

Adelinia and *Andersonglossum* (Boraginaceae), Two New Genera from New World Species of *Cynoglossum*

James I. Cohen

Kettering University, 2212C AB, 1700 University Ave., Flint, Michigan 48504, U. S. A.
(jcohen@kettering.edu)

Communicating Editor: Chuck Bell

Abstract—Recent phylogenetic evidence suggests that *Cynoglossum* (Boraginaceae), a cosmopolitan genus, is not monophyletic, but relationships among members of the genus remain uncertain. This is particularly the case for North American species of *Cynoglossum*. Utilizing DNA sequence data, a phylogeny has been reconstructed to investigate the evolutionary relationships among the New and Old World species of *Cynoglossum* and other members of Boraginaceae. The resulting phylogeny resolved that North American species of *Cynoglossum* are members of a clade distinct from the Old World species, and these North American species belong to two distinct lineages. *Cynoglossum occidentale* and *C. virginianum* are sister species, and *C. grande* is a member of a separate group. Given these evolutionary relationships in conjunction with diagnostic morphological features, two new genera are proposed for these species, *Andersonglossum* and *Adelinia*, with four name transfers: *Andersonglossum boreale*, *Andersonglossum occidentale*, *Andersonglossum virginianum*, and *Adelinia grande*. *Andersonglossum* bears sessile cauline leaves, pedicels recurved in fruit, and pollen with two shapes of pores and no transverse groove. In contrast, *Adelinia* develops petiolate cauline leaves, pedicels erect in fruit, and pollen with only one pore shape and a transverse groove.

Keywords—Amsinckiinae, *Cryptantha*, molecular systematics, *Oncaglossum*, taxonomy.

Cynoglossum L. (Boraginaceae) is a medium-sized genus with a cosmopolitan distribution (Zhu et al. 1995). The genus, which is the type of Cynoglosseae W. D. J. Koch, is characterized by heterocolpate pollen and glochidiate nutlets that bear submedial attachment to the gynobase. Recent phylogenetic work by Cohen (2011, 2014) and Weigend et al. (2013) has demonstrated that *Cynoglossum*, as it has been traditionally defined (e.g. Selvi and Sutorý 2012), is not monophyletic, and this is due to two factors. One is that multiple species from other genera, including *Cynoglossopsis* Brand, *Lindelofia* Lehm., *Paracaryum* Boiss., *Rindera* Pall., *Pardoglossum* Barbier & Mathez, *Solenanthus* Ledeb., *Trachelanthus* Klotzsch, *Paracynoglossum* Popov, and others, are nested among the Old World species of *Cynoglossum*. The second is that the few New World species of *Cynoglossum* are members of clades separate from that of the Old World species of the genus. Indeed, in the analyses of Weigend et al. (2013) the North American species represent an early-diverging group that colonized the continent prior to the explosive diversification of *Cryptantha* Lehm. ex G. Don and its relatives throughout western North and South America, and the South American species is a member of the clade that includes *Omphalodes* Mill. and *Myosotidium* Hook. The objective of the present study is to use plastid and nuclear ribosomal DNA regions to reconstruct a phylogeny of *Cynoglossum* and relatives in order to resolve relationships among North American species of the genus and relatives. Additionally, if upon critical analysis the North American species remain distinct from other members of *Cynoglossum*, then an appropriate taxonomic system that includes diagnostic morphological features will be constructed.

Four species of *Cynoglossum* are native to North America. Using morphological evidence, Sutorý (2010) recently segregated the Mexican endemic *C. pringlei* Greenm. into the genus *Oncaglossum* Sutorý. This separation was later supported by phylogenetic data, with *Oncaglossum* resolved as sister to Amsinckiinae Brand. (Cryptanthinae of Hasenstab-Lehman and Simpson [2012]), which includes *Cryptantha* and relatives (Cohen 2011, 2014). The other three North American species of *Cynoglossum* have been included in a phylogenetic analysis by Weigend et al. (2013). In their analysis, *C. occidentale* A. Gray and *C. virginianum* L. were sister species,

and *C. grande* Douglas ex Lehm. was closely related, but the relationship was ambiguous. The clade of *C. occidentale* + *C. virginianum* and *C. grande* formed a trichotomy with members of Amsinckiinae, including *Dasynotus daubenmirei* I. M. Johnst.

In 2012, Hasenstab-Lehman and Simpson reevaluated the taxonomy of Amsinckiinae (as Cryptanthinae) because their phylogenetic analyses provided evidence that *Cryptantha* and *Plagiobothrys* Fisch. & C. A. Mey. were not monophyletic. To this end, the authors revised the taxonomy for the subtribe, which now includes nine genera: *Amsinckia* Lehm., *Cryptantha*, *Eremocarya* Greene, *Greeneocharis* Gürke & Harms, *Harpagonella* A. Gray, *Johnstonella* Brand, *Oreocarya* Greene, *Pectocarya* DC. ex Meisn., and *Plagiobothrys*. The results of Cohen (2011, 2014) and Weigend et al. (2013) provide evidence that other New World members of Cynoglosseae (e.g. *Cynoglossum*, *Dasynotus* I. M. Johnst., and *Oncaglossum*) are closely related to Amsinckiinae, but these relationships either remain ambiguous or have not been adequately examined. In order to elucidate phylogenetic relationships among these species, the current study includes all four North American species that have been members of *Cynoglossum* as well as other species that are putatively related to Amsinckiinae. Furthermore, given the isolated position of these North American members of *Cynoglossum* from other members of the genus, including the type species *C. officinale* L., it seems likely that these North American species will need to be transferred to other genera.

MATERIALS AND METHODS

Taxon Sampling and Sequence Data—The present study includes 55 species (supplementary Appendix S1) from across Cynoglosseae. This sampling represents both morphological and geographic variation in the tribe. Sequence data from four DNA regions were included in the present study: two protein-encoding plastid DNA (cpDNA) regions (*matK* and *ndhF*), one cpDNA intergenic spacer (*trnL-trnF*), and the nuclear ribosomal DNA (nrDNA) internal transcribed spacer (ITS). Leaf material for new DNA isolations was obtained from individuals from wild populations. Additional sequence data for multiple species were obtained from GenBank. Appendix S1 includes GenBank numbers for all species in the present study as well as voucher information for new sequences.

