SYSTEMATICS OF *ANTIGONON* AND TROPICAL ERIOGONOIDEAE: PHYLOGENY,

TAXONOMY, AND INVASION BIOLOGY

A Dissertation

Presented to the Faculty of the Graduate School

of Cornell University

In Partial Fulfillment of the Requirements for the Degree of

Doctor of Philosophy

by

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May 2011

SYSTEMATICS OF *ANTIGONON* AND TROPICAL ERIOGONOIDEAE: PHYLOGENY, TAXONOMY, AND INVASION BIOLOGY

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Cornell University 2011

The genera of Polygonaceae have historically been segregated into two subfamilies, Eriogonoideae and Polygonoideae, based on a few key morphological characters. Using ITS, morphology and five chloroplast markers, a phylogeny for Eriogonoideae was reconstructed, with an emphasis on sampling of the tropical genera. Results support the placement of nine of twelve woody, tropical genera within Eriogonoideae, where these genera form a paraphyletic assemblage giving rise to Eriogoneae (*Eriogonum* and allies). My work corroborates previous phylogenetic studies, and suggests a broader circumscription of Eriogonoideae. Also based on these results, I propose the resurrection of a third subfamily, Symmerioideae, in Polygonaceae, and propose two new tribes, Gymnopodieae and Leptogoneae, in Eriogonoideae. Within the subfamily, the genus *Antigonon* provides a systematic challenge. Although *Antigonon* is a small, easily-recognized genus, the boundaries of species within it have never been resolved satisfactorily. A taxonomic treatment for the genus is presented, based on morphology and molecular phylogenetic data from two chloroplast markers (*psaI-accD, psbA-trnH*) and one nuclear marker (*LFY* , 2nd intron). Four species are described, and a new subspecies, *Antigonon leptopus* subsp. *coccineum* is proposed. *Antigonon leptopus* is also known as corallita, a pantropical invasive vine particularly problematic on islands. Spread of the invasive populations was investigated using data collected for this systematic project. Label data from herbarium specimens were used to map the spread of invasive *A. leptopus* over time. These data show the

history of corallita introduced as a garden ornamental, with subsequent naturalization and escape. Molecular data from plastid DNA sequence were analyzed in a phylogenetic context. Results suggest introductions outside the native range were not from one seed source, as exemplified by the genetic variation found within one island locality. The known data of biology, spread and control of corallita are reviewed and summarized in an action alert.

BIOGRAPHICAL SKETCH

Janelle Burke was born in St. Charles, Illinois on March 2, 1982 near the calm, yet moderately polluted waters of the Fox River. She spent the first 18 years of her life in the same town, frolicking through the parks of suburbia. She graduated from St. Charles High School in 2000. She then completed her bachelor of arts at the Johns Hopkins University majoring in behavioral biology in 2004, yet she managed to avoid the pre-med track, and is currently pursuing her Ph.D. in Plant Biology at Cornell University. When not pondering broad evolutionary quandaries, she enjoys eating spicy food and knitting; preferably not at the same time.

To Dr Mom, for always setting a good example

ACKNOWLEDGMENTS

molecular techniques and advice.

And of course, I would like to thank all my friends who have given me emotional and/or scientific support and provided many, many laughs and meals over the years. To my original housemates, Hanh Nguyen and Catherine Martel, with whom I have enjoyed spending so much time. All of the Bailey Hortorium graduate students were phenomenal office mates and cohorts. In particular I would like to thank my lab mate Cindy Skema and my "eternal TA" Mariana Yazbek for their friendship and mentorship. Fronny Plume, Jim Cohen, Shannon Straub, Marcela Martinez-Millan, Caroline Kellogg, Mary Futey, Simon Gunner, Gwynne Lim, Tee Havanada, Dan Ilut, and Jeremy Coate: you are great friends and office mates.

I consider myself fortunate to have had an outstanding committee. Dr. Jerrold Davis was always available to listen to my questions, and offered thoughtful feedback. I have especially enjoyed his lectures, sense of humor, and academic advice. Dr. James Reveal is a tremendous resource for all things Polygonaceae, and was willing to review any document I sent his way. Dr. Antonio DiTommaso has helped by encouraging me to publish and present in a field that is not my primary focus. I appreciate his enthusiasm and timely feedback. Dr. Melissa Luckow, my major professor, has been a true mentor and friend. From the time I was a young graduate student looking for a thesis project and a free trip to Venezuela, she has always been available for advice and support. I have learned from her rigid scholarship and I will always appreciate her academic guidance.

I would like to thank my family, who has always ready and willing to visit me in Ithaca, even during bad weather. My father, James Burke, was a great help in helping generate distribution maps. And lastly, I want to thank Ahmad Slaibi, who has provided unwavering support and encouragement.

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CHAPTER 1

INTRODUCTION

The Polygonaceae Juss. are a well-delimited family (Cronquist, 1981), known in the systematic community for a unique vegetative characteristic, the ocrea (Simpson, 2010) as well as for taxonomic complexity within two large temperate genera: *Polygonum* L. and *Eriogonum* Michx. (Freeman and Reveal, 2005). Traditionally, the classification of Polygonaceae included two subfamilies: Polygonoideae Eaton (ocrea present, involucre absent) and Eriogonoideae Arn. (ocrea absent, involucre present), though sometimes a third subfamily, the Coccoloboideae Luerss., was circumscribed to include the woody taxa within the Polygonoideae (Brandbyge, 1993; see Chapter 3 for a history of subfamily taxonomy). The latter are mostly neotropical in distribution, and later workers acknowledged they are likely not monophyletic (Brandbyge, 1993; Lamb Frye and Kron, 2003).

Historically, woodiness was used as a character to circumscribe tribes in the Polygonaceae (e.g. Gross, 1913). These tribes, Coccolobeae and Triplarideae, are mostly Central and South American in distribution (Brandbyge, 1993). Preliminary molecular work with *rbcL* showed that the Coccolobeae Dumort. were not monophyletic, and formed a clade containing the woody *Triplaris* (Triplarideae C. A. Mey), and *Eriogonum* (subfamily Eriogonoideae) nested within it (Lamb Frye and Kron, 2003). Anatomical studies suggested a similar heterogeneity; there were two major patterns of petiolar anatomy within Coccolobeae, segregating *Coccoloba* P. Brown and *Podopterus* Humb. & Bonpl. as a group from *Antigonon* Endl., *Brunnichia* Banks ex Gaertn. and *Muehlenbeckia* Meisn. (Freid, 2000). Later molecular phylogenetic studies with increased sampling confirmed the paraphyly of Coccolobeae and Triplarideae (Sanchez and Kron, 2008; Sanchez and Kron, 2009; Burke et al., 2010). These studies demonstrated that the

phylogenetic relationships among these taxa were not congruent with current taxonomic circumscriptions.

In *Antigonon* (formerly Coccolobeae), generic circumscription is clear, but the species boundaries are poorly defined (Brandbyge, 1993), with accounts of species number ranging from one to eight (Wood and Graham, 1965; Ewing, 1982; Brandbyge, 1988; Aymard and Howard, 2004). Some of the species were thought to only be varieties of the commonly cultivated ornamental and weed *Antigonon leptopus* Hook. & Arn. (Standley and Steyermark 1946; Duke, 1960; Graham and Wood, 1965), or did not constitute 'good species' (Standley and Steyermark, 1946; Duke, 1960). Workers have argued that *A. platypus* Hook. & Arn. is merely a white floral color form of *A. leptopus* (Duke, 1960; Graham and Wood, 1965), and *A. cordatum* M. Martens & Galeotti only differs consistently from *A. leptopus* in its dilated petioles (Duke, 1960). The natural range of the genus extends west from Baja California south into Nicaragua (Raju et al., 2001); however both *A. leptopus* and *A. amabile* W. Bull are commonly cultivated outside their natural range (Duke, 1960).

Ecologically, the taxa within Polygonaceae have a propensity for invasiveness. Many temperate Polygonaceae species (*Reynoutria japonica* Houtt.*, Persicaria perfoliata* [L.] H. Gross) are currently in the research spotlight due to their weedy habit (e.g. Kumar and DiTommaso, 2005; Gammon et al., 2007; Bailey et al., 2009), but there are numerous pests in the tropics as well (Atha, 2004). One invasive species, *Antigonon leptopus,* has been documented as a pest from the South Pacific, to Africa, and India, where it is often a weed in agricultural fields (Raju et al., 2001). It also a roadside weed in its own native range (Howard, 2001; Pichardo and Vibrans, 2009). *Antigonon leptopus* commonly escapes cultivation, and is common along roadsides and in abandoned lots (pers. observation).

The purpose of this dissertation research is to investigate the evolutionary relationships of

Polygonaceae in a phylogenetic context; then using these data to inform and revise the taxonomy of the family. The study taxa are those genera previously placed in Coccolobeae and Triplarideae, with a focus on the genus *Antigonon*. Within *Antigonon*, the objective of the systematic study is to ascertain species number and their evolutionary history. Then, data from the *Antigonon* systematic study are used to speak to the field of invasion biology, through study of the invasive species *Antigonon leptopus*. Phylogenetic methods and ecological theories are integrated to investigate the invasive traits of the species *Antigonon leptopus,* culminating in a review of the current natural history and biology of this species. For the purposes of botanical nomenclature, all taxonomic novelities presented in this dissertation should be treated as provisional, and not validly published.

Chapter 2 presents a phylogenetic study of relationships among the tropical, woody members of the Eriogonoideae. This study adds to previous molecular phylogenetic studies in the family by including complete generic sampling among the wood, tropical Polygonaceae, in addition to utilizing a larger data set, including five plastid markers, ITS and morphology. Based on the results, revised interpretations of morphological evolution in the family are discussed.

Chapter 3 takes findings from Chapter 2, as well as previous studies (Sanchez and Kron, 2008; Sanchez and Kron, 2009), and applies these towards a revised subfamily treatment for Polygonaceae and tribal treatment of Eriogonoideae. This is an evolutionary classification, based on well-supported monophyletic groups. The treatment includes keys to subfamilies and tribes, highlights suites of diagnostic characters to tribes, and provides a discussion of the genera within each.

Chapter 4 is a monograph of the genus *Antigonon*. This chapter includes taxonomic and natural history of the genus, along with a review of morphology. A phylogenetic study, based on data from two intergenic species and one nuclear intro, is included and used to help inform

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species delimitation. Finally, four species and two subspecies are described, along with distribution maps, complete nomenclatural synonymy and notes on identification.

Within Chapter 5, a review of the natural history and invasive potential of *Antigonon leptopus* is presented in the form of an invasion alert. All current knowledge of *A. leptopus* natural history and control methods are included. Based on current distribution and previous control tactics, recommendations are made for control protocols and stricter regulations on sale and movement into new areas.

In Chapter 6, data from the systematic portion of the *Antigonon* study are integrated to address invasive biology questions. Data from herbarium specimen label data are used track the history of introduction over time and space across the globe, and then used to infer introduction pathways, of both primary and secondary spread, through site descriptions. Molecular genetic variation is analyzed in a phylogenetic context, and elucidates remarkable variation between invasive populations. This study exemplifies how systematic data is useful to inform invasive biology, whereby both fields can benefit from collaboration.

Lastly, in Chapter 7 includes a summary of results, and touches upon some broader conclusions from the culmination of the dissertation work.

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CHAPTER 2

PLACING THE WOODY TROPICAL GENERA OF POLYGONACEAE: A HYPOTHESIS OF CHARACTER EVOLUTION AND PHYLOGENY[1]

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- *Premise of the study*: Taxonomic groups have often been recognized on the basis of geographic distinctions rather than accurately representing evolutionary relationships. This has been particularly true for temperate and tropical members from the same family. Polygonaceae

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exemplifies this problem, wherein the woody tropical genera were segregated from temperate members of the family and placed in the subfamily Polygonoideae as two tribes: Triplarideae and Coccolobeae. Modern phylogenetic studies, especially when inferred from many lines of evidence, can elucidate more probable hypotheses of relationships. This study builds on previous work in the family and aims to test the traditional classification of the tropical woody taxa, which have been understudied and undersampled compared to their temperate relatives.

- *Methods*: A phylogenetic study was undertaken with expanded sampling of the tropical genera with data from five plastid markers (*psbA-trnH*, *psaI-accD*, *matK*, *ndhF*, and *rbcL)*, nuclear ribosomal DNA (ITS) and morphology.

- *Key results*: Results support the placement of nine of 12 genera of the Triplarideae and Coccolobeae within Eriogonoideae, in which these genera form a paraphyletic assemblage giving rise to Eriogoneae. The remaining woody tropical genera excluded from Eriogonoideae occur in the paleotropics.

