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Generic Placement of the Former *Condaliopsis* (Rhamnaceae) species

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Abstract

Condaliopsis is a genus of eight thorny shrub species. Previous morphological research shed doubt on the validity of *Condaliopsis* as a distinct genus in Rhamnaceae. *Condaliopsis* species were transferred to one of two genera, *Ziziphus* or *Condalia,* but some authors continue to recognize *Condaliopsis*. A recent phylogenetic study did not support *Condaliopsis* as monophyletic and placement of *Condaliopsis* species in either *Ziziphus* or *Condalia* was not straightforward. To clarify the generic placement of these eight species, we conducted phylogenetic analyses based on two nuclear loci (nrITS and 26S), two chloroplast loci (*trnL-F* and *trnQ-rps16*) and morphological characters. We present evidence that five of the *Condaliopsis* species should remain in *Ziziphus*, one should remain in *Condalia*, and two should be transferred from *Ziziphus* to *Condalia*. One of these species had an existing binomial within *Condalia, Condalia parryi,* and one required a new combination, *Condalia celata*. *Condalia celata* is a federally listed endangered species with a limited range in Florida.

Keywords: *Ziziphus celata*

Introduction

The cosmopolitan mostly woody plant family Rhamnaceae includes 52 genera and roughly 900 species (Stevens 2001, onwards) and includes several economic species including *Ziziphus jujuba* Miller (1768: sin page no.) (Chinese jujube)*, Z. mauritiana* Lamarck (1789: 319) (Ber), and the weedy *Rhamnus cathartica* Linnaeus (1753: 193) (Common buckthorn). Three genera, *Ziziphus* Miller (1754: sin page no.)*, Condalia* Cavanilles (1799: 39)*,* and *Condaliopsis* (Weberb.) Suessenguth (1953: 134), although not closely related (Richardson *et al.* 2000a), share morphological similarities that resulted in the back and forth generic placement of several species (Weberbauer 1895, Johnston 1962, 1963).

All three genera are composed of thorny shrubs that occur in sub-tropical to tropical regions with *Ziziphus* also including tree species with spines or thorns. *Condalia* is a genus of 18 species in North and South America with the highest diversity in Mexico. The genus *Ziziphus* is a paraphyletic, pantropical genus with approximately 100 species (Medan & Schirarend 2004) and is split geographically into two distinct lineages (Record 1939, Record & Hess 1943, Johnston 1963, Schirarend 1991, Islam & Simmons 2006). One well-supported lineage of approximately 30 *Ziziphus* species occurs in the Americas (Islam & Simmons 2006). For evolutionary questions, this group is referred to here as New World (NW) *Ziziphus* and is considered separately from the Old World (OW) lineage as they are not sister lineages (Islam & Simmons 2006).

Given confusion regarding the placement of a number of species as *Condalia, Condaliopsis* or *Ziziphus,* we define *Condaliopsis* species as those species that were placed in *Condaliopsis* by Suessenguth (1953), or following his definition of the genus should have been placed within *Condaliopsis* (Table 1). Under this definition, *Condaliopsis* includes eight species restricted to North America. Because not all of these species have names under *Condaliopsis* (discussed more fully below), when referring to species we use the names proposed by Johnston (1962, 1963) (Table 1) with the addition of *Z. celata* Judd & Hall (1984: 382) named after Johnston's publications but fitting with Suessenguth's definition of *Condaliopsis*.

The history of nomenclature for *Ziziphus*, *Condalia* and *Condaliopsis* is complex, with multiple amendments. In

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1895, Weberbauer placed the three NW *Ziziphus* species, *Z. obtusifolia* (Hook. ex Torr. & A. Gray) Gray (1849: 170), *Z. lycioides* Gray (1850: 168) (syn. of *Z. obtusifolia*), and *Z. parryi* Torrey (1859: 46 as *"Zizyphus"*), with unequal, meristematic, thorn-tipped branchlets into *Condalia*. The other NW *Ziziphus* species with paired non-meristematic, thorn-tipped branchlets (Tourn *et al.* 1990) were left in *Ziziphus*. The species transferred to *Condalia* were placed into subgenus *Condaliopsis* (Table 1), because of the presence of two placentas in their fruits compared to one placenta. All other *Condalia* species with one placenta where placed in subgenus *Eucondalia* (Weberbauer 1895). Suessenguth (1953) raised *Condaliopsis* to the generic level and added *Condalia velutina* Johnston (1939: 236) and *Condalia lloydii* Standley (1923: 714) (syn: *Z. lloydii* (Standl.) Johnston (1962: 367) to *Condaliopsis* (Table 1). Based on his definition of *Condaliopsis*, several species of *Ziziphus* including *Z. mexicana* Rose (1895: 315 as *"Zizyphus"*), *Z. pedunculata* (Brandegee) Standley (1923: 713 as *"Zizyphus"*) (syn: *Condalia pedunculata* Brandegee (1909: 384), *Condalia seleri* Loesener (1911: 355), *Condaliopsis* (?) *seleri* (Loes.) Suessenguth (1953: 135, 392), and *Z. yucatanensis* Standley (1932: 16 as *"Zizyphus"*) should have also been placed within this genus. For this study, we consider these species *Condaliopsis*.

TABLE 1. *Condaliopsis* species tested here compared to nomenclature by earlier authors. We are following Johnston (1962, 1963) as well as recognizing *Z. celata,* which was published after Johnston's publications. Syn = Synonym.