DNA extraction was performed with dried plant tissue using a modified CTAB extraction method (Doyle and Doyle 1990) that included 2% PVP-40 in the CTAB extraction buffer. The PCR amplifications of the DNA regions were conducted using either published primers or those designed by the author (Cohen 2014). PCR mixtures, 25 mL in volume, consisted of 1 × PrimeSTAR GXL Taq Buffer (Takara Bio Inc., Japan), 100 mM dNTPs, 1 mM of primers, 1 mL of PrimeSTAR GXL Taq polymerase, and 0.1 mL to 2.5 mL DNA sample, depending on the DNA concentration. Amplifications were performed with an Eppendorf Mastercycler Pro, using the primers and annealing temperatures listed in Cohen (2014). The PCR products were separated on a 1% agarose gel and stained with ethidium bromide to determine if amplification had occurred. Prior to sequencing, PCR products were purified with the QIAquick PCR purification kit (Qiagen, Germany).

Sequencing reactions were performed with BigDye 3.1 terminators (Applied Biosystems [ABI], California) and locus-specific amplification primers. Sequencing products were precipitated using a modification of the ethanol/EDTA/sodium acetate method (ABI), and automated cycle sequencing was performed, with an ABI 3730 DNA Analyzer, by the Life Sciences Core Laboratory Center at Cornell University. Sequence trace files were compiled, examined, and edited with CodonCode Aligner (CodonCode Corporation, Deadham, Massachusetts). Sequences were deposited in GenBank (Appendix S1), and the matrix is available at TreeBASE (accession number 17336).

Initial alignments were performed with MUSCLE (Edgar 2004) as implemented by the European Bioinformatics Institute's MUSCLE server (<http://www.ebi.ac.uk/Tools/msa/muscle/>) using the default settings. Subsequent adjustments were made in Winclada ver. 1.7 (Nixon 2002). Gaps were coded using simple indel coding (Simmons and Ochoterena 2000). Approximately 33% of the sequence data is missing, but the resulting phylogeny is congruent with previous analyses that include greater taxon sampling (e.g. Weigend et al. 2013; Cohen 2014); therefore, this amount of missing data does not appear to considerably affect relationships in the resulting phylogeny.

Phylogenetic Analyses—Maximum parsimony (MP) and Bayesian inference (BI) phylogenetic analyses were conducted using TNT (Goloboff et al. 2008) and BayesPhylogenies V2 (Pagel and Meade 2004, 2008; Meade and Pagel 2008), respectively. Using nucleotide and structural characters (e.g. gaps), the MP analyses were undertaken, with 1,000,000 trees held in memory, and 10 independent iterations of 1,000 parsimony ratchet iterations (Nixon 1999), with 20 trees held per iteration and a 10% probability of upweighting and a 10% probability of downweighting, followed by 1,000 cycles of tree drifting; afterwards, 100 rounds of tree fusion and random sectorial searches were performed (Goloboff 1999). This search strategy was repeated 100 times, and then followed by TBR-max, swapping among all the most-parsimonious trees until completion.

Clade support was measured with TNT (Goloboff et al. 2008). Ten thousand jackknife replicates (36% removal probability) (Farris et al. 1996) were performed. For each replicate, 10 TBR searches were conducted, with 10 trees held after each replicate, and a total of 99,999 trees held in memory for the duration of the entire jackknife resampling.

For BI analyses, the data was partitioned between DNA sequence data and structural characters. The DNA sequence data was analyzed with a GTR model, which jModelTest (Darrriba et al. 2012) identified as the most appropriate model for the each of the four DNA regions, and four gamma categories and the reversible-jump branch length set mixture model (RJBLS) (Pagel and Meade 2004, 2008; Meade and Pagel 2008). Gaps were analyzed with the simplest model for the data. The BI analysis included 20,000,000 iterations, with a 5,000,000 iteration burnin, and a print frequency of 10,000 iterations. The resulting trees were viewed in BayesTrees V1.3 (<http://www.evolution.reading.ac.uk/BayesTrees.html>).

Micromorphology and Palynology of North American *Cynoglossum*—Leaves, flowers, pollen, and fruits of *C. grande*, *C. occidentale*, *C. virginianum*, and *Dasynotus daubenmirei* were examined using a scanning electron microscope. Dried plant material was mounted on stubs, coated with gold using a Denton Desk 5 sputter coater, and then images were captured at 10 kV with a JEOL model 6610-LVM.

RESULTS

Sequence Data—Together, the four DNA regions yielded 5,458 nucleotides, with *ndhF* the longest region (2,103 base pairs [bp]) and ITS the shortest (495 bp). A total of 343 informative nucleotide sites and 35 structural characters are pres-

TABLE 1. Summary of DNA regions included in analyses.

Region	Aligned length (bp)	Number of informative nucleotide sites	Number of informative structural characters	Total number of informative characters	Percent informative characters
<i>matK</i>	1,649	60	11	71	4.3%
<i>ndhF</i>	2,103	88	4	92	4.3%
<i>trnL-trnF</i>	1,211	95	20	115	9.5%
ITS	495	100	0	100	20.2%
Total	5,458	343	35	378	6.9%

ent among the four regions. Of the four DNA regions included in the present study, *trnL-trnF* yielded the greatest number of informative characters (115), and *matK* provided the fewest (71); however, ITS had the greatest number of informative nucleotides (100). The *trnL-trnF* spacer provided the greatest number of structural characters (20), and *ndhF* had the fewest (4). Statistics of the four DNA regions are presented in Table 1.

Phylogenetic Analyses—The MP analyses resulted in 420 most-parsimonious trees of 928 steps, with a consistency index (CI) of 0.53 and a retention index (RI) of 0.75. The RJBLS model in BayesPhylogenies resulted in four partitions, three for the DNA sequence data and one for the structural data. The consensus tree of the BI analysis had greater resolution and higher support values than the MP strict consensus tree. Indeed, 34 nodes in the BI analyses were supported by >0.90 posterior probability (PP) compared with only five nodes in the MP analyses that received >70% jackknife support (JK).

In the MP and BI analyses, the North American species of *Cynoglossum*, *Dasynotus*, and *Cryptantha* and relatives are members of clade distinct from the Old World species of *Cynoglossum* and relatives (Figs. 1 and 2; 0.95 PP in BI analyses). Additionally, the Old World species of *Cynoglossum* do not form a monophyletic group as species of *Pardoglossum*, *Lindelofia*, *Paracaryum* and others are distributed among members of the clade that includes the Old World species of the genus.

The North American species of *Cynoglossum* are resolved as early-diverging species of the clade that includes *Cryptantha* and relatives (Figs. 1 and 2). *Cynoglossum occidentale* and *C. virginianum* are sisters, forming a well-supported clade (99% JK, 1.00 PP). This clade is sister to one that includes *C. grande*, *D. daubenmirei*, and *Cryptantha* and relatives, with *C. grande* sister to the other species in the clade. *D. daubenmirei* is reconstructed as sister to species of *Cryptantha* and relatives (0.92 PP).