- *Conclusions*: Traditional characters used to delimit Coccolobeae and Triplarideae are not useful for defining monophyletic groups. The six-tepal condition is derived from the five-tepal condition, and unisexual flowers have arisen multiple times in different sexual systems. Ruminate endosperm has arisen multiple times in the family, suggesting this character is highly plastic.

Key words: *Coccoloba,* Eriogonoideae; ocrea; phylogeny; Polygonaceae; ruminate endosperm.

Tropical taxa are often understudied in comparison to their temperate relatives, and in this regard the Polygonaceae are no exception. Many phylogenetic studies have shown that the

circumscription of tropical vs. temperate groups may be artificial, with the tropical group giving rise to the temperate members or vice-versa, such as in Aceraceae/Sapindaceae (Buerki et al., 2009) or Salicaceae/Flacourtiaceae (Chase et al., 2002). Taxonomic problems are often exacerbated when workers repeatedly rely on a set of "key" taxonomic characters, without reassessing their utility for phylogenetics or their homology. Our study not only examines relationships among traditionally recognized tropical and temperate groups in the Polygonaceae, but also investigates key taxonomic characters in a phylogenetic context. Conclusions about the plasticity and evolution of these characters may have broader application to studies of other angiosperm families.

The Polygonaceae Juss. have long been recognized as a distinct, relatively isolated family (e.g., Meisner, 1856; Bentham and Hooker, 1880; Cronquist, 1981; Takhtajan, 1997), distinguished at least in part by the presence of an ocrea, a sheathing structure associated with leaf nodes (e.g., Bartling, 1830; Lindley, 1830; Endlicher, 1837). Molecular phylogenetic studies have supported this distinction; the Polygonaceae are a monophyletic group, sister to the Plumbaginaceae Juss. (Fay et al., 1997; Cuénoud et al., 2002). Much taxonomic work over the last several decades has focused on the temperate taxa within Polygonaceae, in particular, the generic circumscription of *Persicaria* Mill., *Polygonum* L., and *Eriogonum* Michx. (Haraldson, 1978; Ronse Decraene and Akeroyd, 1988; Reveal, 1989; Freeman and Reveal, 2005; Kim and Donoghue, 2008; Galasso et al., 2009). In contrast, the infrafamilial classification is still in flux.

Until recently, the Polygonaceae were divided into two subfamilies, Polygonoideae Eaton and Eriogonoideae Arn. (Haraldson, 1978; Brandbyge, 1993; Freeman and Reveal, 2005), largely based on a suite of diagnostic morphological characters, such as presence/absence of ocrea, monopodial/sympodial growth and presence/absence of an involucre. However molecular phylogenies with a broad sampling of genera (Sanchez and Kron, 2008; Sanchez et al., 2009)

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have supported a rearrangement of the two long-recognized subfamilies. Eriogonoideae s.s. is monophyletic but is nested in a clade among many of the woody, tropical genera (hereafter WTG) previously placed in Polygonoideae, rendering Polygonoideae paraphyletic.

The WTG consist of 11 or 12 genera of trees, shrubs and lianas with a predominately neotropical distribution. Besides a woody habit, the WTG can be distinguished from the rest of the Polygonoideae by the presence of ruminate endosperm and greatly expanded tepals in fruit (Meisner, 1856; Jaretzky, 1925; Brandbyge, 1993). Several workers (Dammer, 1893; Gross, 1913) have even treated the WTG as a third subfamily, Coccoloboideae Luerss. Although generic circumscription is not controversial among these taxa, the relationships among them are not clear.

TABLE 2.1 Traditional tribal circumscription of Coccolobeae and Triplarideae, based on Brandbyge (1993).

Tribe Coccolobeae Dumort.	Tribe Triplarideae C. A. Mey.
Afrobrunnichia Hutch. & Dalziel	*Gymnopodium* Rolfe
Antigonon Endl.	*Leptogonum* Benth.
Brunnichia Banks ex Gaertn.	*Ruprechtia* C. A. Mey.
Brunnichia Banks ex Gaertn.	*Symmeria* Benth.
Coccoloba P. Browne	*Triplaris* Loefl.
Muehlenbeckia Meisn.	
Podopterus Humb. & Bonpl.	

Most previous treatments have subdivided the WTG into two tribes within Polygonoideae based on tepal number and breeding system. Triplarideae C. A. Mey. includes mostly dioecious genera with six tepals while Coccolobeae Dumort. includes trees, shrubs and lianas with five tepals (Table 2.1). Among the WTG, *Coccoloba* P. Browne is the most species-rich with 120-150 species distributed in the Caribbean and the Amazon basin (Howard, 1960; Brandbyge,

1993). This genus is best known by the widespread species *Coccoloba uvifera* L., or sea grape, which grows along beaches. *Antigonon* Endl. and *Brunnichia* Banks ex Gaertn. are lianas, as is *Afrobrunnichia* Hutch. & Dalziel (most recently recognized as distinct from *Brunnichia* by Sanchez and Kron, 2009); *Symmeria* Benth., *Ruprechtia* C. A. Mey. and *Triplaris* Loefl. are dioecious trees found mostly in South America. *Gymnopodium* Rolfe, *Podopterus* Humb. & Bonpl. and *Neomillspaughia* S. F. Blake are restricted to dry forests of Central America where they are used commonly in honey production in the Yucatán Peninsula (Ortiz, 1994). *Leptogonum* Benth. is a genus of small trees endemic to Hispaniola, and members of *Muehlenbeckia* Meisn. are small shrubs, often with adaptations to harsh environments (e.g., *M. vulcanica* Meisn., volcanic soils and high altitudes) across the southern hemisphere.

Table 2.2 details previous comprehensive infrafamilial treatments and the characters that have been used to distinguish either two traditional subfamilies, the WTG, or the tribes Coccolobeae and Triplarideae. This summary demonstrates that most treatments have focused on several key characters, namely, the presence of ocrea, tepal number, habit, sexual system, and endosperm type. The ocrea morphologies are quite variable across the tropical genera. In *Triplaris* and some species of *Coccoloba,* this structure is terminal, conical, and caducous. In *Antigonon* and *Brunnichia*, the stipule is a raised line with 1–2 mm of scarious tissue. This variability led Meisner (1856) to segregate genera such as *Brunnichia* and *Symmeria* in their own subfamilies (Brunnichioideae Meisn., Symmerioideae Meisn.) based on the absence or near absence of ocrea. Likewise, Roberty and Vautier (1964) recognized three subfamilies based on ocrea type, whether it was absent, scarious, caducous or persistent and sheathing. In general, the complete absence of ocrea in the Eriogonoideae s.s. was used to distinguish this group as a separate subfamily or tribe (as Eriogoneae Dumort.), though still included in the Polygonaceae (Meisner, 1856; Bentham and Hooker, 1880).

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TABLE 2.2. Table depicting characters used by various workers to either segregate woody tropical genera from the rest of Polygonaceae or to distinguish tribes from each other. Tepal number and ocrea presence were the morphological characters mostly commonly used.

Citation	Characters used						
	Sexual system	Tepal number	Habit	Presence of ocrea	Endosperm type	Stigma type	Perianth texture in fruit
Meisner 1856	X	X	X	X	X		X
Bentham and Hooker 1880	X	X		X			
Dammer 1893	X	X			X		
Gross 1913		X		X	X		
Jaretzky 1925		X	X	X			
Roberty and Vautier 1964			X	X		X	
Haraldson 1978		X		X		X	X
Brandbyge 1993		X	X	X	X		

Sexual systems among the WTG are variable as well. Several genera are strictly dioecious (*Ruprechtia, Symmeria*, and *Triplaris*). Species of *Coccoloba* may also exhibit a dioecious condition, though after closer inspection they are often found to be polygamodioecious (Howard, 1960). In polygamodioecy, individual plants may have inflorescences with both bisexual flowers and unisexual flowers of only one sex. A sexual system such as this might be thought of as transitional between bisexual flowers and a strictly dioecious condition. Dioecy has often been used as a character in previous classifications (Meisner, 1856; Bentham and Hooker, 1880; Dammer, 1893), but the polygamodioecious condition is more recently documented

(Howard, 1960; Brandbyge, 1993) and has not been widely used taxonomically. Polygamodioecy is found in a wide range of taxa throughout Polygonaceae including *Muehlenbeckia* and other temperate genera such as *Rumex* L., *Reynoutria* Houtt., and *Eriogonum.*

Tepal number has also been used to diagnose subfamilies and tribes (Meisner, 1856; Bentham and Hooker, 1880; Dammer, 1893; Gross, 1913; Jaretzky, 1925; Buchinger, 1957), even though there is a discrepancy in the older literature regarding tepal number for various genera (see Blake, 1921 for discussion). In addition to uncertainty regarding tepal number, there is a rich literature debating the fundamental Polygonaceous flower plan and whether the six-tepal or five-tepal condition is derived (see Bentham, 1836 and Lamb-Frye and Kron, 2003 for contrasting theories), or whether the fundamental floral plan is spirally arranged or whorled (sensu Eichler, 1878).

Ruminate endosperm is found in at least 58 plant families (Bayer and Appel, 1996), and in the Polygonaceae, it is common among the woody, tropical genera. As mentioned, ruminate endosperm was used as a distinguishing morphological character for the WTG (Meisner, 1856; Dammer, 1893; Gross, 1913). The character is defined in Polygonaceae as invaginations of the seed coat into the endosperm (Fig. 2.1). Often this feature occurs in a late stage of development of the seed (Lindau, 1891a). In Polygonoideae, endosperm is present but not ruminate.

Given the apparent disagreement between the revised circumscription of subfamilies supported by recent molecular phylogenies (Sanchez and Kron, 2008; Sanchez et al., 2009) and traditional classifications based on morphology, we set out to study the incongruence between the two. This study incorporates increased sampling of taxa, especially of the WTG, a morphological data set focused on the characters most often used in infrafamilial classification, and more molecular data (five plastid regions and nuclear ribosomal ITS) to construct a phylogeny of the tribes Eriogoneae, Triplarideae, and Coccolobeae. In addition to testing the

subfamilial classification, we examine the utility of traditional morphological characters to delimit natural groups and their effect on branch support and tree topology. We use the phylogeny to explore any incongruence between the different data sets, with the goal of assigning morphological synapomorphies to well-supported natural groups. Proposed scenarios of character evolution, such as the intermediacy of polygamodioecy and the floral bauplan for the Polygonaceae are also tested.

MATERIALS AND METHODS

Taxon sampling—

Taxa were sampled intensively for the WTG, including representatives from all 12 genera in Coccolobeae and Triplarideae sensu Brandbyge (1993) for a total of 42 accessions. For the large genus *Coccoloba* (ca. 150 spp.), 15 species were sampled to encompass geographic range and diversity in growth habit. In addition, 10 accessions representing six genera from Eriogoneae and 39 accessions from 19 genera in Polygonoideae were included to test subfamilial limits.

Members of Plumbaginaceae were chosen as outgroups. *Plumbago auriculata* Lam. (= *Plumbago capensis* Thunb.), previously used by Sanchez and Kron (2008), was sequenced, and available GenBank sequences of *Ceratostigma minus* Stapf ex Prain, *Limonium dufourii* Kuntze, and *Limoniastrum monopetalum* Boiss. were also used (Appendix 2.1).

Figure 2.1 Diversity of ruminate endosperm in Polygonaceae achenes. (A) *Podopterus mexicanus*, Newman 63, US. (B). *Symmeria paniculata*, unknown specimen, GH. (C) *Brunnichia ovata*, Ford 2027, BH. (D) *Afrobrunnichia erecta*, FH1-16715, BH. (E) *Coccoloba latifolia*, Steyermark 114961, A. (F) *Antigonon leptopus*, Britton 3107, NY. Of the species shown, only *Brunnichia ovata* was scored as not ruminate. As seen, there are no invaginations of the seed coat into the endosperm, instead, the whole seed is lobed. All sections are cross sections except *A. leptopus,* which is tangential. Scale bar = 1mm.
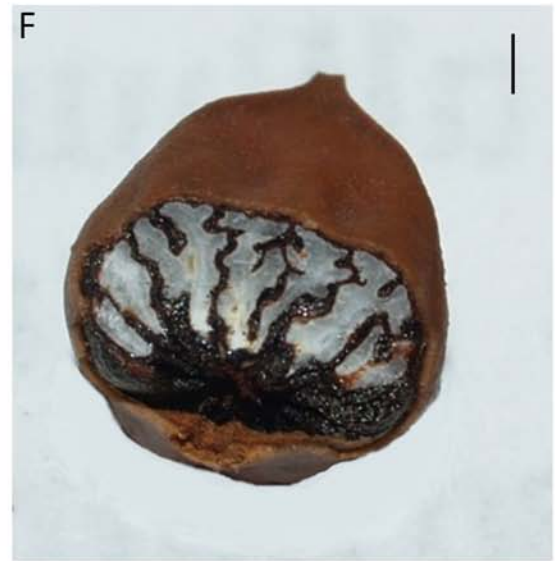
Data presented include nrITS and five plastid gene regions: three coding and two noncoding. Amplification for the regions ITS, *matK*, *ndhF*, and *rbcL* are described in Sanchez and Kron (2008). Primers for *psaI-accD* were from Shaw et al. (2007). Primers for *ycf6-psbM* were designed specific to Eriogonoideae to amplify a 600-bp region: ycf6Fint (5'- GAA GGG GAT ATG GAT GGT AAG- 3') and psbMRint (ATA GAA KAT ACA TAG GGY CCC). These regions were amplified with PCR conditions of a 25 µL volume reaction with 5 µL flexi buffer, 2 µL MgCl$_2$, 1 µL each primer (10µM], 0.13 µL *Taq* polymerase. PCR cycling for *ycf6-psbM* was conducted at 52°C annealing. Products for *psaI-accD* were amplified using the "slow and cold" method of Shaw et al. (2005).