Species	**Gray (1849, 1850); Torrey (1859)**	**Weberbauer (1895)** (subgenus *Condaliopsis*)	**Suessenguth (1953)**	**Johnston (1962, 1963)**
Condalia velutina			*Condaliopsis velutina*	*Condalia velutina*
Z. lloydii			*Condaliopsis lloydii*	*Z. lloydii*
Z mexicana				*Z. mexicana*
Z obtusifolia var. obtusifolia	*Z. obtusifolia*	*Condalia obtusifolia*	*Condaliopsis obtusifolia*	*Z. obtusifolia var. obtusifolia*
Syn: *Z. obtusifolia var. obtusifolia*	*Z. lycioides*	*Condalia lycioides*	*Condaliopsis lycioides*	Syn: *Z. obtusifolia var. obtusifolia*
Z. parryi	*Z. parryi*	*Condalia parryi*	*Condaliopsis parryi*	*Z. parryi*
Syn: *Z. pedunculata*			*Condaliopsis* (?) *seleri*	Syn: *Z. pedunculata*
Z. pedunculata				*Z. pedunculata*
Z. yucatanensis				*Z. yucatanensis*
Z. celata				

After careful examination of *Condalia*, *Condaliopsis*, and *Ziziphus*, Johnston (1962) transferred Suessenguth's *Condaliopsis* species back to *Ziziphus* except for *Condaliopsis velutina* (I.M. Johnst.) Suessenguth (1953: 135, 392), which was transferred back to *Condalia* (Table 1). Johnston (1962) also provided evidence for the *Condaliopsis*-like NW *Ziziphus* species, *Z. mexicana*, *Z. pedunculata*, and *Z. yucatanensis,* to remain in *Ziziphus*. According to Johnston (1962) *Condaliopsis* was no longer a valid genus, however, subsequent studies continue to recognize *Condaliopsis* (Schirarend 1991, Richardson *et al.* 2000b) and names of the species remain unresolved (The Plant List 2013).
Twenty years after Johnston's work, the rare, federally listed Floridian endemic, *Ziziphus celata*, was discovered and named (Judd & Hall 1984) based on a single specimen. This species shares many traits in common with those species previously placed in *Condaliopsis* in that its reproductive characters show affinity with *Ziziphus,* but its vegetative characters are more similar to *Condalia*. The authors, following Johnston, placed the species within *Ziziphus*. Given its federally listed status, we pay special attention to its initial taxonomic placement, and its relationships with other taxa.

Further work, both morphological and explicitly phylogenetic, mirrors the confusion over the generic placement of *Condaliopsis* species. Morphological studies with a limited taxon and character sampling support Suessenguth's *Condaliopsis* as morphologically distinct from other NW *Ziziphus* species based on differences in thorn morphology (as mentioned above), the number of serial buds per node (Tourn *et al.* 1990), and possibly wood anatomy (Schirarend 1991). The first molecular-based phylogenetic analyses by Islam & Simmons (2006) supported Johnston's (1962)

transfer of *Z. obtusifolia* to NW *Ziziphus* but not the placement of *Z. celata*. This species was more closely related to genera in the tribe Rhamneae, which includes *Condalia*. *Ziziphus* belongs to another tribe, which is not closely related to Rhamneae. The same analysis suggested that *Condaliopsis* is not supported as monophyletic, but wholesale transfer of species to *Ziziphus* was also not supported.

Because *Condaliopsis* is not monophyletic and the current morphological characters are homoplastic, we expanded the phylogenetic analysis of Islam & Simmons (2006) to include all putative *Condaliopsis* species as well as additional species from tribe Rhamneae. This additional sampling allowed us to test the generic placement of *Condaliopsis* species in *Condalia* or *Ziziphus*.

Materials and methods

Taxon Sampling

Forty-nine taxa were sampled (Appendix 1). We sampled the following taxa to test the generic placement of putative *Condaliopsis* species: *Condalia velutina*, *Z. celata*, *Z. lloydii*, *Z. mexicana*, *Z. obtusifolia, Z. parryi*, *Z. pedunculata* and *Z. yucatanensis* (Table 1). Because of the morphological similarity among *Condalia, Condaliopsis*, and NW *Ziziphus* and results of Islam & Simmons (2006), both *Condalia* and NW *Ziziphus* species were included to help place the remaining *Condaliopsis* species.

In addition, the ambiguous placement of *Z. celata* with Rhamneae genera in Islam & Simmons (2006) necessitated the inclusion of all Rhamneae genera to find *Z. celata*'s closest relative within this tribe. New World *Ziziphus* is not closely related to Rhamneae so outgroup taxa were sampled from throughout Rhamnaceae based on earlier phylogenies (Richardson *et al.* 2000a, Islam & Simmons 2006). These outgroup taxa included *Hovenia* Thunberg (1781: 7)*, Paliurus* Miller (1754: sin page no.)*,* OW *Ziziphus*, *Reissekia* Endlicher (1840: 1103) and *Pomaderris* Labillardiére (1805: 86, 97). All these taxa occur with NW *Ziziphus* in the informal "ziziphoids" clade (Richardson *et al.* 2000a). More formally, *Hovenia, Paliurus* and OW *Ziziphus* belong to Paliureae, *Pomaderris* to Pomaderreae and *Reissekia* to the more distantly related Gouanieae (Richardson *et al*. 2000a,b).

At least two species were sampled from all genera except for monotypic genera, *Rhamnus* Linneaus (1753: 193), *Frangula* Miller (1754: sin page no.), *Auerodendron* Urban (1924: 221), and the outgroup genera mentioned above. For *Auerodendron*, no successful amplifications were obtained from herbarium or fresh silica dried samples. Given the results of Bolmgren & Oxelman (2004), sampling only one species from *Rhamnus* and *Frangula* is sufficient for this study as these two genera are well-supported as distinct sister genera. To capture diversity within a species, two individuals from all of the *Condaliopsis* species were sampled except for *Z. pedunculata* for which only one individual was successfully amplified. Individuals were sampled from geographically distinct populations. Five of the approximately 30 NW *Ziziphus* species not considered as *Condaliopsis* (see above) were also included.

Character Sampling

Thirty morphological characters (Appendix 2) were sampled to reflect characters important in species and generic delineation. Morphological characters were coded from literature (Endlicher 1840, Standley 1923, Chun & Tsiang 1939, Johnston 1962, 1963, 1964, 1968, Moore & Edgar 1970, Adams 1972, Johnston 1974, Judd & Hall 1984, Smith 1985, Medan 1988, Bornstein 1989, Delaney *et al.* 1989, Schirarend 1991, Fernández Nava 1992, Killeen *et al.* 1993, Schirarend & Hoffmann 1993, Liogier 1994, Schirarend & Olabi 1994, Bhandari & Bhansali 2000, Richardson *et al.* 2000b, Felger *et al.* 2001, Li *et al.* 2004, Medan & Schirarend 2004, Christie *et al.* 2006, Chen & Schirarend 2007, Hyde & Wursten 2008) and herbarium specimens. Herbarium specimens were loaned from the Field Museum of Natural History (F), Missouri Botanical Garden (MO), and New York Botanical Garden (NY).