The phylogenetic relationships resolved from the MP and BI analyses are identical, with three exceptions: the resolution of the consensus tree and the placements of *Cryptantha intermedia* Greene and *Oncaglossum pringlei* (Greenm.) Sutorý. First, the MP consensus tree is less resolved than the BI tree; however, in both trees the North American species of *Cynoglossum* are still members of a clade distinct from the Old World species of the genus. Second, in the BI analysis *C. intermedia* is resolved as sister to the North American species of *Cynoglossum*, *Dasynotus*, and *Cryptantha* and relatives, although this relationship receives low support (0.52 PP). In the MP analysis, *C. intermedia* is nested among *Cryptantha* and relatives and is sister to *C. fendleri* Greene (Fig. 1). In the consensus tree of the BI analyses, both of these species are on longer branches than are other species (Fig. 2). Third, in

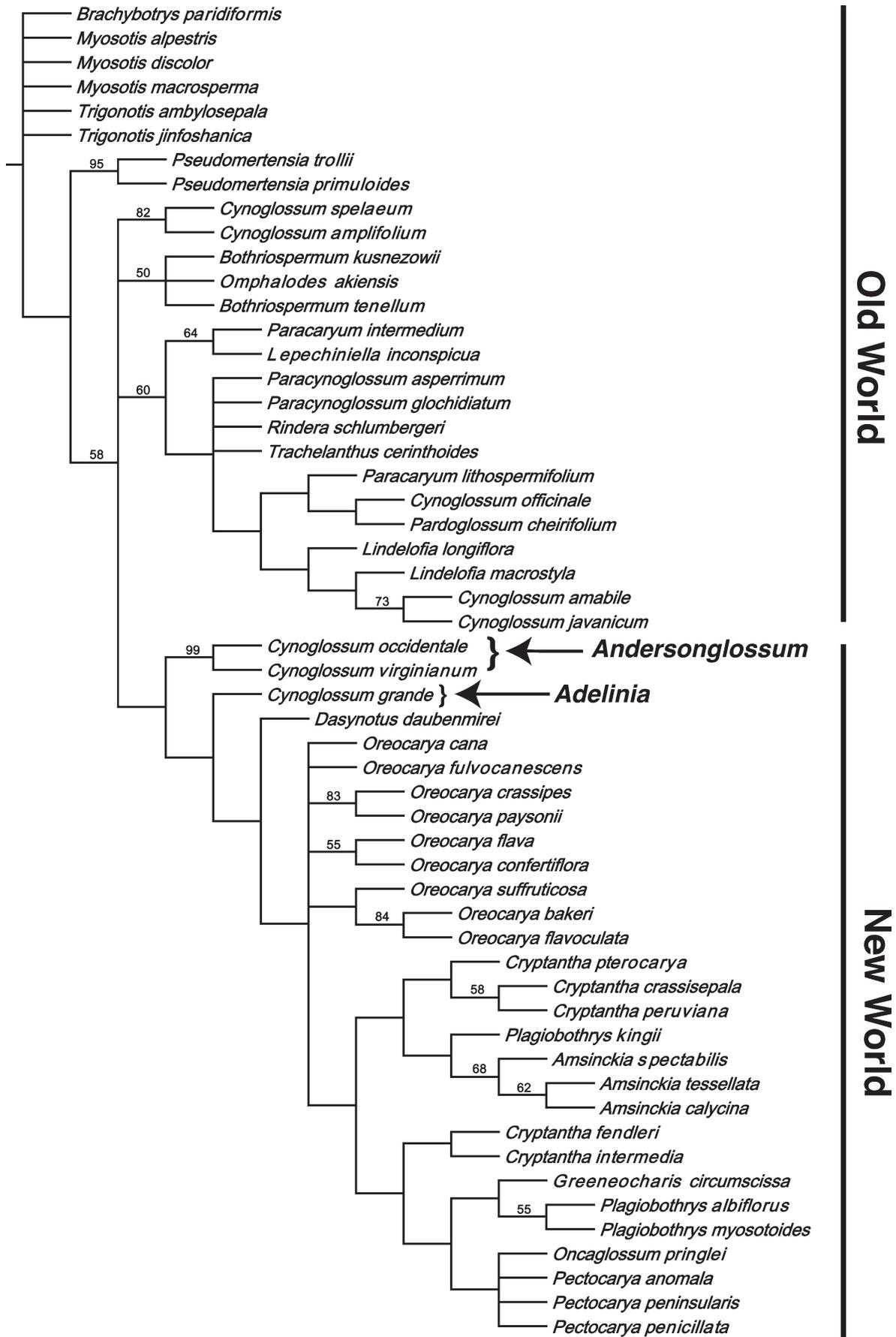


FIG. 1. Strict consensus tree of 420 most-parsimonious trees of 928 steps, CI=0.53, RI=0.75. Numbers above branches are jackknife values >50%.

Delivered by Publishing Technology to: Michael Simpson IP: 146.244.235.206 on: Mon, 21 Sep 2015 23:37:14
Copyright (c) American Society for Plant Taxonomists. All rights reserved.