PCR products were run on a 1% agarose gel stained with ethidium bromide. Because of preferential primer binding, plastid intergenic spacers were cleaned with enzymes Exonuclease I and Antarctic Phosphotase (New England BioLabs, Ipswich, Massachusetts, USA) to remove residual PCR primers before adding one sequencing primer. All other regions were cleaned with Qiagen QIAquick PCR purification columns. Cleaned products were sequenced either at the Cornell Biotechnology Resource Center on an Applied Biosystems (Foster City, California, USA) 3730 DNA analyzer or on an ABI 377 DNA sequencer at Wake Forest University's Automated Sequencing Facility.

Several samples from herbarium specimens, for which there was no other material, were sequenced several times to acquire the best quality sequence. These included *Leptogonum* (ITS, *psaI-accD, ycf6-psbM*) and *Symmeria* (ITS). A complete list of taxa and vouchers, along with GenBank numbers, can be found in Appendix 2.1.

Morphological data—

Twenty-two morphological characters were scored for 41 species in Polygonaceae and four species in Plumbaginaceae as outgroups (Appendix 2.2, see Supplemental Data with the online version of this article). Additional species not in the molecular data set were scored either because they represented morphological diversity for large genera or because ample herbarium material was available for study (*Coccoloba barbadensis* Jacq., *C. densifrons* Mart. ex Meisn., *C. latifolia* Lam., and *C. lehmannii* Lindau). Characters selected were those traditionally used to define tribes Coccolobeae and Triplarideae (Meisner, 1856; Dammer, 1893; Gross, 1913; Blake, 1921; Jaretzky, 1925; Vautier, 1949; Roberty and Vautier, 1964; Haraldson, 1978; Brandbyge, 1993) in addition to novel characters. In the character list below, traditional characters are in lightface, and novel characters are in boldface.

1. Woodiness. Herbaceous (0), Suffrutescent (1), Woody (2)

2. Habit. Erect (0), Climbing (1)

3. **Stem pith.** Hollow (0), Solid (1). This character was coded as inapplicable for nonwoody taxa.

4. **Presence of salt-secreting glands on leaves**. Absent (0), Present (1)

5. Presence of ocrea. Absent (0), Present (1). Here, ocrea was defined as a sheathing structure with at least 1 mm of tissue above a circular scar at the leaf base. Can be caducous or persistent.

6. **Ocrea persistence**. Caducous (0), Persistent (1). Taxa distally caducous were coded as caducous.

7. Sexual system. Bisexual flowers (synoecious) (0), Dioecious (1), Polygamodioecious (2).

8. **Floral stipe winged.** Absent (0), Present (1). All genera of tropical Polygonaceae have an articulation between the proximal stipe and distal pedicel of the flower; hence, a distinction is made between which structure is winged.

9. **Presence of distinct perianth whorls.** Absent (0), Present (1). This character distinguishes the sepals and petals (found in Plumbaginaceae) from tepals (Polygonaceae). Subequal or dimorphic tepals in Polygonaceae were not coded as distinct, due to the cyclic nature of the perianth.

10. Tepal (perianth lobe) number. 4 (0), 5 (1), 6 (2). Because the Polygonaceae do not have a differentiated calyx and corolla, the perianth lobes are traditionally termed tepals.

11. **Perianth accrescent in fruit**. Absent (0), Present (1). A perianth was scored as accrescent if there was a lengthening of perianth between anthesis and fruiting stage, and the perianth completely enclosed the fruit at maturity.

12. Part of accrescent perianth enclosing fruit. Hypanthium (0), Inner tepals (1), Outer tepals (2), Tepal lobes (3), Whole perianth (4). Taxa without accrescent tepals were coded as inapplicable. Most Polygonaceae flowers have a well-developed hypanthium, though this term is not often used in the literature. Howard, in his papers on *Coccoloba* (1960) and for the flora of Nicaragua (Howard, 2001), drew attention to the hypanthium as a structure because it was useful to distinguish the part of the perianth enclosing the fruit: hypanthium (proximal) or tepal lobes (distal). We followed Howard and applied the term hypanthium to accurately describe the fusion of tepal and staminal tissue at the base of the flower.

13. Perianth texture in fruit. Hyaline-chartaceous (0), Coriaceous (1), Fleshy-succulent (2). This character is independent of whether the tepals are accrescent as all taxa had some part of the perianth persistent in fruit.

14. Stamen number. 3 (0), 5 (1), 6 (2), 7 (3), 8 (4), 9 (5), greater than 20 (6).

15. **Filament morphology**. Filiform or flattened (0), Dilated (1), Subulate (2). The filament morphology was based on the proximal half of the stamen. Dilated state was scored when the width of the stamen was wider at the base than the apex. Subulate is similar to dilated, except the base is also recurved and not lying in one plane.

16. **Stamen fusion**. Free until fused to short hypanthium (0), Adnate to perianth for most of length (1), Connate (2).

17. Carpel number. 2 (0), 3 (1), 4 (2), 5 (3).

18. **Style fusion**. Absent (0), Present (1). The difference between style and stigma was discerned based on the presence of papillae or ornamentations on the stigmatic surface. Partially fused styles were coded as present.

19. Stigma morphology. Capitate (0), Peltate (1), Fimbriate (2), Decurrent along adaxial surface (3), Pennicilate (4), Bifid (5).

20. Fruit type. Achene (0), Capsule (1), Utricle (2).

21. **Achene shape.** Shape of the achene was coded based on 3-dimensional form and shape in cross section. Trigonous: cross section bluntly 3-lobed, sides indented (0), Terete: cross section round, oblong (1), Globose to subglobose: cross section circular, spherical; (2), Pyramidal: cross section triangular (3), Lenticular: cross section ellipsoid (4). Members of Plumbaginaceae were coded as inapplicable.

22. Endosperm type. Uniform (0), Ruminate (1). See Fig. 2.1 for explanation.

Five to 10 specimens of each species were coded. Missing data were coded as ambiguous in a parsimony analysis. All characters are unordered. Dissections were made from herbarium specimens, and rehydrated with boiling water with 1–5% detergent. Pictures of dissected

material (Fig. 2.1) have not been altered, except the background has been lightened to increase contrast and remove shadows.

Sequence alignment and phylogenetic analyses—

        Alignment was conducted with the programs MUSCLE (Edgar, 2004) or Mafft (Katoh et al., 2005) and subsequently adjusted by hand. The alignment of coding plastid regions was unambiguous. Sequences of *ycf6-psbM* and *psaI-accD* for *Persicaria virginiana* (L.) Gaertn. were excluded because they were too divergent to align. An expanded sampling for Polygonoideae, to test subfamily delimitations, was not included for the two intergenic spaces due to length variation and ambiguity of alignment. For the region *psaI-accD* two short regions (totaling 71 bp) were excluded due to variation in length of homopolymer repeats. Each gene region was initially partitioned and analyzed separately, then concatenated for a combined molecular data set. Statistics for the molecular matrix are shown in Table 2.3. Insertions/ deletions were not coded as characters in this analysis.

TABLE 2.3. Statistics for gene regions used in the phylogenetic analysis. Ingroup is defined as Polygonaceae taxa. Missing values for the two intergenic spacers are mostly from Polygonoideae.

Statistic/Partition	*matK*	*ndHF*	*rbcL*	*psaI-accD*	*psbM-ycf6*	ITS	Combined plastid	Combined molecular
Aligned length	876	1235	1315	957	748	853	5131	5984
% GC content range by taxon	27.3–34.3	27.8–39.0	40.7–45.8	25.7–29.1	33.9–37.2	45.6–77.9	—	—
Variable sites (%)	490 (55.9)	406 (32.9)	568 (43.2)	335 (35.0)	207 (27.7)	595 (69.7)	2006 (39,1)	2601 (43.5)
Parsimony informative characters (%)	335 (38.2)	247 (20.0)	265 (20.2)	144 (15.0)	100 (13.4)	390 (45.7)	1091 (21.3)	1481 (24.7)
Missing ingroup taxa (%)	11 (12.1)	5 (5.49)	1 (1.10)	43 (47.3)	45 (49.5)	4 (4.40)	105 (23.1)	109 (19.9)
CI	0.50	0.54	0.51	0.67	0.71	0.34	0.50	0.42
RI	0.77	0.80	0.75	0.84	0.87	0.66	0.75	0.71

Alignment was straightforward for ITS across representatives of Polygonaceae in the conserved regions (e.g., 5.8S) but the spacers showed high levels of variability. A total of 114 ambiguous base pairs were excluded due to dubious alignment. Because ITS alignment was variable, a sensitivity analysis was conducted, including several alignments with Mafft, MUSCLE, and DIALIGN (Morgenstern, 2004) used to test the effects of alignment on the recovered topology (available from the first author upon request). Different alignments produced highly congruent topologies, indicating that the phylogenetic results are robust and not highly sensitive to changes in alignment. The aligned matrices of molecular data are available at http://purl.org/phylo/treebase/phylows/study/TB2:S10420, study number 10420. Maximum parsimony analyses were conducted in the program TNT (Goloboff et al., 2008). Matrices were mopped to contain only informative characters and first analyzed with TBR and xmult with 10 starting trees and 10 search replicates per search with 1000 replicates. Trees from each run were then analyzed with at least 600 iterations of the ratchet, 100 replicates of sectorial searches, 100 replicates of tree fusion, and 100 replicates of tree drift. This search was repeated several times until no additional MP trees were recovered.

Maximum likelihood (ML) analyses were performed using the program GARLI (Zwickl, 2006). Before likelihood analyses, each data set was analyzed with the program ModelTest (Posada and Crandall, 1998) in the program PAUP* (Swofford, 2002) for the best model of evolution for the data set. The model GTR+I+G was selected as the optimal model for each data set analyzed and was implemented in GARLI. Configuration settings were kept at default in GARLI except the setting attachments per taxon was changed to more than two times the total taxa analyzed (200 for the combined data set) and "genthreshfortopoterm" was changed to 50,000, with two search replicates per generation.

Support values were calculated with a statistical bootstrap. Parametric bootstraps were conducted in the program TNT with 10 starting trees and 10 search replicates, saving the best tree, for 1000 replicates. Nonparametric bootstrap values for ML were calculated based on 200 replicates with only one search replicate per bootstrap replicate due to the inordinate amount of time required to add additional search replicates.

Before analysis, matrices from different data sets were tested for incongruence using the incongruence length difference (ILD) test (Farris et al., 1994). We decided to combine data sets if they were found to be not significantly incongruent. In cases of moderate significance of incongruence ($P = 0.03$- 0.05), we also assessed support for conflicting topologies of the analysis before deciding whether to combine. We questioned results with moderate significance due to some documented issues with the ILD test such as: (1) possibility of increased type I error for this test (Cunningham, 1997) and (2) ability for the test to reject congruence due to variation in rate of character evolution (Dolphin et al., 2000).

RESULTS

Phylogenetic relationships—

Molecular— Table 2.3 presents a complete list of gene regions and combined data matrix statistics. This study generated 174 new sequences (Appendix 2.1). The remaining sequences were taken from GenBank. Of the six gene regions sampled, ITS was the most variable region (69.7%) and the most parsimony informative (45.7%), and ndhF was the least parsimony informative (20.0%). The two intergenic spacers had the lowest portion of parsimony-informative characters, but taxon sampling was mostly limited to the Eriogonoideae so the numbers are not directly comparable. The combined molecular data set had 19.9% missing data in terms of gene region sampling for ingroup taxa mostly due to the limited number of genera

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and species sampled from Polygonoideae for the two intergenic spacers, as compared to the other molecular regions. The combined data set for all regions was 5984 bp long and contained 24.7% parsimony informative characters. The combined plastid data set was 5131 bp long and contained 21.3% parsimony informative characters.