Molecular characters were obtained by sequencing two loci from the nuclear genome [internal transcribed spacers (nrITS) and 26S rDNA] and two loci from the chloroplast genome [*trnL-trnF* intergenic spacer (*trnL-F*) and *trnQ-5'rps16* intergenic spacer (*trnQ-rps16*)]. These loci were sampled based on use in other studies of Rhamnaceae except for *trnQ-rps16.* Based on preliminary testing of a number of chloroplast loci from Shaw *et al.* (2007) on the study species, *trnQ-rps16* had the highest number of parsimony informative characters. Extraction of genomic DNA was performed using DNeasy Plant Mini Kits (Qiagen Inc., Valencia, CA). Target loci were amplified using the PCR procedures outlined in Islam & Simmons (2006) for nrITS, 26S rDNA, and *trnL-F*. For *trnQ-rps16,* primers and amplification protocol followed Shaw *et al.* (2007). PCR products were purified using ExoSapIT® (Amersham, Piscataway, NJ, USA), and products were sequenced using the same primers for amplification at Macrogen (Seoul, South Korea) or the Cancer Research

Center DNA Sequencing Facility (Chicago) using either Applied Biosystems 3730XL 96-capillary sequencer or a 3130 16-capillary automated DNA sequencer. All sequences have been deposited in GenBank with accession numbers for sequences generated for this study JN900256-JN900385, KT94913 (Appendix 1).

Data Analyses

The nucleotide sequences obtained for each locus were aligned using the online version of MAFFT version 6 (Katoh *et al.* 2002, 2005). Manual adjustments to the alignment were made following Zurwaski & Clegg (1987), and gaps were coded and used in the parsimony analyses following the complex indel coding (Simmons & Ochoterena 2000, Müller 2006) with the aide of SeqState (Müller 2005). Forty-two parsimony informative gap characters in unambiguously aligned regions were included in the analysis (12, nrITS; 9, *trnL-F*; and 21, *trnQ-rps16*). Ambiguously aligned areas across all sequences were eliminated prior to the analyses (132 bp, nrITS; 388 bp *trnQ-rps16*). For individual sequences, ambiguously aligned nucleotides were converted to "?".

Nine data matrices were analyzed: each of the four loci, separate combined analyses of the nuclear loci and the plastid loci, a combined analysis of all four loci, the morphology-only analysis, and a combined analysis of morphological and molecular characters (simultaneous-analysis). All multistate characters were analyzed as unordered with equal weighting. All analyses except for those that include the morphological characters were analyzed using both maximum parsimony and maximum likelihood methods. The morphology-only analysis and the simultaneous-analysis were analyzed using only maximum parsimony.

For each analysis conducted using maximum parsimony, a heuristic search and jackknife (JK) analysis was performed with PAUP* (Swofford 2001). A heuristic search was conducted with 2,000 tree-bisection-reconnection (TBR) searches with a maximum of 10 trees held per search. Maximum parsimony jackknife (JK) analyses (Farris *et al.* 1996) were conducted with the removal probability set to 36.7879%, and "jac" resampling emulated in PAUP* 4.0b10 (Swofford 2001). Two-thousand replicates were performed with 100 random addition TBR searches per replicate and a maximum of 10 trees held per TBR search. Gap and morphological characters were traced onto the tree using unordered parsimony reconstruction in Mesquite ver. 2.74 (Maddison & Maddison 2011).

Maximum likelihood analyses (Felsenstein 1973) were conducted for molecular characters only and excluded gap characters. For each likelihood analysis, the best-fit likelihood model was selected using jModelTest 2.1.3 (Guindon & Gascuel 2003, Darriba *et al.* 2012) and the Akaike Information Criterion (Akaike 1974). Eighty-eight models were tested. All models selected included invariant sites and the gamma distribution with Q-matrices that were variants of TIM, TVM, and GTR except for *trnL-F*, which did not include a gamma distribution, and the combined plastid loci matrix, which did not include invariant sites. Analyses were conducted with RAxML-HPC2 version 7.2.6 (Stamatakis 2006) in CIPRES on Abe (Portal 3, Miller *et al.* 2009).

RAxML cannot implement the more restrictive Q-matrices recommended for several of the matrices. One-thousand searches were performed to find the best tree using the GTRGAMMA model and randomized stepwise parsimony trees generated by RAxML. For the combined molecular analyses, the data were partitioned for each locus to allow for different estimates and optimization of the alpha-shape parameters, GTR-rates, and empirical base frequencies for each partition. Maximum likelihood bootstrap analyses (BS) were also conducted in RaxML on CIPRES. Two-thousand searches were performed with one replicate per search using the standard bootstrap search (-b) for each analysis. Results of the bootstrap analyses were drawn on to the best tree for that dataset in RAxML. The MP strict consensus of all characters (simultaneous-analysis) tree, the ML all loci best tree, all matrices, and analyses from this study are available on TreeBase (S14619). Tree shown in Fig. 1 was drawn using TreeGraph 2 (Stöver & Müller 2010) with support values mapped on the strict consensus tree following Simmons & Freudenstein (2011).

Results

We present the parsimony simultaneous-analysis strict consensus tree in Fig. 1. Summary statistics for all maximum parsimony analyses are given in Table 2. The percentage of data matrix cells scored as missing for all loci and morphology was 35.6% (Table 2). One morphological character, presence or absence of glandular dots, was not included in the morphology-only or simultaneous-analysis but mapped on the strict consensus trees as above.

No moderately to well-supported (≥70 JK or BS) incongruence resulted between the maximum parsimony and maximum likelihood analyses for each of the four loci, the two genomes, or simultaneous molecular analyses. There was only one well-supported conflict between the simultaneous maximum likelihood analysis and simultaneous

parsimony analysis. In the maximum likelihood analysis, *Z. mexicana* (V.W. Steinman #3088, NY) was sister to a well-supported clade (100 BS) including the other *Z. mexicana* specimen (P. Carillo-Reyes 1683, NY), *Z. pedunculata*, and *Z. yucatanensis*.