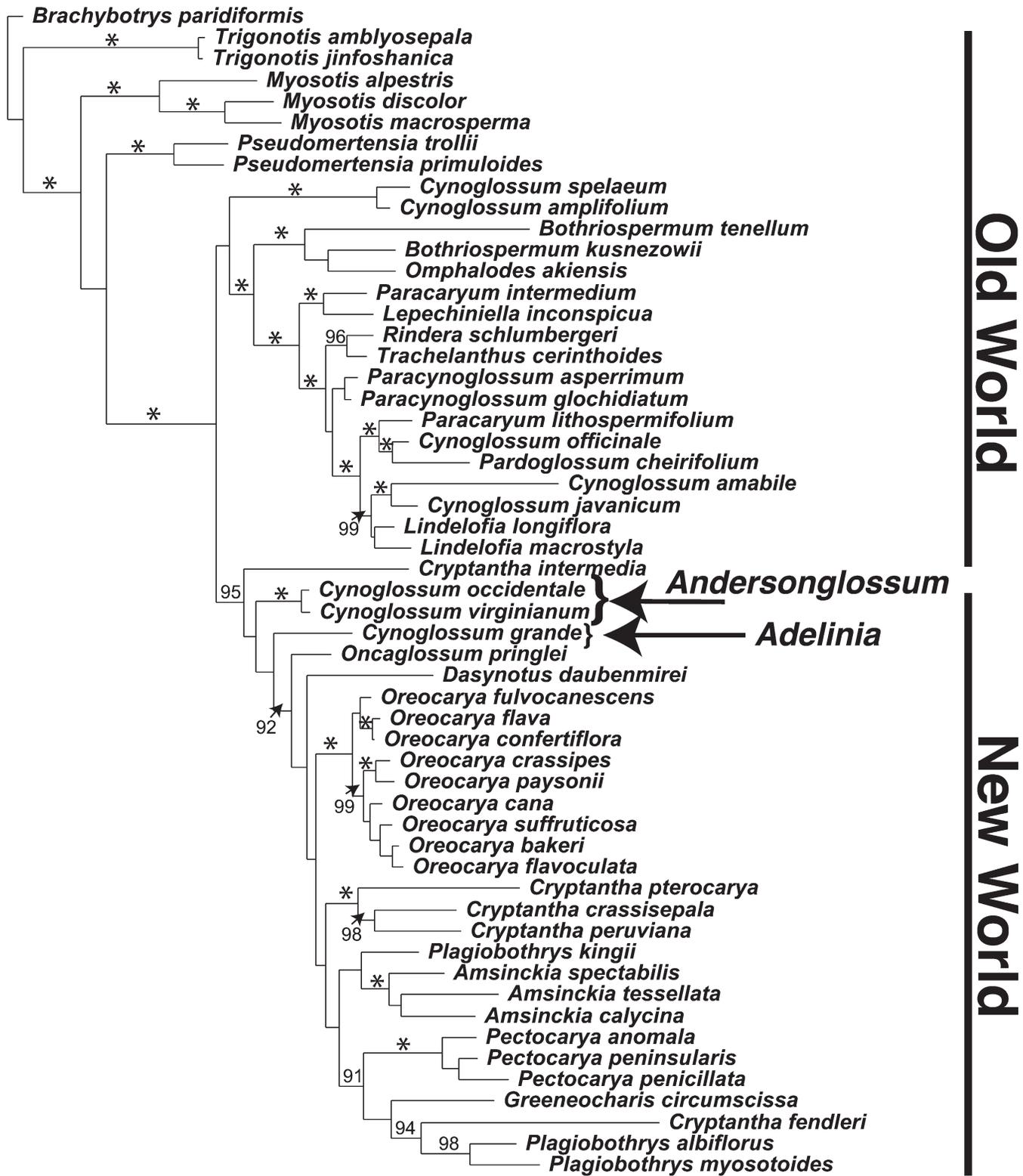


FIG. 2. Consensus tree of Bayesian inference phylogeny. Numbers above branches are posterior probabilities >0.9, and asterisks (*) denote posterior probabilities of 1.

the MP analysis *O. pringlei* is a member of a small clade that also includes three species of *Pectocarya*, but in the BI analysis, *O. pringlei* is sister to a larger clade composed of *Dasynotus* and *Cryptantha* and relatives. Support values (JK and PP) are

low for both placements, but in both topologies, *O. pringlei* is closely related to species that bear glochidiate nutlets (although the type of glochid differs between *Pectocarya* and species of *Cynoglossum*).

Micromorphology and Palynology of North American *Cynoglossum*—The micromorphology of the leaves of the three North American species of *Cynoglossum* is quite similar, with all bearing trichomes with papillae (Fig. 3A). The nutlets are also similar among the three species. The nutlets are glochidiate, with recurved hooks at the apex of each glochid (resembling a grappling hook), and small protuberances on the nutlet surface (Fig. 3B). Although the number of hooks at the apex each glochid varies, *C. occidentale* and *C. virginianum* tend to produce nutlets with a greater number of hooks (4–6) than those from *C. grande* (3–5 hooks).

The pollen of the three North American species of *Cynoglossum* and of *Dasynotus daubenmirei* is ellipsoid with three colpi and three pseudocolpi. The pollen grains range in size from 11–15 mm in length and 8–10 mm in width. The pollen of *C. grande* and *D. daubenmirei* (Fig. 4A, D) develops a transverse groove sensu Hargrove and Simpson (2003) and Spaeth (2014), but this is not the case for the other two species of *Cynoglossum*. *Cynoglossum occidentale* and *C. virginianum* produce pollen in which the shape of the colpi and pseudocolpi differs (Fig. 4B, C). In contrast, the pollen grains of *C. grande* and *D. daubenmirei* have colpi and pseudocolpi that are the same shape (Fig. 4A).

DISCUSSION

The North American species of *Cynoglossum* are not members of the same clade as the Old World species of *Cynoglossum*, a result Cohen (2011, 2014) and Weigend et al. (2013) also recovered. Cohen (2011, 2014), utilizing 10 cpDNA regions and three cpDNA regions and ITS in two studies respectively, recovered *Oncaglossum* as sister to members of Amsinckiinae, although sampling was quite limited in the earlier study. Weigend et al. (2013) employed two cpDNA regions to resolve *C. grande*, *C. occidentale*, and *C. virginianum* as close relatives to the species of Amsinckiinae, including *Dasynotus*. Although these authors recovered congruent results to those in the present study, their analyses could not resolve the relationships among these three species and members of Amsinckiinae, and their study did not include *Oncaglossum*.

The present study includes all four of the North American species that have been members of *Cynoglossum*, and the results provide evidence that these North American species are not members of a monophyletic group. *Cynoglossum occidentale* and *C. virginianum* are sisters (Figs. 1 and 2), and this relationship is well supported (99% JK, 1.00 PP), a result also identified by Weigend et al. (2013). The clade of *C. occidentale* and *C. virginianum* is sister to *C. grande* and other members of Amsinckiinae. The exception is *Cryptantha intermedia* in the BI analysis, which is sister to the North American species of *Cynoglossum* and other members of Amsinckiinae. *Cynoglossum grande* is sister to *Dasynotus* and *Cryptantha* and relatives. *O. pringlei*, a Mexican species that was included in *Cynoglossum* until recently (Sutorý 2010), is resolved in two different regions of the tree depending on the type of analysis (Figs. 1 and 2), but, just as with the other North American species of *Cynoglossum*, *Oncaglossum pringlei* is not closely related to the Old World species of *Cynoglossum*.

Given these phylogenetic relationships, the North American species of *Cynoglossum* should no longer be included in *Cynoglossum*; instead, *C. occidentale* and *C. virginianum* (including *C. boreale* Fernald, a species sometimes segregated from

C. virginianum, but not by the author) should be transferred to one genus (*Andersonglossum*) and *C. grande* to another (*Adelinia*). These relationships are supported by more than DNA sequence data and branching patterns. *Andersonglossum* and *Adelinia* differ from the Old World species of *Cynoglossum* by their shorter, broadly triangular areolae (Weigend et al. 2013) and the lack of leaves or bracts subtending flowers and inflorescences.