ITS and combined plastid data sets were found to be incongruent with moderate significance ($P = 0.03$). The decision was made to combine the molecular data sets, based on the lack of support for conflicting topologies in the ITS tree. These topological incongruences are discussed below. The ILD test also rejected congruence with high significance ($P = 0.0196$) for the combined molecular and morphological data sets. In this case, we did not combine. Instead we present a tree generated from molecular data, which had higher support values and resolution, and mapped morphological characters on it (Fig. 2.3), although we also discuss some of the results from the total evidence analysis.

Phylogenetic trees reconstructed from ITS and combined plastid regions were largely concordant (results not shown) under a maximum parsimony criterion. Plastid and ITS trees supported the same members of the major clades, with only one topological incongruence regarding the WTG taxa. *Afrobrunnichia* was placed sister to Polygonoideae based on the plastid data set (44% bootstrap) and was at the base of the tree with evidence from ITS (72% bootstrap). Under the maximum likelihood criterion, the ITS data set recovered a most likely tree where *Symmeria* and *Brunnichia + Antigonon* were sister to Polygonoideae, though with little support (11%/22% bootstrap, respectively). The placement of *Symmeria* and *Afrobrunnichia* for the plastid ML analysis was different from MP as well. For ML, *Symmeria* is nested within the six tepal clade, and *Afrobrunnichia* is sister to this same clade (results not shown).

Figure 2.2. Cladogram obtained from the strict consensus of the maximum parsimony (MP)

analysis of the combined molecular data. The maximum likelihood (ML) phylogram can be

found online and in Appendix 2.3. Numbers below branches indicate bootstrap values for

MP/ML. A hyphen (-) indicates a topology not supported by the ML tree. If only one number is

present, both ML and MP had the same values, denoted by an asterisk (*).The dashed-line

branch accents the lack of support for the phylogenetic placement of *Podopterus.* This position

varies depending on the gene region and taxon sampling used in the analysis. Boldfaced taxa

indicate members of the woody tropical genera. Recommended subfamily classification is

depicted on right where *Symmeria* and *Afrobrunnichia* are incertae sedis (*).

Phylogenetic tree (cladogram)

OG

*

Polygonoideae

Eriogonoideae

Taxa (top to bottom):

- Plumbago auriculata
- Ceratostigma minus
- Limoniastrum monopetalum
- Limonium dufourii
- **Symmeria paniculata**
- **Afrobrunnichia erecta**
- Antenoron filiforme
- Persicaria virginiana
- Persicaria pensylvanica
- Persicaria sagittata
- Bistorta attenuatifolia
- Bistorta tenuicaulis
- Rubrivena polystachya
- Polygonum paniculatum
- Aconogonon molle
- Koenigia forestii
- Koenigia islandica
- Pteropyrum aucheri
- Pteropyrum olivieri
- Calligonum microcarpum
- Calligonum aphyllum
- Calligonum eriopodum
- Fagopyrum urophyllum
- Fagopyrum cymosum
- Fagopyrum esculentum
- Emex spinosa
- Rumex obtusifolius
- Rumex acetosella
- Rumex induratus
- Oxyria digyna
- Oxyria sinensis
- Rheum nobile
- Rheum pinchonii
- Knorringia sibrica
- Atraphaxis spinosa
- Atraphaxis pyrifolia
- Polygonum aviculare
- Polygonum erectum
- Polygonella americana
- Polygonella articulata
- Reynoutria japonica
- Reynoutria sachalinensis
- Fallopia dumetorum
- Fallopia scandens
- **Muehlenbeckia complexa**
- **Muehlenbeckia platyclada**
- Fallopia aubertii
- **Muehlenbeckia tamnifolia**
- **Brunnichia ovata**
- Antigonon leptopus
- Antigonon cinerascens
- Antigonon guatimalense
- Neomillspaughia emarginata
- Coccoloba acapulcensis
- Coccoloba brasiliensis
- Coccoloba latifolia
- Coccoloba belizensis
- Coccoloba swartzii
- Coccoloba northropiae
- Coccoloba venosa
- Coccoloba diversifolia
- Coccoloba spicata
- Coccoloba tenuifolia
- Coccoloba uvifera
- Coccoloba rugosa
- Coccoloba krugii
- Coccoloba pallida
- Coccoloba pubescens
- **Podopterus cordifolius**
- **Podopterus mexicanus**
- **Leptogonum domingense**
- **Gymnopodium floribundum B48**
- **Gymnopodium floribundum B70**
- Gilmania luteola
- Pterostegia drymarioides
- Chorizanthe brevicornu
- Eriogonum umbellatum
- Eriogonum alatum
- Eriogonum inflatum
- Johanneshowellia crateriorum
- Eriogonum esmeraldense
- Dedeckera eurekensis
- Eriogonum clavellatum
- **Ruprechtia triflora**
- **Triplaris cumingiana**
- **Triplaris americana**
- **Triplaris weigeltiana**
- **Triplaris poeppigiana**
- **Triplaris setosa**
- **Ruprechtia laxiflora**
- **Ruprechtia chiapensis**
- **Ruprechtia coriacea**
- **Ruprechtia cruegeri**
- **Ruprechtia pallida**
- **Ruprechtia tangarana**

Support values on branches:

99/100, 86*, 100/99, 93/45, 96/100, 100, 70*, 99/100, 98/100, 64/-, 100*, 53/95, 100*, 100*, 97/100, 100*, 92/99, 94/97, 100*, 100*, 42/-, 100, 100*, 100/97, 100*, 79/96, 100*, 52/73, 92/100, 94/98, 89/97, 99/100, 67/98, 100*, 90/97, 67/84, 64/81, 84/97, 53/81, 23/29, 16/24, 72/57, 48/-, 100*, 99/100, 100*, 100*, 99/100, 93/96, 87/98, 52/73, 41/59, 37/46, 18/36, 26/70, 30/66, 70/78, 25/61, 76/52, 89/88, 98/89, 100*, 30/61, 100/88, 100*, 100*, 98/100, 100*, 99/100, 34/-, 57/66, 44/60, 36/-, 99/100, 80/87, 83/78, 99/95, 100/98, 63/72, 100/64, 46/49, 75/74, 98/99

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Figure 2.3. One most parsimonious tree recovered from the molecular data set, with most Polygonoideae taxa pruned. When morphology is included in the analysis, *Gymnopodium* is placed sister to *Ruprechtia + Triplaris*. Characters were mapped, and the optimization was unambiguous, except in the character of ruminate endosperm. Both five tepals and presence of ocrea were reconstructed as ancestral for Polygonaceae, while ruminate endosperm was ambiguous, here mapped as DELTRAN. The traditional tribal designations are shown on the tree with dashed lines to indicate they are not monophyletic. T = Triplarideae, C = Coccolobeae.
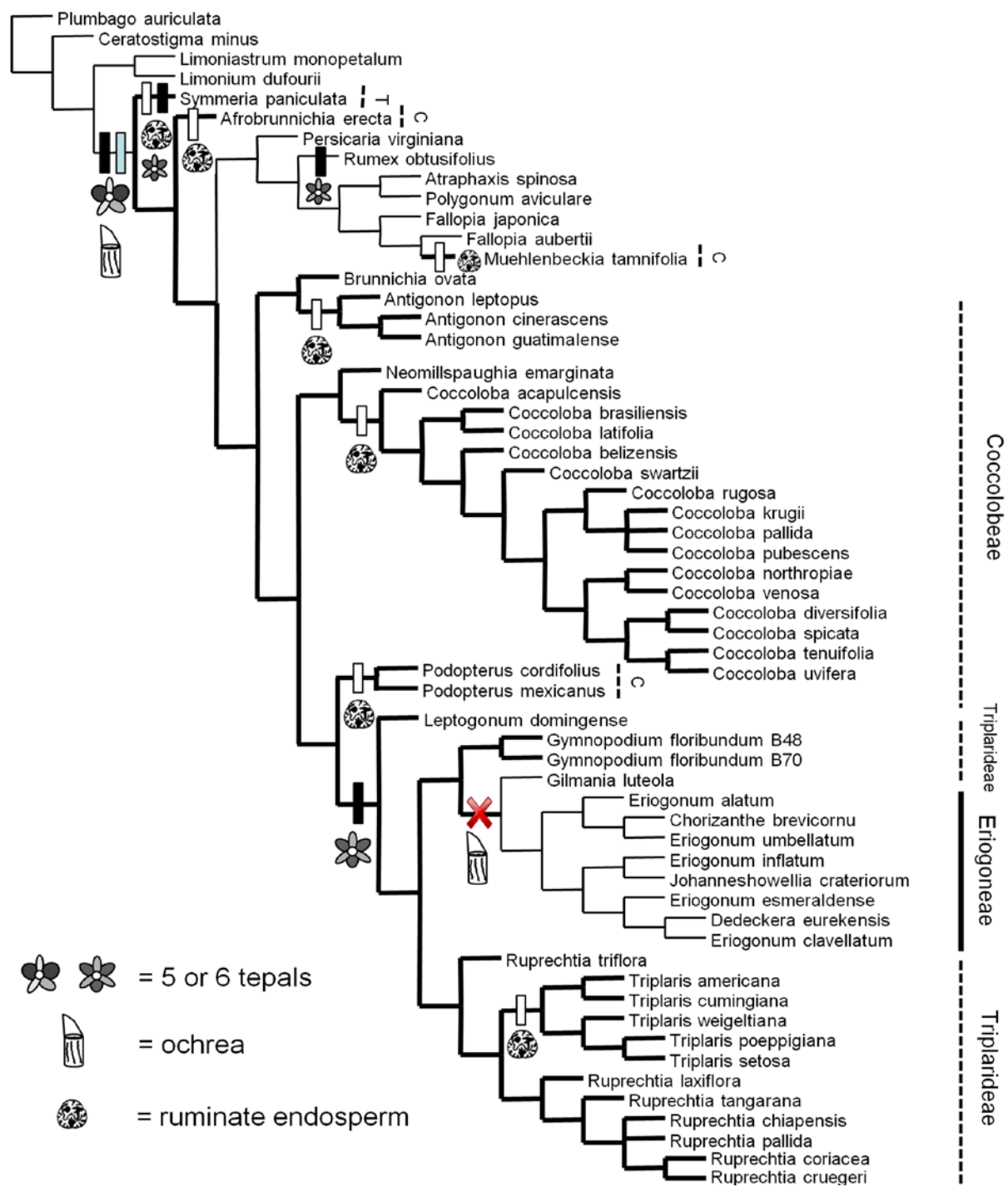
Results from the maximum parsimony analysis (MP) for the combined molecular data set recovered nine trees (L = 5742, CI = 0.42, RI = 0.71). The tree with the lowest likelihood score from maximum likelihood analyses (ML) was Ln = -46868.69 (Appendix 2.3, see online Supplemental Data). Results from combined molecular analyses for both MP and ML recovered with 89/88% bootstrap scores, respectively, for a broad Eriogonoideae (sensu Sanchez and Kron, 2008), excluding *Afrobrunnichia, Symmeria* and *Muehlenbeckia* (Fig. 2.2). *Symmeria* and *Afrobrunnichia* are at the base of the tree with 100% and 93% parsimony bootstrap support, respectively. In the ML analysis, *Symmeria* is at the base of the tree and *Afrobrunnichia* is sister to the rest of Polygonoideae with very little bootstrap support (28%, Fig. 2.2, Appendix 2.3). *Muehlenbeckia* is nested within Polygonoideae, consistent with previous analyses (Lamb-Frye and Kron, 2003; Won et al., 2007; Galasso et al., 2009; Sanchez et al., 2009).

The first diverging lineage in Eriogonoideae is a strongly supported clade of *Antigonon + Brunnichia* (100% bootstrap support). The next two major clades distinguish taxa with five tepals (*Coccoloba, Neomillspaughia)* from those with six tepals, with the exception of *Podopterus*, which is sister to the six-tepal clade (30% and 61% for MP and ML). The second clade includes the six-tepaled taxa: *Leptogonum*, *Triplaris*, *Ruprechtia*, *Gymnopodium*, and the genera of Eriogoneae. *Leptogonum* is sister to the other genera with moderate support (80% and 87% for ML and MP, respectively). Two subclades are strongly supported as monophyletic within the six-tepaled taxa: a clade of *Triplaris* and *Ruprechtia* (Fig. 2.2) and Eriogoneae (monophyletic with 100% bootstrap support). *Gymnopodium* is placed as sister to Eriogoneae (100/88% bootstrap) in both analyses.