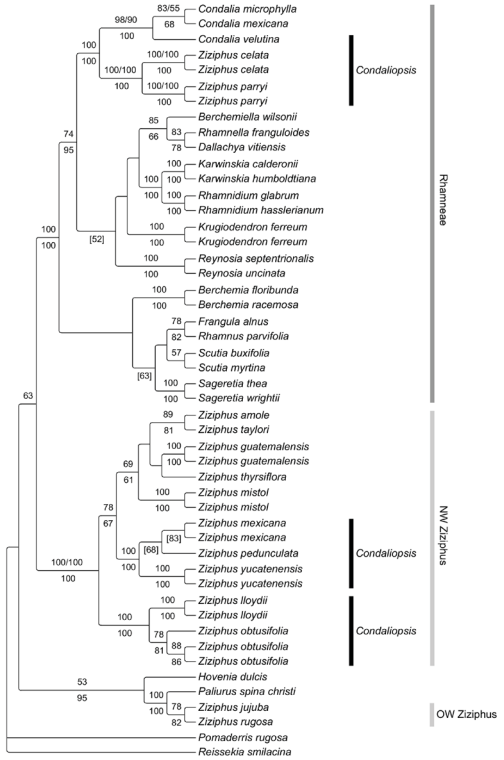

FIGURE. 1. Simultaneous-analysis strict consensus parsimonious tree with parsimony jackknife support values ≥50% above each branch and likelihood bootstrap support values ≥50% below each branch. If a support value is in brackets [], then the clade is contradicted in the likelihood analysis, and the bootstrap support for the contradictory clade with the highest support is reported.

TABLE 2. Statistics for the nine parsimony analyses including ensemble consistency index (CI) after removal of parsimony-uninformative characters and ensemble retention index (RI).

Matrix	# terminals	# characters analyzed	# of parsimony informative characters	% missing / inapplicable	Most parsimonious tree length	# of most parsimonious trees	CI	RI
nrITS rDNA	47	807	236	17.6	859	29	0.48	0.96
26S rDNA	48	876	51	5.5	217	696	0.46	0.84
nrDNA (26S, nrITS)	49	1,683	287	13.9	955	2	0.47	0.80
trnL-F	46	492	64	17.6	197	9,590	0.79	0.96
trnQ-rps16	47	1,834	202	57.5	331	4,925	0.75	0.93
Plastid (*trnL-F*, *trnQ*-rps16)	49	2,326	266	51.5	447	10,547	0.74	0.94
All molecular	49	4,009	553	35.7	1,787	6	0.55	0.85
Morphology only	49	30	30	17.0	107	2,000	0.40	0.74
All characters	49	4,039	583	35.6	1,924	1	0.53	0.84

The results do not provide conclusive evidence for deeper sister group relationships. Paliureae (*Hovenia, Paliurus,* and OW *Ziziphus*), *Reissekia* and *Pomaderris* were included as outgroups for the generic placement of *Condaliopsis* species. Five species, *Z. mexicana, Z. pedunculata, Z. yucatanensis, Z. lloydii,* and *Z. obtusifolia*, were strongly supported within the NW *Ziziphus* clade (Fig. 1, 100 JK/100 BS). In the simultaneous-parsimony analysis, Paliureae were sister (<50 JK) to the NW *Ziziphus* and Rhamneae. The all-molecular likelihood analysis weakly (<50 BS) contradicted these relationships. It is unclear if the sister to the Paliureae is Rhamneae or NW *Ziziphus*. The former genus *Condaliopsis* was not supported as monophyletic. *Condalia velutina* was strongly supported (Fig. 1, 98 JK/90 BS) as sister to the other two sampled *Condalia* species. The other two *Condaliopsis* species, *Z. celata* and *Z. parryi*, were strongly supported as sister to *Condalia* (Fig. 1, 100 JK/100 BS) within the Rhamneae tribe (Fig. 1, 100 JK/100 BS). Tribe Rhamneae was strongly supported (Fig. 1, 100 JK/100 BS). Sister to *Condalia* s.l. clade, *Condalia-Ziziphus celata-Z. parryi,* was the poorly supported *Reynosia-Berchemiella* (Fig. 1, <50% JK) clade.

Discussion

Our results shed light on a long-standing problematic group of thorny shrubs, including a federally listed species whose generic placement has been in doubt.

Generic Placement of Condaliopsis

Condaliopsis was not supported as monophyletic (Fig. 1). Our results support the eight putative *Condaliopsis* species (Table 1) as most closely related to either NW *Ziziphus* or *Condalia*. Five of the *Condaliopsis* (or *Condaliopsis*-like) species formed a well-supported clade with NW *Ziziphus* and separate from the OW *Ziziphus* species. These species formed a grade sister to the other NW *Ziziphus* species likely reflecting the morphological differences that led to different authors placing the species in either *Condalia, Condaliopsis* or *Ziziphus*. The type of *Condaliopsis, Condaliopsis lycioides*, has long been recognized as a synonymy of *Z. obtusifolia.* In our analyses, *Z. obtusifolia*, a widespread species occurring from southwest US into northern Mexico and the Baja California peninsula (USA and Mexico), is sister to *Z. lloydii*. *Ziziphus lloydii,* also considered *Condaliopsis* (Table 1)*,* occurs in northern Mexico as well but is restricted to low, arid, limestone outcroppings of the Sierra Madre Oriental Mountains in Nuevo León. *Ziziphus mexicana, Z. pedunculata,* and *Z. yucatanensis*, which based on Suessenguth's definition of *Condaliopsis* should have been placed within the genus, are sister to other sampled NW *Ziziphus* species (Fig. 1) and occur in southern Mexico. These five species should remain in NW *Ziziphus*. The other native *Ziziphus* species in Mexico*, Z. amole* Johnston (1963: 1021–1022) and *Z. guatemalensis* Hemsley (1878: 6) (Pool 2015)*,* which were never considered within *Condaliopsis,* differ from these five species in thorn morphology. *Ziziphus amole* and *Z. guatemalensis* have paired, unmeristematic thorns, and these species all possess unequal, meristematic (albeit short in *Z. yucatanensis*), thorn-tipped branchlets.

