatsch 1337 (LSU00062045)
Gutierrezia ramulosa (Greene) M.A.Lane	Sanders 6408 (SDS124908)
Gutierrezia sarothrae (Pursh) Britton & Rusby	Urbatsch 10386 (LSU00062052)
Gutierrezia texana (DC.) Torr. & A.Gray	Lane 1957 (LSU00062059)
Gymnosperma glutinosum Less.	Urbatsch 3012 (LSU00041279)
Haplopappus macraeanus A.Gray	Gray s.n. (TEX00382772)
Hazardia detonsa Greene	Urbatsch 12150 (LSU s.n.)
Herrickia glauca (Nutt.) Brouillet	Urbatsch 11088 (LSU00137531)
Heterothalamus alienus (Spreng.) Kuntze	Wurdack 20385 (TEX00532276)
Heterotheca subaxillaris (Lam.) Britton & Rusby	Szubryt 770 (LSU00218374)
Hinterhubera ericoides Wedd.	Stergios 20385 (TEX532276)
Ionactis linariifolia (L.) Greene	Abbott 23572 (FLAS233185)
Isocoma acradenia Greene	Tiehm s.n. (Unknown)
Isocoma menziesii (Hook. & Arn.) G.L.Nesom	Urbatsch 12143 (LSU00181263)
Kalimeris altaica Nees ex Fisch., C.A.Mey. & Avé-Lall.	Unknown (Unknown)
Laennecia sophiifolia (Kunth) G.L.Nesom	Reina 2010-805 (TEX s.n.)
Linochilus apiculatus (S.F.Blake) Saldivia & O.M.Vargas	Vargas 332 (ANDES s.n.)
Linochilus colombianus (Cuatrec.) Saldivia & O.M.Vargas	Vargas 299 (ANDES s.n.)
Linochilus floribundus Benth.	Vargas 499 (ANDES s.n.)
Linochilus huertasii (Cuatrec.) Saldivia & O.M.Vargas	Vargas 518 (ANDES s.n.)

APPENDIX (CONT.)

Species	Voucher
Linochilus jugibioyi (Cuatrec.) Saldivia & O.M.Vargas	Vargas 504 (ANDES s.n.)
Linochilus obtusus (S.F.Blake) Saldivia & O.M.Vargas	Dorr 9246 (US s.n.)
Linochilus rhododendroides (Hieron.) Saldivia & O.M.Vargas	Vargas 233 (ANDES s.n.)
Linochilus rupestris (Kunth) Saldivia & O.M.Vargas	Vargas 504 (ANDES s.n.)
Linochilus venezuelensis (Cuatrec.) Saldivia & O.M.Vargas	Norrbom 89V33 (US s.n.)
Llerasia caucana (S.F.Blake) Cuatrec.	Vargas 444 (ANDES s.n.)
Lorandersonia baileyi (Wooton & Standl.) Urbatsch, R.P.Roberts & Neubig	Urbatsch 7970 (LSU00076523)
Lorandersonia linifolia (Greene) Urbatsch, R.P.Roberts & Neubig	Urbatsch 11068 (LSU00137512)
Lorandersonia microcephala (Cronquist) Urbatsch, R.P.Roberts & Neubig	Fletcher 7145 (Unknown)
Lorandersonia microcephala (Cronquist) Urbatsch, R.P.Roberts & Neubig	Lightfoot 22 (Unknown)
Lorandersonia pulchella (A.Gray) Urbatsch, R.P.Roberts & Neubig	Urbatsch 7973 (LSU00179288)
Lorandersonia salicina (S.F.Blake) Urbatsch, R.P.Roberts & Neubig	Urbatsch s.n. (LSU s.n.)
Lorandersonia spathulata (L.C.Anderson) Urbatsch, R.P.Roberts & Neubig	Urbatsch 7983 (LSU00076527)
Machaeranthera tanacetifolia (Kunth) Nees	Szubryt 1000 (LSU00218241)
Monoptilon bellioides H.M.Hall	Hemkamp 2856 (LL s.n.)