The WTG of Polygonaceae are not monophyletic in the recovered tree nor are the tribes Coccolobeae or Triplarideae (compare Fig. 2.2 and Table 2.2). *Afrobrunnichia* and *Muehlenbeckia* are in the Polygonoideae clade, and the remaining genera of the Coccolobeae

(*Antigonon*, *Brunnichia*, *Coccoloba*, *Neomillspaughia*, and *Podopterus*) form a paraphyletic assemblage, giving rise to the six-tepaled taxa. In turn, the genera of Triplarideae (*Gymnopodium*, *Leptogonum*, *Ruprechtia*, and *Triplaris*), excluding *Symmeria*, form a paraphyletic group giving rise to Eriogoneae.

Morphology— The strict consensus tree from parsimony analysis of morphological characters (L = 102, N = >10000) was largely unresolved (results not shown). The Polygonaceae were recovered as strongly monophyletic. In contrast to molecular results, the genera of Eriogoneae make up the basal lineages of the tree, with the tropical genera nested within, although none of these relationships are well supported (<50% bootstrap).

Combined morphology and molecular— A combined parsimony analysis of both data sets for a subset of taxa (59) produced 312 most parsimonious trees (L = 3597) with a topology almost identical to the molecular tree (Fig. 2.2), with the exception of Gymnopodium, which is placed, with low support, as sister to Ruprechtia and Triplaris (results not shown). The bootstrap value for Eriogonoideae was 71%; support for other internal clades was also lower than with molecules alone, with the exception of Eriogoneae, which was recovered with 100% support and the Brunnichia + Antigonon clade with 99% support.

Of the 22 morphological characters examined, none provided an unreversed synapomorphy for Eriogonoideae, neither when included in the analysis with molecular data nor when mapped a tree generated from molecular data. However, several characters added support to clades within Eriogonoideae such as tepal number, supporting a six-tepaled clade, and absence of ocrea, in Eriogoneae (Fig. 2.3). Many of the traditional taxonomic characters were homoplasious. The least consistent characters within Polygonaceae were endosperm type (no. steps = 7, c_i = 0.14, Fig. 2.3), stipe wings (no. steps = 6, c_i = 0.16), ocreae persistence (no. steps = 7, c_i = 0.14), stem pith (no. steps = 6, c_i = 0.16), and stamen fusion (no. steps = 12, c_i = 0.16).

Characters with higher consistency indices were stamen number (no. steps = 8, c_i = 0.62), gynoecium merosity (no. steps = 4, c_i = 0.50), achene shape (no. steps = 6, c_i = 0.66), tepal number (no. steps = 5, c_i = 0.40, Fig. 2.3), and ocrea presence (no. steps = 2, c_i = 0.50, Fig. 2.3).

DISCUSSION

Monophyly and relationships among genera—

Based on many taxonomic treatments, the WTG were thought of as either representing a separate subfamily or derived from within Polygonoideae (Dammer, 1893; Gross, 1913; Roberty and Vautier, 1964). Heintze (1927) departed from the common evolutionary scenario when he postulated that both Polygonoideae and Eriogonoideae were derived from a more primitive Coccoloboideae (synonymous here with WTG). Reveal (1978) considered the WTG and Eriogoneae to be monophyletic groups derived from the same Polygonaceous tropical ancestor. None of these evolutionary hypotheses is supported by our data. Instead, this study corroborates previous molecular phylogenetic studies in the family (Sanchez and Kron, 2008; Sanchez et al., 2009). Eriogonoideae is a monophyletic subfamily containing most members of WTG, excluding the genera *Afrobrunnichia*, *Muehlenbeckia*, and *Symmeria* (Figs. 2.2, 2.3). Even with increased sampling of gene regions and outgroups compared to previous studies, the position of *Symmeria* and *Afrobrunnichia* remains at the base of the tree (as in Sanchez and Kron, 2009; Sanchez et al., 2009). We are confident that *Symmeria* is not closely related to the rest of Eriogonoideae; however, the position of *Afrobrunnichia* changes depending on the gene region used as data; hence, we are not confident about its position and have excluded it from Eriogonoideae until additional supporting evidence is discovered.

A number of other relationships have strong support based on molecular data. *Antigonon* and *Brunnichia* are monophyletic (Figs. 2.2, 2.3), with morphological synapomorphies such as the climbing habit and short, caducous ocrea. Our analyses also clarify the position of

Neomillspaughia emarginata S. F. Blake as sister to *Coccoloba*. Previous to its segregation as a new genus by Blake (1921), *Neomillspaughia* had been placed either in *Campderia* Benth. (Donnell Smith, 1899) or *Podopterus* (Gross, 1913). *Podopterus* and *Neomillspaughia* were placed together taxonomically based on their similar habit (dry forest shrubs) and presence of membranaceous tepals surrounding the fruit (Gross, 1913). Although *Neomillspaughia* lacks the fleshy tepals in fruit and globose achene found in most species of *Coccoloba*, the two genera share numerous vegetative characters, including coriaceous leaves and similar ocrea morphologies. Given the affinity of *Neomillspaughia* to *Coccoloba* in our analyses, it appears that membranaceous tepals in fruit are plesiomorphic, and fleshy tepals have been derived in *Coccoloba.*

There have not been many subgeneric classifications of *Coccoloba. Campderia* was segregated as a genus by Bentham and Hooker (1880) and Donnell Smith (1899) but was subsequently recognized as a section of *Coccoloba* by Lindau (1891b). The characters distinguishing sect. *Campderia* from the other *Coccoloba* were the accrescent tepal lobes (instead of a hypanthium) in fruit and a perianth not adherent to the achene (Bentham and Hinds, 1844; Lindau, 1891b). For our morphological analyses, species that were previously placed in *Campderia* are *Coccoloba lehmannii*, *C. venosa* L., and *C. tenuifolia* L.; these do not form a monophyletic group in either the molecular or combined analysis. *Coccoloba venosa* and *C. tenuifolia* are in different subclades based on the molecular data, and *Coccoloba lehmannii* is placed as sister to the rest of *Coccoloba* based on morphological data alone. The latter differs from the other *Coccoloba* species sampled in the presence of coriaceous instead of fleshy tepals in fruit. Fleshy tepals seem to be a synapomorphy for the rest of the genus, but the combined analysis samples only 18 of ca. 150 species, so a more thorough assessment of variation across the genus is needed to determine the diagnostic value of this character.

Our results are ambiguous about the affinities of *Podopterus* relative to other genera (Figs. 2.2, 2.3). The genus consists of three species, two of which are sampled here and were recovered as sister with strong support (100%). This relationship is upheld by floral morphology, although they have different growth habits. *Podopterus mexicanus* Humb. & Bonpl. is a shrub of dry forests in southeastern Mexico, with white flowers and the terminal buds on branches modified into spines. *Podopterus cordifolius* Rose & Standl. is a remarkable species with only a few populations documented so far in Mexico: Oaxaca and the type locality in Colima. They are large lianas, often with numerous stems and foliar growth in the dry forest canopy. Flowers appear in February and April, after the first rains, and are lilac, a unique character in Polygonaceae. There are several morphological similarities that suggest *Podopterus* is related to *Neomillspaughia*, such as membranaceous tepals with dorsal wings (Blake, 1921; Roberty and Vautier, 1964), but our study finds no convincing molecular evidence for such a relationship. In Sanchez et al. (2009) a relationship of *Podopterus* to *Neomillspaughia* and *Coccoloba* was supported by a bootstrap of 52–62%, but the addition of more molecular data and increased taxon sampling has changed this hypothesized relationship.

The six-tepaled clade is supported as monophyletic (Figs. 2.2, 2.3), with *Leptogonum* at the base of the clade. *Leptogonum* is a monospecific genus, rare and endemic to the serpentine soils on Hispaniola (J. Salazar, Universidad Autónoma de Santo Domingo, personal communication). Although *Leptogonum* is nested within Eriogonoideae and is sister to the remaining genera of the six-tepaled clade, it appears to have retained ancestral characters. It is distinguished by leaves that are clustered apically on the shoots and by the absence of an accrescent perianth (Brandbyge, 1990), unlike other tropical members of Eriogonoideae. Brandbyge (1990) attributed the limited evolutionary success of the genus, as assessed by its limited range, to a lack of adaptations to dispersal, and he interpreted this feature as an ancient

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condition. To the contrary, it could be argued that *Leptogonum* has evolved to become exclusively adapted to serpentine soils and hence cannot expand its range beyond this soil type.

The South American, dioecious tree genera *Triplaris* and *Ruprechtia* form a clade with high support (95/99% bootstrap; Fig. 2.2) in which *Triplaris* is monophyletic but *Ruprechtia* is not. *Ruprechtia triflora* Griseb. is at the base of the clade but without strong support. Because of the morphological gradation between many characters, generic circumscription has been a taxonomic issue for these genera (Cocucci, 1961; Roberty and Vautier, 1964; Brandbyge and Øllgard, 1984; Pendry, 2004). One of the diagnostic characters that has been used is the extent to which the accrescent hypanthium is fused to cover the achene (Cocucci, 1961), a quantitative character. *Ruprechtia triflora* exhibits only 1 mm of hypanthium fusion, though this elongates in fruit. From the phylogenetic trees (Figs. 2.2, 2.3), this lack of fusion seems to be the ancestral trait, with more fusion (as it occurs in *Triplaris*) derived. More sampling of species from both genera is needed to test the monophyly of these genera and whether the generic circumscriptions hold.

Our analyses place *Gymnopodium* as the sister group to Eriogoneae (100/88% bootstrap), which is also supported by some morphological characters. *Gymnopodium* shares floral traits with this clade, such as filiform filaments having relatively small anthers. In addition, the ocreae exhibited by *Gymnopodium* are scarious and minute (1–2 mm), a possible intermediate state before the loss of ocrea observed in Eriogoneae.

Afrobrunnichia, *Muehlenbeckia*, and *Symmeria* were previously placed in Eriogonoideae but are not closely related to them in the present analysis. *Muehlenbeckia* is sister to *Fallopia*, where it shares characters such as vine habit and presence of extrafloral nectaries (Haraldson, 1978; Brandbyge, 1993). The genus *Symmeria* is monospecific, morphologically variable, and has a disjunct distribution with individuals occurring throughout the Amazon Basin (though

restricted to Igapó forests) and West Africa (Brandbyge, 1988; Aymard and Howard, 2004). It also has many autapomorphic characters unique to Polygonaceae, such as dilated petiole wings covering the apical meristem (instead of a true ocrea), pyramidal achenes with three tepals adnate to the fruit wall, and male flowers with more than 20 stamens. All these characters suggest that *Symmeria* is highly derived. The other tropical genus excluded from Eriogonoideae is *Afrobrunnichia* (Sanchez and Kron, 2009) which differs from *Brunnichia ovata* (Walter) Shinners in its West African distribution and the presence of ruminate endosperm (absent in *Brunnichia*, Fig. 2.1). A more thorough discussion of these genera can be found in Sanchez and Kron (2009). The original placement of these genera among the other WTG genera likely was based on convergence of morphological characters such as habit, endosperm type, or fleshy tepals in fruit. Some of these characters are discussed later.

Character evolution—

The ocrea, or sheathing structure surrounding leaf nodes, is observed in most members of Polygonaceae and is often thought of as a distinctive vegetative character for the family (Zomlefer, 1994; Simpson, 2005). This term was introduced into botanical usage and defined by Willdenow (1799, p. 440), but the character had been used to recognize the group previously (e.g., Jussieu, 1789). Most species in Polygonaceae have outgrowths associated with leaf bases, but they may not be "ocrea-like", i.e., sheathing, persistent, and hyaline. In the phylogenetic hypothesis presented here (Fig. 2.3), the ocrea is a synapomorphy for Polygonaceae (with the possible exception of *Symmeria*), with one reversal in the Eriogoneae clade (depending on the placement and coding of some species of *Chorizanthe* R. Br. ex Benth., which may have a vestigial stipular structure; see Freeman and Reveal, 2005). The absence of ocrea led early

workers, such as Bentham (1836) to treat Eriogoneae as a separate tribe, a taxonomic division we accept in this study.