The remaining *Condaliopsis*-like species, *Ziziphus celata, Z. parryi,* and *Condalia velutina* belong in *Condalia* (Fig. 1). *Ziziphus celata* and *Z. parryi* share two morphological synapomorphies with *Condalia* within Rhamneae, 1) secondary branch meristems that form thorns, and 2) ring-porous wood (Schirarend 1991). Morphologically, *Z. celata* and *Z. parryi* share many traits in common (Delaney *et al.* 1989). For those morphological characters sampled only one is a synapomorphy for the two species, a tapered and forked style. In contrast, other *Condalia* species have entire, terete styles like many other species in Rhamneae.

Ziziphus celata is a federally endangered species with 14 wild populations, which are composed of a few clonal individuals, in the sandhills or former sandhill habitats of the Lake Wales Ridge of Florida (Weekley *et al.* 2012). Over 3,200 kilometers away, *Z. parryi* occurs in the chaparral of Southern California and is sympatric with another *Condalia* species, *C. globosa* Johnston (1924: 1086). North American *Condalia* species occur in southwest US (Texas, New Mexico, Arizona, and California) and throughout Mexico. The geographically closest *Condalia* relative of *Z. celata* is almost 1,300 kilometers away in Texas. This disjunct distribution may be the result of fragmentation of the southwestern US xeric flora during the Pliocene leaving *Z. celata*, like other Floridian scrub species, a relict of this once widespread flora (Delaney *et al.* 1989, Germain-Aubrey *et al.* 2014). The ridges of central Florida were often isolated from the mainland, along with their flora and fauna, episodically during the last 23ma (White 1970). The Lake Wales Ridge was one of the few ridges to remain emergent throughout this period and contains a high number of endemic species (Huck *et al.* 1989, Germain-Aubrey *et al.* 2014), like *Z. celata*.

Of the 18 *Condalia* species, only two species were sampled, one native to Argentina and the other Mexico,

which although sufficient to place *Z. celata* and *Z. parryi* as closest relatives was not sufficient to find their closest relatives within *Condalia*. The three *Condalia* species, including *C. velutina*, share a morphological synapomorphy not shared with these two former *Ziziphus* species; persistent sepals on the fruits. Addition of other *Condalia* species may not support the putative sister relationship between *Z. parryi* and *Z. celata*. The most conservative nomenclatural recommendation is the removal of *Z. celata* and *Z. parryi* from the genus *Ziziphus* and placement in the genus *Condalia*.

Taxonomic Treatment

Ziziphus parryi already has a binomial within *Condalia* as *Condalia parryi* (Torr.) Weberbauer (1895: 404). The new combination for *Z. celata* is as follows.

Condalia celata (Judd & D.W.Hall) M.B.Islam, comb. nov., *Ziziphus celata* Judd & Hall (1984: 382). TYPE:—USA. Florida: Highlands Co. on sand dunes, vicinity of Sebring., 18 March 1949, *Garrett s.n.* (holotype: FLAS! (136888)).

Conclusions

This study investigated the generic placement of a number of Rhamnaceae species that were shifted between two genera based on the importance placed on different sets of morphological characters. Some authors put more weight on vegetative characters while other authors placed more weight on reproductive. By testing the generic placement of the *Condaliopsis* species using a combination of molecular and morphological characters, we were able to place these species within either *Condalia* or NW *Ziziphus*; two genera that despite their morphological similarities are not closely related. The results show that a combination of vegetative and reproductive traits are important for classification versus reliance on a limited set of characters, which although not a novel conclusion, is the current state of generic recognition for a number of genera in Rhamnaceae with the few detailed studies possessing a regional focus. This type of study could benefit many of the other Rhamnaceae genera that Medan & Schirarend (2004) note are in need of review.

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APPENDIX 1. List of taxa sampled with information related to taxonomy, voucher information, and GenBank accession numbers. For sequences obtained from GenBank the accession number is placed in brackets [ ]. Abbreviations for the botanical gardens are as follows: Desert Botanical Garden (DBG), Montgomery Botanical Center (MBC), and U.S. National Arboretum (USNA).