Neonesomia palmeri (A.Gray) Urbatsch & R.P.Roberts	Urbatsch 3043 (LSU00179257)
Nestotus macleanii (Brandegee) R.P.Roberts, Urbatsch & Neubig	Culder 24968 (UAL27425)
Nestotus stenophyllus (A.Gray) R.P.Roberts, Urbatsch & Neubig	Atwood 13554 (OSC s.n.)
Noticastrum acuminatum (DC.) Cuatrec.	Tressens 6592 (LSU s.n.)
Oclemena reticulata (Pursh) G.L.Nesom	Abbott 22505 (Unknown)
Oreochrysum parryi Rydb.	Urbatsch 7934 (LSU00179302)
Oreostemma alpigenum (Torr. & A.Gray) Greene	Urbatsch 7704 (LSU00062348)
Oritrophium peruvianum (Lam.) Cuatrec.	Vargas 448 (ANDES s.n.)
Parastrephia quadrangularis (Meyen) Cabrera	Vargas 440 (HUSA s.n.)
Pentachaeta exilis (A.Gray) A.Gray	Taylor 15980 (ARIZ432594)
Petradoria pumila (Nutt.) Greene	Urbatsch 11077 (LSU00137520)
Pityopsis falcata Nutt.	Unknown (Unknown)
Psilactis asteroides A.Gray	Stuessy 980 (TEX00138733)
Rayjacksonia phyllocephala DC.	Szubryt 774 (LSU00218375)
Rigiopappus leptocladus A.Gray	Tiehm 1123 (LSU00062449)
Sericocarpus tortifolius Nees	Urbatsch 11432 (LSU00178890)
Solidago decurrens Lour.	Unknown (Unknown)
Solidago rugosa Mill.	Abbott 23610 (MO100795087)
Solidago sp.	Vanderpool 429 (STAR014693)
Stenotus acaulis (Nutt.) Nutt.	Evert 16458 (RM577351)
Stenotus armerioides Nutt.	Nelson 35157 (LSU00116961)
Stenotus lanuginosus Greene	Evert 8019 (Unknown)
Stenotus pulvinatus (Moran) G.L.Nesom	Rebman 4159 (UCR s.n.)
Symphyotrichum dumosum (L.) G.L.Nesom	Abbott 23667 (FLAS s.n.)
Symphyotrichum subulatum (Michx.) G.L.Nesom	Unknown (Unknown)
Thurovia triflora Rose	Rosen 6165 (TEX00466706)
Toiyabea alpina (L.C.Anderson & Goodrich) R.P.Roberts, Urbatsch & Neubig	Tiehm 14043 (UTC00162139)
Tonestus eximius A.Nelson & J.F.Macbr.	Matson s.n. (LSU00063473)
Tonestus graniticus (Tiehm & L.M.Shultz) G.L.Nesom & D.R.Morgan	Tiehm 15338 (NY1153651)
Tonestus lyallii A.Nelson	Pojar s.n. (LSU00063476)
Tonestus peirsonii (D.D.Keck) G.L.Nesom & D.R.Morgan	Urbatsch 9258 (LSU00179176)
Tonestus pygmaeus A.Nelson	Hartman 69602 (LSU00063479)
Townsendia exscapa (Richardson) Porter	Rosche 75 (Unknown)
Tracyina rostrata S.F.Blake	Orndulb 10106 (UWL274773)
Triniteurybia aberrans (A.Nelson) Brouillet, Urbatsch & R.P.Roberts	Urbatsch 7812 (LSU00179317)
Xanthocephalum benthamianum Hemsl.	Panero 2257A (TEX00029083)
Xanthocephalum centauroides Willd.	Lane 2452d (TEX00139179)
Xanthocephalum sericocarpum A.Gray	Hendricks 482 (Unknown)
Xanthocephalum sphaerocephalum (A.Gray) Shinners	Bollwinkel 68 (Unknown)
Xylovirgata pseudobaccharis (S.F.Blake) Urbatsch & R.P.Roberts	Urbasch 2786 (LSU00179254)