In Polygonoideae, ocrea morphology is relatively uniform, with long ocreae having hyaline texture, though reduced ocreae are still common (e.g., *Calligonum, Koenigia*). Ocreae in this group are often persistent, though commonly split distally with age. Among the Eriogonoideae, we see a wide range in ocrea morphologies. In *Coccoloba*, as well as *Neomillspaughia* and *Triplaris*, the stipule functions to enclose the emerging leaves and apical meristem and can be large, though it does not persist and soon abscises to leave a circular scar. In *Coccoloba*, ocreae are foliaceous and often distally caducous. In *Triplaris*, the shape of the stipule is conical and soon deciduous. Genera such as *Antigonon*, *Brunnichia*, and some species of *Ruprechtia* have reduced ocreae consisting of several millimeters of scarious tissue above a stipular line. And in *Podopterus cordifolius*, the ocreae are long, sheathing, and hyaline, more similar to those found in Polygonoideae. Overall, the leaf node structure as seen in Eriogonoideae may not be ocrea-like in the strict sense. Though not quantified here, it seems that the ocrea is more variable in subfamily Eriogonoideae than in Polygonoideae and has not become "fixed" on one morphology.

Tepal number and floral bauplan in the progenitors to the family Polygonaceae have been debated for centuries. The most common condition in Polygonaceae is five or six tepals, with occasional reduction to three or four in such genera as *Koenigia* L*., Oxyria* Hill, and *Persicaria* (L.) Mill. The debate regarding the perianth of Polygonaceae has focused on ancestral merosity (five or six) and fundamental arrangement (spiral or whorled). Early on, Bentham (1836) postulated trimerous flowers with six tepals in two whorls as the primitive state. Later, Eichler (1878) published his ideas about floral arrangement in studies across the plant kingdom. He divided perianth arrangements into either cyclic (spirally arranged) or acyclic (whorled). This

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division was adopted by Dammer (1893) in his treatment of Polygonaceae. He placed the five-tepal taxa into the cyclic category, and the six tepals were treated as acyclic, thereby not limiting the floral bauplan in Polygonaceae to one condition.

Toward the 1920s, the theory shifted toward the tepals being spirally arranged, instead of in separate whorls (sensu Eichler), and the debate also focused on the ancestral condition for the family. Bauer (1922) conducted ontogenetic studies and concluded that the five-tepal, spirally arranged condition is fundamental, and four or six tepals represent the derived state, with the four or six tepal condition the result of variability in nutrient availability to the developing flower. Lundbald (1922), also using ontogenetic studies, concluded the opposite: the six tepal, spirally arranged condition is primitive, and the transitional arrangement in a five tepal flower is a "double tepal" and not homologous to the others. Figure 2.4 depicts the position of this transitional tepal. According to Lundbald's hypothesis, it is formed from the fusion of the adjacent tepals in the spiral arrangement, thereby reducing the tepal number from six to five. Vautier (1949) also investigated the evolution of tepal number through careful anatomical studies. She maintained the view of a transitional tepal, but distinguished whether this tepal was inserted in a clockwise or counterclockwise fashion. Based on his own anatomical studies and a synthesis of previous literature, Laubengayer (1937) supported the six tepal condition as primitive. However, he found contradictory evidence: the tepal primordia were arranged in a spiral sequence, while the vasculature was arranged in whorls. Our results support the five-tepal condition as ancestral and the six-tepal condition as derived within the Eriogonoideae (Fig. 2.3). Our study also refutes the "transitional tepal" theory, in which the joined tepal is formed by reduction. The transition to six tepals is likely formed from an addition of a primordium in a spiral arrangement as opposed to a switch from a fundamental floral plan from spiral to whorled.

Within the Eriogonoideae there are a number of different sexual systems. Strict dioecy appears as a synapomorphy for one clade: *Ruprechtia* and *Triplaris*. Sexual systems in species of *Coccoloba* have not been well documented and it is often hard to assess functionality of sexual organs based on herbarium specimens. Nevertheless, it is clear that both dioecy and polygamodioecy are found in the genus (Howard, 1960). We hypothesized that a "leaky" system such as polygamodioecy would be transitional between plants with bisexual flowers (ancestral) and strict dioecy. However, this does not appear to be the case; the strictly dioecious genera (*Triplaris*, *Ruprechtia*) are in a separate clade from *Coccoloba* (Fig. 2.3), suggesting that these systems have evolved independently. In fact, polygamodioecy has evolved multiple times in Polygonaceae: the condition also occurs in some species of *Eriogonum*, *Muehlenbeckia*, *Oxygonum* Burch., *Persicaria*, *Reynoutria*, and *Rumex*. Dioecy also occurs outside of Eriogonoideae, as in *Rheum* and *Symmeria* (Brandbyge, 1993; Freeman and Reveal, 2005).

Figure 2.4. Photomicrograph of *Antigonon cordatum* (*Burke 34*, BH) with tepals labeled as acyclic, with a transitional or "double tepal" sensu Eichler or Lundbald. O = outer tepal, I = inner tepal, T = transitional. The transitional tepal has been interpreted as a fusion of one tepal from each whorl, a hypothesis contradicted by our analysis.

The presence of ruminate endosperm was previously used as a character to distinguish subfamily Coccoloboideae consisting of all the WTG (Dammer, 1893; Gross, 1913). As mapped on our tree, this character appears to have evolved multiple times in Eriogonoideae (Fig. 2.3). Optimization is ambiguous at the base of Polygonaceae, so it is unclear if the presence of ruminate endosperm is plesiomorphic. In Fig. 2.3, it is optimized favoring parallelisms (DELTRAN). We chose this optimization because ruminate endosperm has evolved in parallel many times in the angiosperms (Bayer and Appel, 1996), and we lack evidence that this is a synapomorphy for Polygonaceae. We also discovered that ruminate endosperm varies among genera (Fig. 2.1). The amount of seed coat invagination is variable by stage of development and was only apparent in mature seeds, making it difficult to quantify different types of ruminate endosperm in seeds unless the seeds are all at the same stage of maturity. In some cases, what appear to be seed coat invaginations into the endosperm is actually a deeply lobed seed, as in *Brunnichia* (Fig. 2.1). Lack of homology in this character further supports the separation of *Brunnichia* from *Afrobrunnichia* because the latter has true ruminate endosperm. In *Coccoloba,* the one species investigated that did not appear to have ruminate endosperm was *C. lehmannii.* This species is placed as sister to the rest of *Coccoloba* in a morphological analysis (not shown). Combined with the lack of a fleshy hypanthium in fruit, this supports its position as a basal species without some of the derived characters exhibited by the rest of the *Coccoloba* species.

Future work will include a search for additional morphological characters with the potential to support natural groups. From his morphological studies, Galle (1977) concluded that the relationship of the flower to the stem and the ocreolae (fused bracteoles subtending the primary inflorescence) were the most phylogenetically informative characters. From this, he assumed an affinity between some tropical genera and Eriogoneae. Other characters worthy of investigation in Eriogonoideae may be palynological. Even though pollen morphology does not

vary much within Eriogoneae, there is variability in organization of colpi, pores, and ornamentation among the other genera of Eriogonoideae (Nowicke and Skvarla, 1977; Mondal, 1997). Pollen characters have previously been used to posit an affinity between Polygonaceae and Plumbaginaceae (Nowicke and Skvarla, 1977) or to place Polygonaceae as a transitional family within Caryophyllales (Wodehouse, 1931).

Conclusions—

This study is the first to address thoroughly the relationships among taxa in Eriogonoideae using morphological and molecular characters. The subfamily Eriogonoideae is supported as monophyletic if one excludes *Afrobrunnichia* and *Symmeria*. Coccolobeae and Triplarideae are not monophyletic, although there is strong support for a six-tepaled clade comprising Eriogoneae, *Gymnopodium*, *Leptogonum*, *Ruprechtia*, and *Triplaris*. We recommend that the circumscription of Coccolobeae be modified to include *Coccoloba*, *Neomillspaughia*, and possibly *Podopterus.* Triplarideae, to remain a monophyletic group, should only include the genera *Ruprechtia* and *Triplaris.* These tribes can easily be distinguished based on morphological synapomorphies. A more comprehensive tribal treatment of the family is forthcoming (Sanchez et al., 2011; Burke and Sanchez, in press).

Morphological work did not elucidate synapomorphies for the subfamily Eriogonoideae, but we discovered that several characters traditionally used to delimit subfamilies and tribes are homoplasious. The ocrea is a highly variable character in Eriogonoideae, and its presence, in the strict morphological sense, may be restricted to the subfamily Polygonoideae. The six-tepaled condition is derived from five tepals and likely results from additional primordium to the floral plan. Polygamodioecy has evolved multiple times in Polygonaceae, and endosperm rumination is a variable character, sometimes confounded with a deeply lobed seed coat.

Our findings indicate that the woody, tropical genera of Polygonaceae have given rise to the temperate Eriogoneae, a tribe which is supported as strongly monophyletic. The latter is extremely diverse in the western North America, with some 325 species. Often tropical genera are treated as their own family or subfamily. Our study supports the origin of a diverse temperate group from a heterogeneous tropical assemblage, which was not previously hypothesized before the advent of molecular phylogenetics. This phylogenetic arrangement elicits broader evolutionary questions about dispersal from a tropical region, and rapid radiation in a new habitat.

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APPENDICES

APPENDIX 2.1 Voucher information for DNA extractions used in this study. Sequences obtained from GenBank are given with their respective site specific numbers. New sequences generated for this study provide the following information: taxon, collector(s), collection number (in italics), and GenBank accession numbers. Specimens are deposited at WFU (Wake Forest University) unless another herbarium is given. Herbarium acronyms follow Index Herbariorum, K = Royal Botanic Gardens Kew, E = Royal Botanic Gardens Edinburgh, BH= Cornell University, MO = Missouri Botanical Garden, NCU = University of North Carolina. Gene abbreviations are as follows: R = *rbcL*, M = *matK*, N = *ndhF,* P = *psbM-ycf6*, A = *psaI-accD* and I = ITS. NA= not used in this study.

(**1**) **Sequences obtained from GenBank.** *Aconogonon molle* (D. Don) Hara, R-EF653764, M-GQ206190, N-GQ206271, P-NA, Y-NA, I-EF653687; *Afrobrunnichia erecta* Hutch. & Dalziel, R-FJ154447, M-FJ154489, N-FJ154501, I-FJ154459; *Antenoron filiforme* (Thunb.) Roberty & Vautier (*Polygonum filiforme* Thunb. *subsp. neofiliforme* (Nakai) Kitam.), R-GQ206211, M-NA, N-GQ206272, P-NA, Y-NA, I-GQ206237; *Antigonon guatimalense* Meisn., R-FJ154449, M-FJ154491, N-FJ154503, I-FJ154461; *Antigonon leptopus* Hook. & Arn., R-AF297146, M-EF437988, N-EF438027, I-FJ154462; *Atraphaxis pyrifolia* Bunge., R-GQ206212, M-GQ206191, N-GQ206273, P-NA, Y-NA, I-NA; *Atraphaxis spinosa* L., R-AF297123, M-EF437989, N-EF438028, I-FJ154463; *Bistorta attenuatifolia* Miyam. & H. Ohba, R-GQ206213, M-NA, N-NA, P-NA, Y-NA, I-GQ206239; *Bistorta tenuicaulis* Petrov, R-GQ206214, M-NA, N-GQ206274, P-NA, Y-NA, I-GQ206240; *Brunnichia ovata* (Walter) Shinners, R-FJ154451, M-EF437990, N-EF438029 I-FJ154465; *Calligonum aphyllum* (Pall.) Gürke, R-GQ206215, M-GQ206192, N-GQ206275, P-NA, Y-NA, I-GQ206241; *Calligonum eriopodum* Bunge, R-GQ206216, M-GQ206193, N-GQ206276, P-NA, Y-NA, I-GQ206242; *Calligonum microcarpum* Borszcz., R-GQ206218, M-GQ206195, N-GQ206278, P-NA, Y-NA, I-GQ206244; *Chorizanthe brevicornu* Torr. var. *brevicornu*, R-EF437974, M-EF437991, N-EF438030, I-FJ154466; *Coccoloba swartzii* Meisn., R-AF297150, M-EF437995, N-EF438034, I-FJ154469; *Coccoloba uvifera* (L.) L., R-AF206753, M-EF437996, N-NA, I-GQ206246; *Dedeckera eurekensis* Reveal & J. T. Howell, R-EF437976, M-EF437997, N-EF438036, I-FJ154470; *Emex spinosa* (L.) Campd., R-AF297142, M-AY042582, N-EF438037, P-NA, Y-NA, I-FJ154471; *Eriogonum alatum* Torr. var. *alatum*, R-EF437977, M-EF437998, N-EF438038, I-FJ154472; *Eriogonum clavellatum* Small, R-EF437979, M-EF438000, N-EF438040, I-GQ206247; *Eriogonum esmeraldense* S. Watson var. *toiyabense* J. T. Howell, R-EF437981, M-EF438003, N-EF438043, I-GQ206248; *Eriogonum inflatum* Torr. & Frém., R-EF437984, M-EF438006, N-EF438046, I-GQ206249; *Fagopyrum cymosum* Meisn., R-D86286, M-