Berchemia floribunda (Wall.) Brongn—Lai Shushen & Shan Hanrong 2573, 1998 (MO), 26S JN900265, *trnL-F* JN900318, *trnQ-rps16* JN900341. ***Berchemia racemosa*** Siebold & Zucc.—S. Tsugaru 14944, 1991 (MO), 26S JN900266, nrITS JN900290, *trnL-F* JN900314, *trnQ-rps16* JN900342. ***Berchemiella wilsonii*** (C.K. Schneid.) Nakai—Deng Maobin 93007, 1998 (MO), 26S JN900268, nrITS JN900305, *trnL-F* JN900321, *trnQ-rps16* JN900343. ***Condalia mexicana*** Schltdl.—C. Dziekanowski *et al.* 3312, 1979 (MO), 26S JN900275, nrITS JN900301, *trnQ-rps16* JN900344. ***Condalia microphylla*** Cav.—Kiesling *et al.* 5967 (K), 1986, [26S DQ146522], *trnQ-rps16* JN900345. ***C. microphylla*—**Richardson *et al.* 2000b, [*trnL-F* AJ390334]. ***C. microphylla*—**Bolmgren and Oxelman 2004, [nrITS AY626456]. ***Condalia velutina*** I.M. Johnst.—R. Fernández N. 719, 1981 (MO), 26S JN900273, nrITS JN900302, *trnQ-rps16* JN900345. ***Dallachya vitiensis*** (Benth.) F. Muell.—P.I. Forster *et al.* 27619, 2001 (NY), 26S JN900267, nrITS JN900300, *trnL-F* JN900333, *trnQ-rps16* JN900357. ***Frangula alnus*** Mill.—Revaz Gagnidze & Shamil Shetekauri 286, 2002 (MO), 26S JN900264, nrITS JN900292, *trnL-F* JN900316, *trnQ-rps16* JN900346. ***Hovenia dulcis*** Thunb.—USNA Acc. #24752, C. Bordelon s.n., [26S DQ146516, nrITS DQ146607, *trnL-F* DQ146563], *trnQ-rps16* JN900366. ***Karwinskia calderonii*** Standl.—R. Villacorta 2383, 1996 (MO), 26S JN900277, nrITS JN900296, *trnL-F* JN900326, *trnQ-rps16* JN900347. ***Karwinskia humboldtiana*** Zucc.—J.L. Tapia M. & F. May 1071, 1999 (MO), 26S JN900278, nrITS JN900297, *trnL-F* JN900327, *trnQ-rps16* JN900350. ***Krugiodendron ferreum*** (Vahl) Urb.—MBC Acc#9701323A; M. Islam 07-013 (CU), 26S JN900270, nrITS JN900298, *trnL-F* JN900331, *trnQ-rps16* JN900348. ***K. ferreum***—MBC Acc#95598A; M. Islam 07-011 (CU), 26S JN900271, nrITS JN900299, *trnL-F* JN900332, *trnQ-rps16* JN900349. ***Paliurus spina-christi*** Miller—University of Copenhagen Botanical Garden Acc.#E5716-0003; K.I. Christensen s.n., 2003, [26S DQ146520, nrITS DQ146613, *trnL-F* DQ146570], *trnQ-rps16* KT949413. ***Pomaderris rugosa*** Cheeseman—Chase 857, (K), [26S DQ146525, nrITS DQ146615], *trnQ-rps16* JN900385. ***P. rugosa*—**Richardson *et al.* 2000b, [*trnL-F* AJ390363]. *Reissekia smilacina* Endl., Richardson *et al.* 2000a, [trnL-F AJ390345]. *R. smilacina*, Arbo *et al.* 4925, 1991 (K), [nrITS DQ146614, 26S DQ146524]. ***Rhamnidium glabrum*** Reissek.—M. Nee 50493, 1999 (NY), 26S JN900272, nrITS JN900286, *trnL-F* JN900324, *trnQ-rps16* JN900351. ***Rhamnidium hasslerianum*** Chodat—Pastoreo 9515, 1969 (NY), 26S JN900269, nrITS JN900287, *trnL-F* JN900325, *trnQ-rps16* JN900353. ***Rhamnus parvifolia*** Bunge—Wang Shilong 1080, 1999 (MO), 26S JN900263, nrITS JN900291, *trnL-F* JN900322, *trnQ-rps16* JN900352. ***Rhamnella franguloides*** (Maxim.) Weberb.—Y. Miyagi 9151, 1980 (NY), 26S JN900258, nrITS JN900306, *trnL-F* JN900334, *trnQ-rps16* JN900354. ***Reynosia septentrionalis*** Urb.—D. Seigler & P. Waterman 13779, 1992 (MO), 26S JN900256, nrITS JN900288, *trnL-F* JN900319, *trnQ-rps16* JN900355. ***Reynosia uncinata*** Urb.—Al Gentry & Elsa Zardini 50476, 1985 (MO), 26S JN900257, nrITS JN900289, *trnL-F* JN900320, *trnQ-rps16* JN900356. ***Scutia buxifolia*** Reissek.—M.Nee 50694, 1999 (MO), 26S JN900262, nrITS JN900293, *trnL-F* JN900323, *trnQ-rps16* JN900358. ***Scutia myrtina*** (Burm. f.) Kurz.—G. Gobbo *et al.* 707, 2000 (MO), 26S JN900261, *trnL-F* JN900328, *trnQ-rps16* JN900359. ***Sageretia thea*** (Osbeck) M.C. Johnst.—Kuang-Yuh Wang *et al.* 439, 1994 (MO), 26S JN900259, nrITS JN900294, *trnL-F* JN900329, *trnQ-rps16* JN900360. ***Sageretia wrightii*** S. Watson—J.S. Miller 7729, 1992 (MO), 26S JN900260, nrITS JN900295, *trnL-F* JN900330, *trnQ-rps16* JN900361. ***Ziziphus amole*** (Sesse´ & Moc.) M.C. Johnst.—O. Dorado *et al.* 1585 (NY), [26S DQ146491, nrITS DQ146579, *trnL-F* DQ146535], *trnQ-rps16* JN900371. ***Z. celata*** Judd & D.W. Hall—Acc. HO1-3 #387, C. Weekley s.n., [26S DQ146493, nrITS DQ146581, *trnL-F* DQ146537], *trnQ-rps16* JN900362. ***Z. celata*—**Acc. PO2-1E/2004, C. Weekley s.n., [26S DQ146494, nrITS DQ146582, *trnL-F* DQ146538], *trnQ-rps16* JN900363. ***Ziziphus guatemalensis*** Hemsl.—J.F. Morales 2906 (MO), [26S DQ146497, nrITS DQ146585, *trnL-F* DQ146541], *trnQ-rps16* JN900372. ***Z. guatemalensis*—**D. Stevens *et al.* 17116 (NY), [26S DQ146496, nrITS DQ146584, *trnL-F* DQ146540]. ***Ziziphus jujuba*** Mill.—Dixie Damrel DBG. 682201016, 2003 (DES), [26S DQ146488, nrITS DQ146576, *trnL-F* DQ146532], *trnQ-rps16* JN900367. ***Ziziphus lloydii*** (Standl.) M.C. Johnst.—M.C. Johnston, T.L. Wendt, & F. Chiang 11202, 1973 (F), 26S JN900279, nrITS JN900312, *trnL-F* JN900335, *trnQ-rps16* JN900373. ***Z. lloydii*—**F. Chiang, T. Wendt, & M.C. Johnston 7983, 1972 (NY), 26S JN900280, nrITS JN900313, *trnL-F* JN900336, *trnQ-rps16* JN900374. ***Ziziphus mexicana*** Rose—V.W. Steinmann 3088, 2003 (NY), 26S JN900283, nrITS JN900309, *trnL-F* JN900340, *trnQ-rps16* JN900377. ***Z. mexicana*—**P. Carrillo-Reyes 1683, 2001 (NY), 26S JN900284, nrITS JN900310, *trnQ-rps16* JN900378. ***Ziziphus mistol*** Griseb.—M. Nee 51192, (NY), [26S DQ146503, nrITS DQ146590, *trnL-F* DQ146547], *trnQ-rps16* JN900375. ***Z. mistol*—**Simon Goodwin 619812, Royal Botanic Gardens Sydney Acc. #14930, 2004 (NSW), [nrITS DQ146591, *trnL-F* DQ146548], *trnQ-rps16* JN900376. ***Ziziphus obtusifolia*** (Hook.