Andersonglossum and *Adelinia* differ from each other by vegetative, pollen, and fruit characteristics. The pollen of *Andersonglossum* and *Adelinia* is similar in size and shape (Fig. 4), but species of the two genera differ in the presence of a transverse groove (sensu Hargrove and Simpson [2003] and Spaeth [2014]) and the shape of the pollen pores. The pollen of *Andersonglossum* lacks a transverse groove, and the pollen pores differ in shape between the colpi and pseudocolpi. In contrast, the pollen of *Adelinia* has a transverse groove, and the pollen pores are the same shape (Fig. 4). Other species of Amsinckiinae also develop pollen with a transverse groove (Hargrove and Simpson 2003; Spaeth 2014), including *Dasynotus daubenmirei*, a perennial species endemic to Idaho. *D. daubenmirei* also develops pollen with colpi and pseudocolpi that differ in shape (Fig. 4D). Weigend et al. (2013) mentioned that due to the presence of a keeled nutlet, a feature of many members of Amsinckiinae, *D. daubenmirei*, which is resolved as sister to *Cryptantha* and relatives (Figs. 1 and 2), is transitional between the North American species of *Cynoglossum* and the other species of Amsinckiinae. The pollen, as well as the presence of hairs, but not glochids, on the nutlets of *D. daubenmirei*, appears to be an additional transitional feature between the two groups. Some species of Amsinckiinae develop pollen with polar pseudoapertures (Hargrove and Simpson 2003; Spaeth 2014), and this is the case for *O. pringlei* (Sutorý 2010). This pollen feature can help distinguish the Mexican species from its northern New World relatives.

In addition to pollen characteristics that differ between *Andersonglossum* and *Adelinia*, species of the two genera also differ in vegetative features. *Andersonglossum* develops cauline leaves that are sessile, and the blade ranges in shape from spatulate to lanceolate to oblanceolate. *Adelinia* bears cauline leaves that are petiolate, and the blade is deltate.

In flower, the pedicels of the species of both genera are erect, but this changes during fruit development. In *Andersonglossum*, the pedicel bends backwards and becomes recurved 180° when fruits develop, but the pedicel of *Adelinia* remains erect during fruit development.

The recognition of two new genera derived from the North American species formerly in *Cynoglossum* should highlight two additional issues that will require taxonomic modifications. The first relates to the Old World species of *Cynoglossum*. Weigend et al. (2013) and Cohen (2014) have resolved that *Cynoglossum* is not monophyletic, and the present study provides a useful taxonomic scheme for the North American species; however, the Old World species remain members of a geographically widespread non-monophyletic genus. As with the North American species, the Old World species of *Cynoglossum* and close relatives should be reevaluated in order to identify the most appropriate taxonomic system for the group. The second issue is that Amsinckiinae has previously included *Cryptantha* and relatives (e.g. *Plagiobothrys*, *Amsinckia*, etc.), but Simpson (<http://www.sci.sdsu.edu/plants/boraginaceae/>) has proposed a broader circumscription for

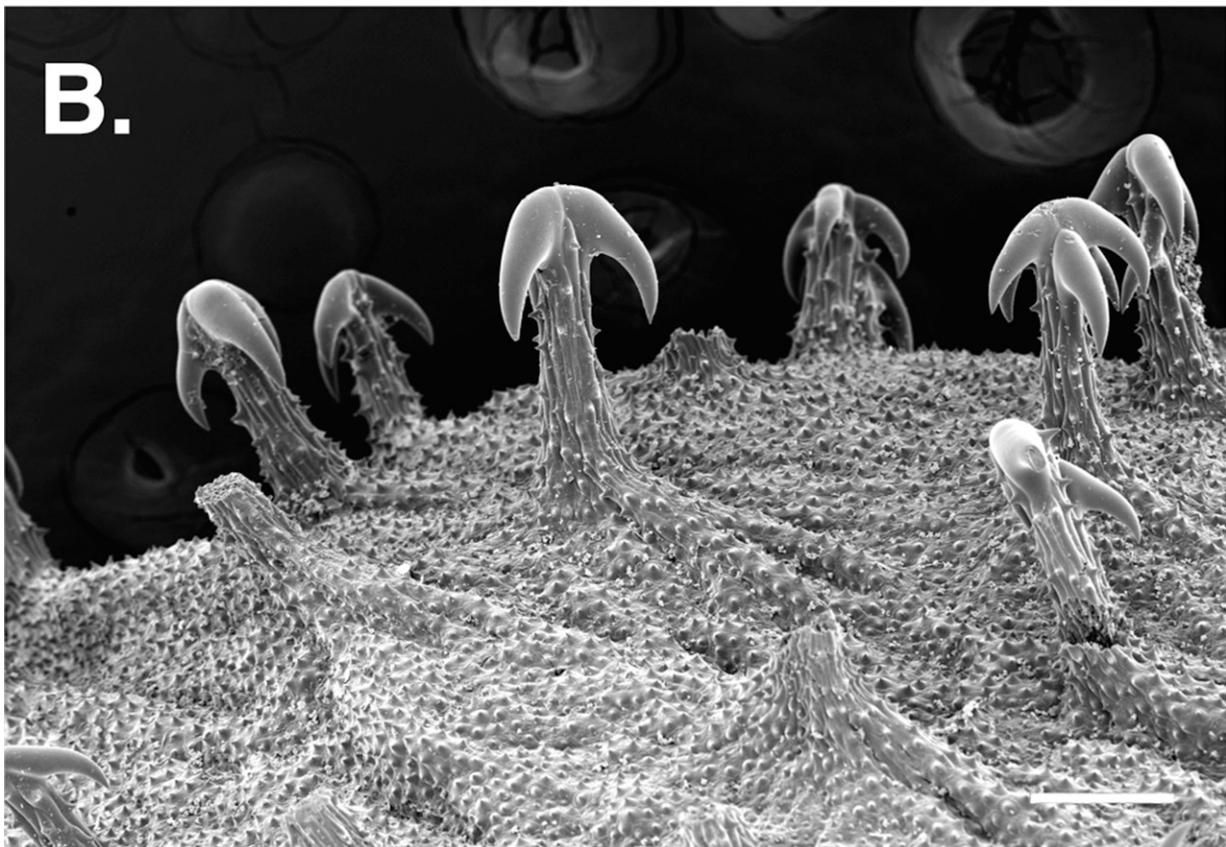
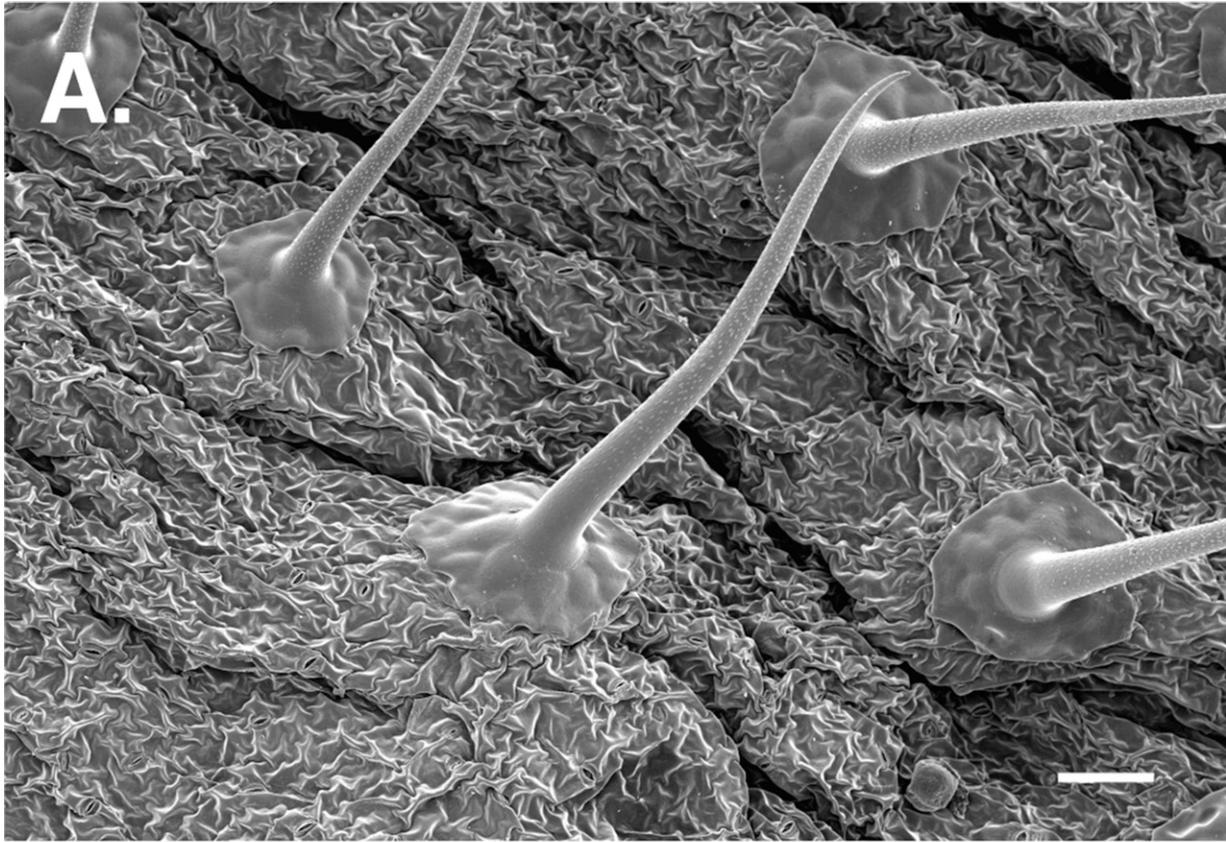