EF438008, N-GQ206280, P-NA, Y-NA, I-AB000329; *Fagopyrum esculentum* Moench, R-D86285, M-AB093087, N-EU254477, P-NA, Y-NA, I-AB000331; *Fagopyrum urophyllum* (Bureau & Franch.) H. Gross, R-D86288, M-AB026332, N-NA, P-NA, Y-NA, I-AB000342; *Fallopia dumetorum* (L.) Holub, R-FM883613, M-AM503813, N-AM503835, P-NA, Y-NA, I-AF040068; *Fallopia scandens* (L.) Holub, R-EF653785, M-NA, N-NA, P-NA, Y-NA, I-AF040069; *Gilmania luteola* (Coville) Coville, M-EF438010, N-EF438049, I-GQ206250; *Gymnopodium floribundum* Rolfe, R-GQ206220, M-GQ206197, N-GQ206282, I-GQ206251; *Johanneshowellia crateriorum* Reveal, R-EF437986, M-EF438011, N-EF438050, I-GQ206252; *Knorringia sibirica* (Laxm.) S.P. Hong (= *Polygonum sibiricum* Laxm.), R-GQ206222, M-NA, N-GQ206284, P-NA, Y-NA, I-GQ206253; *Koenigia forrestii* (Diels) Měsíček and Soják, R-AF297144, M-EF438012, N-EF438051, P-NA, Y-NA, I-GQ206254; *Koenigia islandica* L., R-EF653789, M-NA, N-EU840371, P-NA, Y-NA, I-EF653686; *Leptogonum domingense* Benth, R-GQ206223, M-GQ206199, N-GQ206285, I-GQ206256; *Neomillspaughia emarginata* (H. Gross) S.F. Blake, R-GQ206225, M-GQ206201, N-GQ206287, I-GQ206257; *Muehlenbeckia complexa* (A. Cunn.) Meisn., R-GQ206224, M-GQ206200, N-GQ206286, P-NA, Y-NA, I-AF040076; *Muehlenbeckia platycladum* (F.J. Müll.) L.H. Bailey, R-GQ206221, M-GQ206198, N-GQ206283, P-NA, Y-NA, I-AF189738; *Muehlenbeckia tamnifolia* Meisn. R-FJ154453, M-FJ154499, N-FJ154511, I-FJ154473; *Oxyria digyna* Hill, R-FJ154454, M-FJ154500, N-FJ154512, P-NA, Y-NA, I-FJ154474; *Oxyria sinensis* Hill, R-AF297148, M-EF438013, N-EF438053, P-NA, Y-NA, I-GQ206258; *Persicaria pensylvanica* (L.) M. Gómez, R-AF297133, M-EF438017, N-EF438056, P-NA, Y-NA, I-FJ154475; *Persicaria sagittata* (L.) H. Gross, R-AF287141, M-EF438018, N-GQ206288, P-NA, Y-NA, I-FJ154476; *Persicaria virginiana* (L.) Gaertn., R-AF297135, M-EF438019, N-EF438058, I-FJ154477; *Polygonella americana* (Fisch. & C.A. Mey.) Small, R-GQ206226, M-GQ206202, N-GQ206289, P-NA, Y-NA, I-GQ206259; *Polygonella articulata* (L.) Meisn., R-EF653760, M-NA; N-GQ206290, P-NA, Y-NA, I-EF653683; *Polygonum aviculare* L., R-AF297127, M-EF438020, N-EF438059, P-NA, Y-NA, I-FJ154478; *Polygonum erectum* L. R-AF297128, M-GQ206203, N-NA, P-NA, Y-NA, I-GQ206260; *Polygonum paniculatum* Blume, R-AF297129, M-GQ206204, N-GQ206291, P-NA, Y-NA, I-GQ206255; *Pteropyrum aucheri* Jaub. & Spach, R-GQ206227, M-GQ206205, N-GQ206292, P-NA, Y-NA, I-GQ206261; *Pteropyrum olivieri* Jaub. & Spach, R-GQ206228, M-NA, N-GQ206293, P-NA, Y-NA, I-GQ206262; *Pterostegia drymarioides* Fisch. & C.A. Mey., R-GQ206229, M-GQ206206, N-GQ206294, P-NA, Y-NA, I-GQ206263; *Reynoutria japonica* Houtt., R-AF297131, M-AY042586, N-EF438048, P-NA, Y-NA, I-AF189734; *Reynoutria sachalinensis* F. Schmidt Petrop., R-AF297125, M-EF438009, N-GQ206281, P-NA, Y-NA, I-AF189737; *Rheum nobile* Hook. & Thomson, R-AF297147, M-EF438021, N-EF438060, P-NA, Y-NA, I-GQ206264; *Rheum pichonii* Pierre ex F.B.Forbes & Hemnsl., R-GQ206231, M-GQ206208, N-GQ206296, P-NA, Y-NA, I-GQ206265; *Rubrivena polystachya* (Wall. ex Meisn.) M. Král *(=Polygonum polystachyum* Wall. ex Meisn.), R-GQ206232, M-NA, N-GQ206297, P-

NA, Y-NA, I-GQ206266; *Rumex acetosella* L., R-D86290, M-EF438022, N-GQ206298, P-NA, Y-NA, I-AF189730; *Rumex induratus* Boiss. & Reut., R-AF297122, M-AY042647, N-EF438061, P-NA, Y-NA, I-FJ154480; *Rumex obtusifolius* L., R-AF297126, M-EF438023, N-EF438062, I-FJ154481; *Ruprechtia chiapensis* Lundell ex Standl. & Steyerm. R-FJ154456, M-FJ154495, N-FJ154506, I-FJ154482; *Ruprechtia laxiflora* Meisn., R-EF437987, M-EF438024, N-EF438063, P-NA, Y-NA, I-FJ154484; *Ruprechtia tangarana* Standl*.,* R-GQ206233, M-EF438025, N-EF438064, I-FJ154485; *Ruprechtia triflora* Griseb., *Pendry* (E), R-GQ206234, N-GQ206299, P-NA, Y-NA, I-GQ206267; *Symmeria paniculata* Benth., R-GQ206235, M-GQ206209, N-GQ206300, P-NA, Y-NA, I-GQ206268; *Triplaris americana* L., R-Y16910, M-AY042668, N-FJ154508; I-FJ154486; *Triplaris cumingiana* Fisch. & C.A. Mey. ex C.A. Mey., R-GQ206236, M-GQ206210, N-GQ206301, I-GQ206269; *Triplaris poeppigiana* Wedd., R-AF297137 M-FJ154497, N-FJ154509, I-FJ154487; *Triplaris setosa* Rusby, R-FJ154458, M-FJ154498, N-FJ154510, I-FJ154488; *Ceratostigma minus* Stapf ex Prain, R-Z97641, M-AY042566, N-NA, P-NA, Y-NA, I-NA; *Limonium dufourii* Kuntze, R-AJ286363, M-NA, N-NA, P-NA, Y-NA, I-AJ222840; *Limoniastrum monopetalum* Boiss., R-Z97642, M-AY042609, N-NA, P-NA, Y-NA, I-NA; *Plumbago auriculata* Lam., R-M77701, M-EF438026, N-EF438065, P-NA, Y-NA, I-GQ206270.

(2) **Sequences generated in this study.** Materials obtained from herbarium specimens are indicated with an asterisk (*) after the collection number. *Afrobrunnichia erecta* Hutch. & Dalziel, *Stone J., G. Walters, T. Nzabi & T. Mboumbore 3272* (MO), P-HM137447, A-HM137493; *Antigonon cinerascens* M.Martens & Galeotti, *Burke 8* (BH), R-HM137363, M-HM137385, N-HM137406, P-NA, A-HM137494, I-HM137427; *Antigonon guatimalense* Meisn., *Luckow 4634* (BH), P-HM137448, A-HM137495; *Antigonon leptopus* Hook. & Arn., *Luckow 4630* (BH), P-HM137449, A-HM137496; *Atraphaxis spinosa* L., *Anon. s.n.* (E), P-NA, A-HM137497; *Brunnichia ovata* (Walter) Shinners, *Alford 3851* (USMS), P-HM137450, A-HM137498; *Chorizanthe brevicornu* Torr. var. *brevicornu*, *Reveal 8462*, P-HM137451, A-HM137499; *Coccoloba acapulcensis* Standl., *Bruke 61* (BH), R-HM137364, M-HM137386, N-HM137407, P-HM137452, A-HM137500, I-HM137428; *Coccoloba belizensis* Standl., *Burke 72* (BH), R-HM137365, M-HM137387, N-HM137408, P-HM137453, A-HM137501, I-HM137429; *Coccoloba brasiliensis* Nees & Mart., *Harley 27120** (A), R-HM137366, M-HM137388, N-HM137409, P-HM137454, A-HM137502, I-HM137430; *Coccoloba diversifolia* Jacq., *Sanchez 102*, R-HM137367, M-HM137389, N-HM137410, P-HM137455, A-HM137503, I-HM137431; *Coccoloba krugii* Lindau, *Sanchez 108,* R-HM137368, M-HM137390, N-HM137411, P-HM137456, A-HM137504, I-NA; *Coccoloba latifolia* Lam., *Sanchez 106,* R-HM137369, M-HM137391, N-HM137412, P-HM137457, A-HM137505, I-HM137432; *Coccoloba northropiae* Britton, *Sanchez 110,* R-HM137370, M-HM137392, N-HM137413, P-HM137458, A-HM137506, I-HM137433; *Coccoloba pallida* C. Wright ex Griseb., *Sanchez 112,* R-HM137371, M-HM137393, N-HM137414, P-HM137459, A-HM137507, I-

NA; ***Coccoloba pubescens*** L., *Sanchez 103,* R-HM137372, M-HM137394, N-HM137415, P-HM137460, A-HM137508, I-HM137434; ***Coccoloba rugosa*** Desf., *Sanchez 101,* R-HM137373, M-HM137395, N-HM137416, P-HM137461, A-HM137509, I-HM137435; ***Coccoloba spicata*** Lundell, *Burke 54* (BH), R-HM137374, M-HM137396, N-HM137417, P-HM137462, A-HM137510, I-HM137436; ***Coccoloba swartzii*** Meisn., *Sanchez 109,* P-HM137463, A-HM137511; ***Coccoloba tenuifolia*** L., *Sanchez 111*, R-HM137375, M-HM137397, N-HM137418, P-HM137464, A-HM137512, I-HM137437; ***Coccoloba uvifera*** (L.) L., *Burke s.n.* (BH), P-HM137465, A-NA; ***Coccoloba venosa*** L., *Burke 126* (BH), R-NA, M-NA, N-NA, P-HM137466, A-HM137513, I-NA; ***Dedeckera eurekensis*** Reveal & J. T. Howell, *Reveal 8456*, P-HM137467, A-NA; ***Eriogonum alatum*** Torr. var. ***alatum***, *Reveal 8515,* P-NA, A-HM137514; ***Eriogonum clavellatum*** Small, *Reveal & Broome 8478*, P-HM137468, A-HM137515; ***Eriogonum esmeraldense*** S. Watson var. ***toiyabense***, *Tiehm 14537*, P-HM137469, A-HM137516; ***Eriogonum inflatum*** Torr. & Frém., *Reveal 8458*, P-HM137470, A-NA; ***Eriogonum umbellatum*** Torr., *Reveal 8526*, R-HM137376, M-NA, N-HM137419, P-HM137471, A-HM137517, I-HM137438; ***Fallopia aubertii*** (L. Henry) Holub, *Burke s.n.* (BH), R-HM137377, M-HM137398, N-HM137420, P-NA, A-HM137518; ***Gilmania luteola*** (Coville) Coville, *Reveal 8465* R-HM137378, P-HM137473, A-HM137520; ***Gymnopodium floribundum*** Rolfe, *Burke 48* (BH), P-HM137474, A-HM137521; ***Gymnopodium floribundum*** Rolfe, *Burke 70* (BH), R-HM137379, M-HM137399, N-HM137421, P-HM137475, A-HM137522, I-HM137440; ***Johanneshowellia crateriorum*** Reveal, *Reveal 8469,* P-HM137476, A-HM137523; ***Leptogonum domingense*** Benth, *Gustafson 3077** (RSA), P-HM137477, A-HM137524; ***Muehlenbeckia tamnifolia*** Meisn., *Burke 18* (BH), P-HM137478, A-HM137525; ***Neomillspaughia emarginata*** (H. Gross) S.F. Blake, *Burke 66* (BH), P-HM137479, A-HM137526; ***Persicaria virginiana*** (L.) Gaertn., *Burke s.n.* (BH), P-NA, A-HM137527; ***Podopterus cordifolius*** Rose & Standl., *Burke 30* (BH), P-HM137480, A-HM137528; ***Podopterus mexicanus*** Bonpl., *Burke 27* (BH), R-HM137380, M-HM137400, N-HM137422, P-HM137481, A-NA, I-HM137441; ***Polygonum aviculare*** L., *Kron s.n.,* P-NA, A-HM137529; ***Reynoutria japonica*** Houtt., *Burke s.n.*, P-HM137472, A-HM137519; ***Rumex obtusifolius*** L., *Burke s.n.*, P-HM137482, A-HM137530; ***Ruprechtia chiapensis*** Lundell ex Standl. & Steyerm. *Burke s.n.* (BH), P-HM137483, A-HM137531; ***Ruprechtia coriacea*** (H. Karst.) S.F. Blake, *Sanchez 104,* R-HM137381, M-HM137401, N-HM137423, P-HM137484, A-HM137532, I-HM137442; ***Ruprechtia cruegeri*** Griseb. ex Lindau, *Luckow 4587* (BH), R-HM137382, M-HM137402, N-HM137424, P-HM137485, A-HM137533, I-HM137443; ***Ruprechtia pallida*** Standl., *Burke 129* (BH), R-HM137383, M-HM137403, N-HM137425, P-HM137486, A-HM137534, I-HM137445; ***Ruprechtia tangarana*** Standl*., Silman s.n.** (WFU), P-HM137487, A-HM137535; ***Triplaris americana*** L., Luckow 4635 (BH), P-HM137489, A-HM137537; ***Triplaris cumingiana*** Fisch. & C.A. Mey. ex C.A. Mey., *Sanchez 100*, P-HM137490, A-HM137538; ***Triplaris poeppigiana*** Wedd., *Sanchez 89,* P-HM137491, A-HM137539; ***Triplaris setosa*** Rusby, *Fuentes 5351* (MO), P-HM137492, A-HM137540; ***Triplaris***