ex. Torr. & A. Gray) **var. *canescens*** (A. Gray) M.C. Johnst.—DBG Acc. #1987- 01550105, 2003 (DES), D. Damrel s.n. (DES), [26S DQ146507, nrITS DQ146595, *trnL-F* DQ146552], *trnQ-rps16* JN900380. ***Ziziphus obtusifolia* var. *obtusifolia*—**DBG Acc. #1977- 047601-01, 2003 (DES), D. Damrel s.n. (DES), [26S DQ146506, nrITS DQ146594, *trnL-F* DQ146551], *trnQ-rps16* JN900379. ***Z. obtusifolia* var. *obtusifolia*—**DBG Acc. #1983-007110, D. Damrel s.n. (DES), [26S DQ146508, nrITS DQ146596, *trnL-F* DQ146553], *trnQ-rps16* JN900381. ***Ziziphus parryi*** Torr.—John P. Rebman 10045, 2004 (SD), 26S JN900276, nrITS JN900303, *trnL-F* JN900317, *trnQ-rps16* JN900364. ***Z. parryi*—**Jeannie Gregory 888, 2004 (SD), 26S JN900274, nrITS JN900304, *trnL-F* JN900315, *trnQ-rps16* JN900365. ***Ziziphus pedunculata*** (Brandg.) Standl.—Pedro Tenorio con E. Martinez C. 17366, 1991 (F), 26S JN900285, nrITS JN900311, *trnL-F* JN900337, *trnQ-rps16* JN900368. ***Ziziphus rugosa*** Lam.—W. John Kress #03-7371, 2003 (US), [26S DQ146512, nrITS DQ146601, *trnL-F* DQ146557], *trnQ-rps16* JN900382. ***Ziziphus taylori*** (Britton) M.C. Johnst.—D.S. Correll 41621 (MO), [26S DQ146514, nrITS DQ146605, *trnL-F* DQ146561], *trnQ-rps16* JN900384. ***Ziziphus thyrsiflora*** Benth.—X. Cornejo & C. Bonifaz 7796 (GUAY), [26S DQ146515, nrITS DQ146606, *trnL-F* DQ146562], *trnQ-rps16* JN900383. ***Ziziphus yucatanensis*** Standl.—P. Simá 2106, 1997 (F), 26S JN900281, nrITS JN900307, *trnL-F* JN900338, *trnQ-rps16* JN900369. ***Z. yucatanensis*—**P. Sima y R. Duran 2126, 1997 (NY), 26S JN900282, nrITS JN900308, *trnL-F* JN900339, *trnQ-rps16* JN900370.

APPENDIX 2. Morphology Matrix.

1) Primary branch meristem structure: not thorn-tipped (0), thorn-tipped (1); 2) Secondary branch meristem structure: not thorn-tipped (0), thorn-tipped (1); 3) Tertiary branch meristem structure: not thorn-tipped (0), thorn-tipped (1); 4) Short shoots: absent (0), present (1); 5) Leaf venation: palmate (0), pinnate (1); 6) Leaf position: alternate (0), opposite (1); 7) Stipule form: free lateral (0), intrastipular (1), 8) Inflorescence complexity: simple (0), compound (1); 9) Inflorescence position: axillary (0), terminal (1); 10) Ventral disc position (flower): adnate to calyx tube & ovary (0), adnate to calyx tube or free (1); 11) Petals: present (0), absent (1); 12) Sepal abaxial surface: pubescent (0), glabrous (1); 13) Sepal persistence on mature fruit: persistent (0), deciduous (1); 14) Style form: tapered and forked (0), entire and terete (1); 15) Style persistence: persistent in fruit (0), absent in fruit (1); 16) Ovary surface: pubescent (0), glabrous (1); 17) Carpel number: one (0), two (1), three (2); 18) Ovary position: superior (0), semi-inferior (1), inferior (2); 19) Fruit wall at maturity: dry-indehiscent (0), dry-dehiscent (1), fleshy (2); 20) Carpel endodermis development: compound stone-indehiscent (0), single stones-dehiscent (1), single stone(s)-indehiscent (2); 21) Ray type: multiseriate (0), exclusively uniseriate (1); 22) Vessel perforation: simple (0), some scalariform to reticulate (1); 23) Tangential to diagonal axial parenchyma band: present (0), absent (1); 24) Growth rings: present (0), faintly developed (2) ; 25) Wood type: ring-porous (0), diffuse-porous (1); 26) Parenchyma distribution: not banded or marginal (0), banded (1), marginal (2); 27) Gum deposits: present (0), absent (1); 28) Intervessel pits: vestured (0), non-vestured (1); 29) Pollen exine architecture: reticulate-rugulate (0), perforate (1), regulate (3), striate-rugulate (4), tectate to semitectate (5), striate-reticulate (6), suprareticulate-rugulate (7), fossulate-perforate (8); 30) Endosperm type: albuminous-ruminate (0), exalbuminous (1), albuminous-non-ruminate (2).