FIG. 3. Scanning electron microscope images of: A. Leaf surface of *Cynoglossum occidentale* (scale bar = 100 μ m, 100 \times). B. Nutlet surface of *Cynoglossum grande* (scale bar = 200 μ m, 75 \times).

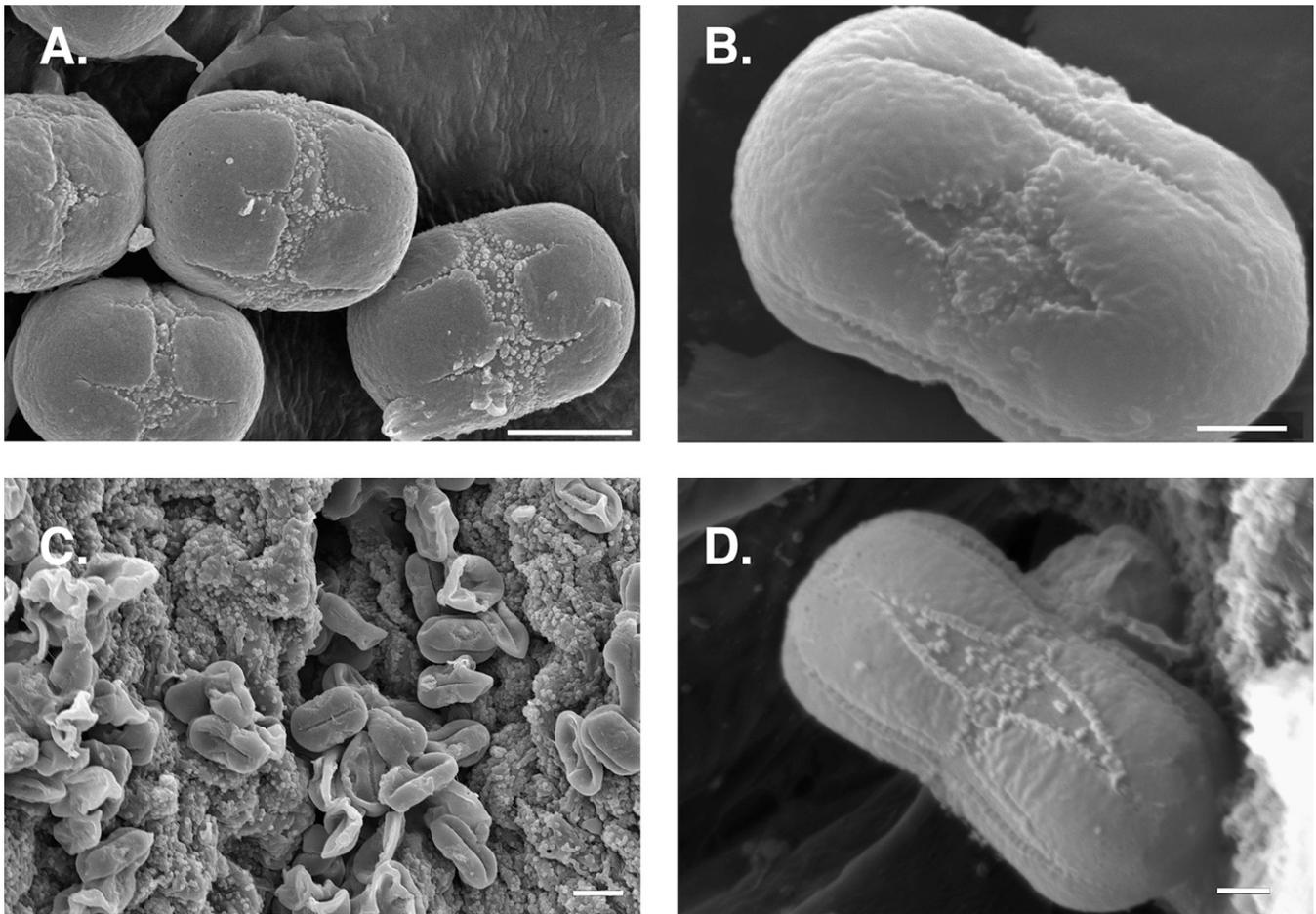


FIG. 4. Scanning electron microscope images of pollen. A. *Cynoglossum grande* (scale bar = 5 µm, 5,000×). B. *Cynoglossum virginianum* (scale bar = 2 µm, 9,000×). C. *Cynoglossum occidentale* (scale bar = 10 µm, 1,000×). D. *Dasynotus daubenmirei* (scale bar = 1 µm, 10,000×).

the subtribe to include *Dasynotus* and the North American species formerly in *Cynoglossum* (i.e. *Adelinia*, *Andersonglossum*, and *Oncaglossum*). As the broader limits of the subtribe become well defined, future studies should focus on identification of diagnostic features and synapomorphies to distinguish Amsinckiinae from other taxa in Cynoglosseae and Boraginaceae.

It is interesting to note that *Adelinia* and *Andersonglossum* develop corollas that are blue to white or purple to red, and, with the exception of white corollas, these colors are uncommon among members of Amsinckiinae (Simpson and Hasenstab 2009). Blue, purple, and red corollas are present among other North American members of Cynoglosseae, such as *Mertensia* Roth and *Hackelia* Opiz, but most species of Amsinckiinae bear corollas that are white, yellow, or orange. Perhaps this shift in corolla color is associated with a change in fruit type from one with glochids to one that is eglochidiate.

TAXONOMIC TREATMENT

Adelinia J. I. Cohen, gen. nov.—Type: *Adelinia grande* (Douglas ex Lehm.) J. I. Cohen

Similar to *Cynoglossum*, but the cauline leaves are deltate and petiolate, compared to elliptical or lanceolate cauline leaves that are sessile; the inflorescences are ebracteate;

the pollen has a transverse groove; and pedicels are erect in fruit.

Erect perennial herbs to 75 cm. Stem glabrous. Taproot. Leaves alternate, simple, cauline and basal, basal leaves epetiolate, cauline leaves petiolate, 5–21 × 2–10 cm, leaf margin entire, indument glabrous to strigose to sericeous, Inflorescences terminal, 15–25 flowered scorpioid cymes, ebracteate. Flowers pedicellate, actinomorphic, pentamerous, calyx 5-lobed to the base with linear to lanceolate lobes; corolla blue and white, salverform, glabrous, 5-lobed, lobes elliptical, flared, faucal appendages present, white; stamens 5, included, anthers ellipsoid; gynoecium superior, ovary 4-parted, gynobase pyramidal, style included, stigmas 2, terminal. Nutlets 4 or fewer by abortion, ovoid, glochidiate, brown to yellow, submedial attachment, attachment scar broad triangular.

Etymology—This genus is named for my daughter, Adeline Etta Cohen (b. 2014), who makes every day better.

Adelinia grande (Douglas ex Lehm.) J. I. Cohen, comb. nov. *Cynoglossum grande* Douglas ex Lehm. Nov. Stirp. Pug. 2: 25. 1830.—TYPE: CANADA. British Columbia: In shady pine wood near Fort Vancouver. 1825, *Douglas s. n.* (neotype [designated here]: K [image!]; BM [image!]).

In his book, Lehmann (1830) mentions that *C. grande* is based on a manuscript by Douglas, but no type was designated nor were any specimens cited, and none of Douglas'

specimens bear an annotation designating one as a type. Therefore, in the spirit of Lehmann and Douglas, Douglas' 1825 specimen at Kew, which seems likely to be one of the specimens Lehmann saw before describing the species, is designated as the neotype for *A. grande*.

Andersonglossum J. I. Cohen, gen. nov.—Type: *Andersonglossum virginianum* (L.) J. I. Cohen

Similar to *Cynoglossum*, but the cauline leaves are sessile; the inflorescences are ebracteate; the apertures and pseudoapertures of the pollen grains differ in shape; and pedicels are recurved in fruit.

Erect perennial herbs to 1 m. Stem hispid to strigose to pilose to sericeous, Taproot. Leaves alternate, simple, cauline and basal, petiolate, 3–38 × 0.5–11 cm, leaf margin entire, indument strigose to sericeous, Inflorescences terminal, 15–25 flowered scorpioid cymes, ebracteate. Flowers pedicellate, actinomorphic, pentamerous, calyx 5-lobed to the base with linear lobes; corolla blue and white to red to purple, salverform, glabrous, 5-lobed, lobes elliptical, erect to flared, faucal appendages present, white to red to purple; stamens 5, included, anthers ellipsoid; gynoecium superior, ovary 4-parted, gynobase pyramidal, style included, stigmas 2, terminal. Nutlets 4 or fewer by abortion, ovoid, glochidiate, brown to yellow, submedial attachment, attachment scar broad triangular.

Etymology—This genus is named for William Russell Anderson (1942–2013; Daniel and Weller 2009), an incomparable professor, botanist, and person, who inspired me to study plant systematics.

Andersonglossum boreale (Fernald) J. I. Cohen, comb. nov. *Cynoglossum boreale* Fernald *Rhodora* 7: 250. 1905. *Cynoglossum virginianum* subsp. *boreale* (Fernald) A. Haines *Stantec Bot. Notes* 13: 3. 2010. *Cynoglossum virginianum* var. *boreale* (Fernald) Cooperr. *Michigan Bot.* 23: 166. 1984.—TYPE: CANADA. Quebec: Little Cascapedia River, July 17, 1905, E. F. Williams, J. F. Collins, & M. L. Fernald s. n. (lectotype: GH [image!]).

Although the author does not accept *A. boreale* as distinct from *A. virginianum*, given that it is accepted by other botanists, the appropriate new combination has been made.

Andersonglossum occidentale (A. Gray) J. I. Cohen, comb. nov. *Cynoglossum occidentale* A. Gray *Proc. Amer. Acad. Arts* 10: 58. 1874.—TYPE: U.S.A. California: Sierra Co. and California, 1874, J. G. Lemmon 667 (holotype: GH [image!]).