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30
Berchemia floribunda	0	0	0	0	1	0	1	1	0/1	0	0	1	1	1	0	1	1	0	2	0	?	?	?	?	?	?	?	?	?	2
Berchemia racemosa	0	0	0	0	1	0	1	1	0/1	0	0	1	0/1	1	0	1	1	0	2	0	0	0	1	2	1	0	1	1	?	2
Berchemiella wilsonii	0	0	0	0	1	0	1	1	0/1	1	0	1	0	1	?	?	0	0	2	0	?	?	?	?	?	?	?	?	?	?
Condalia mexicana	0	1	1	1	1	0	1	0	0	1	1	0	0	1	0	1	1	0	2	0	?	?	?	?	?	?	?	?	?	2
Condalia microphylla	0	1	1	1	1	0	1	0	0	1	1	0/1	?	1	0	1	1	0	2	0	0	0	1	0	0	?	0	0	8	2
Condalia velutina	0	1	0	1	1	0	1	0	0	1	0	0	0	1	0	0	1	0	2	0	?	?	?	?	?	?	?	?	?	2
Frangula alnus	0	0	0	0	1	0	0	0	0	1	0	1	1	1	1	1	1/2	0	2	1	0	0	?	0	0/1	?	?	?	1	2
Hovenia dulcis	0	0	0	0	0	0	0	1	0/1	0	0	1	1	0	0	1	2	1	0	2	0	?	?	0	0	?	?	?	3	2
Karwinskia calderonii	0	0	0	0	1	1	1	1	0	1	0	1	0	1	1	1	1	0	2	0	0	0	1	2	1	2	0	0	?	?
Karwinskia humboldtiana	0	0	0	0	1	1	1	1	0	1	0	1	1	1	1	1	1	0	2	0	0	0	1	2	1	2	0	0	0	2
Krugiodendron ferreum	0	0	0	0	1	1	?	1	0	1	1	?	0	0	0	1	1	0	2	0	0	0	1	2	1	0	1	1	0	1
Paliurus spina-christi	0	0	0	0	1	0	0	0	0	1	0	1	0	0	1	1	1/2	1	0	0	1	1	1	0	1	2	1	1	?	1
Pomaderris rugosa	0	0	0	0	1	0	0	1	0/1	1	0	?	1	0	?	0	2	2	1	1	?	?	?	?	?	?	?	?	?	2
Reissekia smilacina	0	0	0	?	?	0	?	0	0/1	0	0	?	?	?	?	?	2/3	2	1	2	?	?	?	?	?	?	?	?	5	2

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APPENDIX 2. (Continued)

Reynosia septentrionalis	0	0	0	1	1	1	1	0	0	1	0	1	1	1	0	1	1	0	2	0	0	0	1	2	1	1	0	1	0	0
Reynosia uncinata	0	0	0	1	1	1	1	0	0	1	0	1	1	1	0	1	1	0	2	0	?	?	?	?	?	?	?	?	0	0
Rhamnella franguloides	0	0	0	0	1	0	0	1	0/1	1	0	1	1	1	0	0	0/1	0	2	0	0	0	1	0	0	0	1	1	7	?
Dallachya vitiensis	0	0	0	0	1	0	0	0	0/1	1	0	1	1	0	0	1	0	0	2	2	0	0	1	2	1	2	0	1	?	?
Rhamnidium glabrum	0	0	0	0	1	1	1	1	0	1	0	0	0	1	1	1	1	0	2	0	0	0	?	2	1	2	0	?	?	1
Rhamnidium hasslerianum	0	0	0	?	1	0	1	1	0	1	0	1	1	1	1	1	1	0	2	0	?	?	?	?	?	?	?	?	?	1
Rhamnus parvifolia	1	0	0	1	1	1	0	0	0	1	0	?	1	0	1	1	1	0	2	2	?	?	?	?	?	?	?	?	?	2
Sageretia thea	1	0	0	0	1	0/1	0	1	0/1	1	0	0	1	1	?	1	2	0	2	2	?	?	?	?	?	?	?	?	7	2
Sageretia wrightii	1	1	1	0	1	0/1	0	1	1	1	0	1	1	1	1	1	?	0	2	2	?	?	?	?	?	?	?	?	7	?
Scutia buxifolia	0	1	0	0	1	1	0	0	0	1	0	1	1	1	1	1	2	1	2	2	?	?	?	?	?	?	?	?	0	1
Scutia myrtina	0	1	0	0	1	1	0	0	0	1	0	0/1	1	1	1	1	1	1	2	2	?	?	?	?	?	?	?	?	?	?
Ziziphus celata	0	1	1	1	1	0	?	0	0	1	0	1	1	0	0	1	1/2	0	2	0	?	?	?	?	?	?	?	?	?	?
Ziziphus guatemalensis	0	1	0	?	0	0	0	1	0	?	0	0	1	0	1	1	1	0	2	0	0	0	0	0	1	1/2	0	0/1	?	1
Ziziphus jujuba	0	0	0	1	0	0	0	0	0	0	0	1	1	0	1	2	1	0	2	0	1	1	1	0	1	1/2	0	1	?	1

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APPENDIX 2. (Continued)

Ziziphus lloydii	0/1	1	1	1	1	0	0	0	0	1	0	0	1	0	1	1	1	0	2	0	?	?	?	?	?	?	?	?	?	1
Ziziphus mexicana	1	0	0	1	0	1	0	1	0	1	0	1	1	0	1	0	1	0	2	0	?	?	?	?	?	?	?	?	?	1
Ziziphus mistol	0	0	0	1	0	0	0	1	0/1	1	0	0	1	0	1	0/1	1	0	2	0	0	0	1	0	1	1/2	0	0/1	?	1
Ziziphus obtusifolia	0	1	0/1	1	0	0	0	1	0/1	1	0	0	1	0	1	1	1	0	2	0	0	0	1	0	1	2	0	0/1	?	1
Ziziphus obtusifolia var. canescens	0	1	0/1	1	0	0	0	1	0/1	1	0	0/1	1	0	1	0/1	1	0	2	0	0	0	1	0	1	2	0	0/1	?	1
Ziziphus parryi	0	1	1	1	1	0	0	0	0	1	0	1	1	0	0	1	1/2	0	2	0	0	0	1	0	0	2	0	0/1	?	2
Ziziphus pendunculata	0	1	1	1	0	0	0	1	0	1	0	1	1	0	1	1	1	0	2	0	?	?	?	?	?	?	?	?	?	1
Ziziphus rugosa	0	0	0	0	0	0	0	1	0/1	1	1	0	1	0	1	0	1	0	2	0	1	1	1	0	1	1/2	1	1	6	1
Ziziphus taylori	0	1	0	0	1	0	0	0	0/1	?	?	?	?	0	?	?	?	?	2	0	?	?	?	?	?	?	?	?	4	1
Ziziphus thyrsiflora	0	1	0	0	0	0	0	1	1	?	?	0/1	0	0	?	0/1	1	0	2	0	0	0	0	0	1	1/2	0	0/1	?	1
Ziziphus yucatanensis	0	1	0	1	0	0	0	1	0	1	0	0	1	0	1	1	1	0	2	0	?	?	?	?	?	?	?	?	?	1
Ziziphus amole	0	1	0	1	0	0	0	1	0/1	1	0	0	1	0	1	1	1	0	2	0	0	0	0	0	1	1/2	0	0/1	?	1