Andersonglossum virginianum (L.) J. I. Cohen, comb. nov. *Cynoglossum virginianum* L. *Sp. Pl.* 1: 134. 1753.—TYPE: U.S.A. Virginia: Habitat in Virginia, Clayton 257 (lectotype: BM [image!]).

KEY TO *ADELINIA*, *ANDERSONGLOSSUM*, AND *ONCAGLOSSUM* (THE NORTH AMERICAN SPECIES FORMERLY INCLUDED IN *CYNOGLOSSUM*)

1. Corolla green to lemon yellow to brown, inflorescence somewhat bracteate, pollen with equatorial apertures and pseudoapertures and polar pseudoapertures; plants of Mexico *Oncaglossum pringlei*
1. Corolla white to blue to red to purple, inflorescences ebracteate, pollen with only equatorial apertures and pseudoapertures; plants of the U. S. A and Canada 2
 2. Cauline leaves petiolate, pedicels not recurved in fruit, pollen pores of the same shape, stems glabrous *Adelinia grande*
 2. Cauline leaves sessile, pedicels recurved in fruit, pollen pores of different shapes, stems pubescent 3
 3. Corolla blue to white, style < 3.5 mm in length; plants of the northern and eastern (not western) U. S. A. and Canada *Andersonglossum virginianum*
 3. Corolla purple to red, style > 4 mm in length; plants of California and Oregon *Andersonglossum occidentale*

ACKNOWLEDGMENTS. The author would like to thank M. H. Alford and S. C. Meyers for providing plant material, and C. D. Kellogg, C. Anderson, three anonymous reviewers, and C. D. Bell for carefully reading and commenting on the manuscript. L. Solis and M. Gallegos took wonderful SEM images of the studied species. CodonCode Corporation provided a free license of CodonCode Aligner through the CodonCode Aligner License Grant Program. Texas A&M International University provided funding for the project. I am grateful to MICH, TEX/LL, and WTU for loaning specimens or allowing me to visit in order to better understand the morphological variation of the studied species.

LITERATURE CITED

- Cohen, J. I. 2011. A phylogenetic analysis of morphological and molecular characters of Lithospermum L. (Boraginaceae) and related taxa: Evolutionary relationships and character evolution. *Cladistics* 27: 559–580.
- Cohen, J. I. 2014. A phylogenetic analysis of morphological and molecular characters of Boraginaceae: Evolutionary relationships, taxonomy, and patterns of character evolution. *Cladistics* 30: 139–169.
- Daniel, T. F. and S. G. Weller. 2009. William R. Anderson – Recipient of the 2008 Asa Gray Award. *Systematic Botany* 34: 1–3.
- Darriba, D., G. L. Taboada, R. Doallo, and D. Posada. 2012. jModelTest2: More models, new heuristics and parallel computing. *Nature Methods* 9: 772.
- Doyle, J. J. and J. L. Doyle. 1990. Isolation of plant DNA from fresh tissue. *Focus (San Francisco, Calif.)* 12: 13–15.
- Edgar, R. C. 2004. MUSCLE: multiple sequenced alignment with high accuracy and high throughput. *Nucleic Acids Research* 32: 1792–1797.

- Farris, J. S., V. A. Albert, M. Källersjö, D. Lipscomb, and A. G. Kluge. 1996. Parsimony jackknifing outperforms neighbor-joining. *Cladistics* 12: 99–124.
- Goloboff, P. 1999. Analyzing large data sets in reasonable times: Solutions for composite optima. *Cladistics* 15: 415–428.
- Goloboff, P., J. S. Farris, and K. C. Nixon. 2008. TNT, a free program for phylogenetic analysis. *Cladistics* 24: 774–786.
- Hargrove, L. and M. G. Simpson. 2003. Ultrastructure of heterocolpate pollen in *Cryptantha* (Boraginaceae). *International Journal of Plant Sciences* 164: 137–151.
- Hasenstab-Lehman, K. and M. G. Simpson. 2012. Cat's eyes and popcorn flowers: Phylogenetic systematics of the genus *Cryptantha* s.l. (Boraginaceae). *Systematic Botany* 37: 738–757.
- Lehmann, J. G. C. 1830. *Novarum et Minus Cognitarum Stirpium Pugillus*. Hamburg: Hamburgensium Gymnasio Academico.
- Meade, A. and M. Pagel. 2008. A phylogenetic mixture model for heterotachy. Pp. 29–41 in *Evolutionary biology from concept to application*, ed. P. Pontarotti. Heidelberg: Springer Verlag.
- Nixon, K. C. 1999. Parsimony ratchet, a new method for rapid parsimony analysis. *Cladistics* 15: 407–414.
- Nixon, K. C. 2002. WinClada ver. 1.7. Ithaca, New York: Published by author.
- Pagel, M. and A. Meade. 2004. A phylogenetic mixture model for detecting pattern-heterogeneity in gene sequence or character-state data. *Systematic Biology* 53: 571–581.
- Pagel, M. and A. Meade. 2008. Modelling heterotachy in phylogenetic inference by reversible-jump Markov chain Monte Carlo. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences* 363: 3955–3964.
- Selvi, F. and K. Sutorý. 2012. A synopsis of the genus *Cynoglossum* (Boraginaceae-Cynoglosseae) in Italy. *Plant Biosystems* 146: 461–479.

- Simmons, M. P. and H. Ochoterena. 2000. Gaps as characters in sequence-based phylogenetic analyses. *Systematic Biology* 49: 369–381.
- Simpson, M. G. and K. E. Hasenstab. 2009. *Cryptantha* of southern California. *Crossosoma* 35: 1–59.
- Spaeth, R. 2014. *Morphological character mapping on a molecular phylogeny using pollen variation in the Cryptanthinae (Boraginaceae)*. M.S. thesis. Rohnert Park, California: Sonoma State University.
- Sutorý, K. 2010. *Oncaglossum*, a new genus of Boraginaceae, tribe Cynoglosseae, from Mexico. *Novon* 20: 463–469.
- Weigend, M., F. Luebert, F. Selvi, G. Brokamp, and H. H. Hilger. 2013. Multiple origins for Hound's tongues (*Cynoglossum* L.) and Navel seeds (*Omphalodes* Mill.) – The phylogeny of the borage family (Boraginaceae s.str.). *Molecular Phylogenetics and Evolution* 68: 604–618.
- Zhu, G., H. Riedl, and R. V. Kamelin. 1995. Boraginaceae. Pp. 329–427 in *Flora of China* vol. 16 (Gentianaceae through Boraginaceae), eds. Z. Y. Wu and P. H. Raven. Beijing and St. Louis: Science Press and Missouri Botanical Garden Press.