weigeltiana (Rchb.) Kuntze, *Michelangeli s.n.,* R-HM137384, M-HM137405, N-HM137426, P-HM137488, A-HM137536, I-HM1374.

APPENDIX 2.2. Morphological matrix (nexus format) used for phylogenetic analysis.

#NEXUS

BEGIN DATA;

DIMENSIONS NTAX=45 NCHAR=22;

FORMAT MISSING=? SYMBOLS= " 0 1 2 3 4 5 6 7 8 9";

OPTIONS MSTAXA=POLYMORPH ;

CHARLABELS

	[1]	Woodiness
	[2]	Climbing_habit
	[3]	Stem_pith
	[4]	Salt-secreting_glands_on_stems_or_leaves
	[5]	Ocrea_presence
	[6]	Ocrea_persistance
	[7]	Flower_sex
	[8]	Stipe_wings
	[9]	Distinct_perianth_whorls
	[10]	Perianth_lobe_number
	[11]	Perianth_accresent_in_fruit
	[12]	Part_of_accrescent_perianth_enclosing_fruit
	[13]	Perianth_texture_in_fruit
	[14]	Stamen_Number
	[15]	Filament_morphology
	[16]	Stamen_fusion
	[17]	Gynoecium_merosity
	[18]	Style_fusion
	[19]	Stigma_type
	[20]	Fruit_type
	[21]	Achene_shape
	[22]	Endosperm_type

        ;

        STATELABELS

	1	herbaceous suffrutescent woody,
	2	erect climbing,
	3	hollow solid,
	4	absent present,
	5	absent present,
	6	caducous persistent,
	7	Bisexual_fls Dioecious Polygamous_(various_forms),
	8	absent present,
	9	absent present,
	10	3 4 5 6,
	11	absent present,
	12	hypanthium outer_whorl inner_whorl all_tepal_lobes whole_perianth,
	13	hyaline_to_chartaceous coriaceous fleshy_to_succulent,
	14	3 5 6 7 8 9 numerous,
	15	filiform_or_flattened dilated subulate,
	16	free_until_short_hypanthium adnate_to_perianth connate,
	17	2 3 4 5,
	18	absent present,

19   capitate peltate fimbriate decurrent_along_inner_surface filiform bifid,
20   achene capsule utricle,
21   trigonous terete globose_to_subglobose pyramidal lenticular,
22   uniform ruminate,
;

MATRIX

Afrobrunnichia_erecta
2100110102101401105001
Antigonon_cordatum
1110100002130412101001
Antigonon_amabile
1110100002130412101001
Antigonon_leptopus
1110100002130412101001
Brunnichia_ovata
1110100102101411101000
Coccoloba_barbadensis
2010112002102422101021
Coccoloba_brazilensis
2(01)10102002102422101021
Coccoloba_densifrons
2(01)10111002102422101021
Coccoloba_latifolia
2000101002142422101021
Coccoloba_lehmanii
2000101002131422101020
Coccoloba_pubescens
2010101002102422101021
Coccoloba_uvifera
2000112002102422101021
Coccoloba_venosa
2010102002131422101021
Gymnopodium_floribundum
20101000031305001000?
Leptogonum_domingense
20101000030-0011100000
Neomillspaughia_emarginata
20101001021305(45)22101000
Podopterus_cordifolius
21001101021305(45)22101001
Podopterus_mexicanus
2010100002130412101001
Ruprechtia_chiapensis
201010100312050210300?
Ruprechtia_coriacea
201011100310050010300?
Ruprechtia_cruegeri
20(01)0101003130510103000
Ruprechtia_laxiflora
2010111003130500(12)0300?
Ruprechtia_triflora
2010101003140510103000
Symmeria_paniculata
2(01)101010031216602102031
Triplaris_americana
2000101003100501103001

Triplaris_cumingiana
20001010031005011103001
Triplaris_poeppigiana
20001010031005011103001
Triplaris_weigeltiana
2000101003100501110300?
Chorizanthe_brevicornu
00-00-00030-00?000?040
Eriogonum_alatum
00-00-00030-0501100000
Eriogonum_esmeraldense
00-00-00030-0500100000
Eriogonum_inflatum
00-00-00030-050(01)100010
Gilmania_luteola
00-00-00030-0511105000
Johanneshowellia_crateriorum
00-00-00030?050110300?
Atraphaxis_spinosa
20101100011102120000040
Fallopia_aubertii
2110100102130(234)12100000
Muehlenbeckia_tamnifolia
1(01)(01)011200214241?1000(02)1
Persicaria_virginiana
00-01100010-0111003040
Polygonum_aviculare
00-011000(12)0-0(124)11(01)00000
Reynoutria_japonica
00-01(01)21021304412102000
Rumex_obtusifolius
00-01(01)2003120200102000
Ceratostigma_minus
10110-00120-01103141-0
Limoniastrum_monopetalum
10110-00120-01013141-0
Limonium_dufourii
00-10-00120-01013042-0
Plumbago_auriculata
10110-00120-0110(13)141-0
;
ENDBLOCK;

BEGIN ASSUMPTIONS;

OPTIONS DEFTYPE=unord PolyTcount=MINSTEPS ;

ENDBLOCK;

APPENDIX 2.3. Maximum likelihood tree from combined molecular dataset. Ln= -46868.69.

Ceratostigma minus
Plumbago auriculata
Limoniastrum monopetalum
Limonium dufourii

Outgroups

Symmeria paniculata *
Afrobrunnichia erecta †

Incertae sedis

Antenoron filiforme
Persicaria virginiana
Persicaria pensylvanica
Persicaria sagittata
Rubrivena polystachya
Bistorta attenuatifolia
Bistorta tenuicaulis
Polygonum paniculatum
Aconogonon molle
Koenigia forrestii
Koenigia islandica
Fagopyrum urophyllum
Fagopyrum cymosum
Fagopyrum esculentum
Pteropyrum aucheri
Pteropyrum olivieri
Calligonum microcarpum
Calligonum aphyllum
Calligonum eriopodum
Emex spinosa
Rumex obtusifolius
Rumex acetosella
Rumex induratus
Oxyria digyna
Oxyria sinensis
Rheum nobile
Rheum pinchonii
Knorringia sibirica
Atraphaxis spinosa
Atraphaxis pyrifolia
Polygonum aviculare
Polygonum erectum
Polygonella americana
Polygonella articulata
Reynoutria japonica
Reynoutria sachalinensis
Fallopia dumetorum
Fallopia scandens
Muehlenbeckia complexa †
Muehlenbeckia platyclada †
Fallopia aubertii
Muehlenbeckia tamnifolia †

Polygonoideae

Brunnichia ovata †
Antigonon leptopus †
Antigonon cinerascens †
Antigonon guatimalense †
Neomillspaughia emarginata †
Coccoloba acapulcensis †
Coccoloba brasiliensis †
Coccoloba latifolia †
Coccoloba belizensis †
Coccoloba northropiae †
Coccoloba venosa †
Coccoloba rugosa †
Coccoloba pubescens †
Coccoloba krugii †
Coccoloba pallida †
Coccoloba swartzii †
Coccoloba diversifolia †
Coccoloba spicata †
Coccoloba tenuifolia †
Coccoloba uvifera †
Podopterus cordifolius †
Podopterus mexicanus †
Leptogonum domingense *
Gymnopodium floribundum B48 *
Gymnopodium floribundum B70 *
Gilmania luteola
Pterostegia drymarioides
Eriogonum alatum
Chorizanthe brevicornu
Eriogonum umbellatum
Eriogonum inflatum
Dedeckera eurekensis
Eriogonum clavellatum
Eriogonum esmeraldense
Johanneshowellia crateriorum
Ruprechtia triflora *
Triplaris cumingiana *
Triplaris americana *
Triplaris weigeltiana *
Triplaris poeppigiana *
Triplaris setosa *
Ruprechtia laxiflora *
Ruprechtia chiapensis *
Ruprechtia pallida *
Ruprechtia coriacea *
Ruprechtia cruegeri *
Ruprechtia tangarana *

Eriogoneae

Eriogonoideae

† = placed in traditional Coccolobeae

* = placed in traditional Triplarideae

— 0.01 substitutions/site

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CHAPTER 3

REVISED SUBFAMILY CLASSIFICATION FOR POLYGONACEAE, WITH A TRIBAL CLASSIFICATION FOR ERIOGONOIDEAE[2]

JANELLE M. BURKE AND ADRIANA SANCHEZ

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Abstract. Recent phylogenetic studies have provided a revised hypothesis of the evolutionary relationships within Polygonaceae, particularly regarding placement of certain tropical taxa. Based on phylogenetic data, we recognize three subfamilies: Eriogonoideae, Polygonoideae and Symmerioideae. Within the Eriogonoideae we accept six tribes, two of which, **Leptogoneae** and **Gymnopodieae**, are new.

Key Words: classification, Eriogonoideae, Polygonoideae, Polygonaceae, Symmerioideae

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[2] Burke and Sanchez. *In press*. *Brittonia.*

Polygonaceae Juss. have long been recognized as a distinct, cohesive group (Jussieu, 1789) based on the presence of ocrea (sheathing outgrowths of leaf bases), a single, basal ovule, a perianth composed of usually five or six tepals, and the fruit, an achene. The family, comprised of about 49 genera and some 1200 species, has a cosmopolitan distribution. *Eriogonum* Michx. is the most species-rich genus with just over 250 species, mainly in western North America. *Rumex* L. (200 spp.), *Coccoloba* P. Browne (130 spp.) and *Persicaria* Mill. (100 spp.) also comprise a substantial portion of the diversity in Polygonaceae. The family has minor economic value as crop plants: species of rhubarb (*Rheum* L.), dock (*Rumex* L.) and buckwheat (*Fagopyrum* Mill.) are cultivated for food. However the family also has a detrimental economic impact. Several species (*Reynoutria japonica* Houtt., *Emex spinosa* [L.] Campd., *Persicaria perfoliata* [L.] H. Gross) have received notoriety as invasive species. Many species are cultivated as ornamentals: *Eriogonum* for xeriscaping, *Antigonon leptopus* Hook. & Arn. as an ornamental vine, and *Persicaria*, *Rheum*, and *Reynoutria* Houtt. for their large, showy inflorescences.

The subfamilial classification for Polygonaceae has not been stable over the past 200 years. Recent classifications (Haraldson, 1978; Brandbyge, 1993) recognized two subfamilies: Eriogonoideae Arn. and Polygonoideae Eaton. The Eriogonoideae were clearly distinguished based on a suite of morphological characters such as lack of ocrea, sympodial growth, and an involucre subtending the inflorescence; the Polygonoideae were distinguished based on presence of ocrea, monopodial growth and lack of an involucres. Recently, molecular data have showed Polygonoideae are not monophyletic (Lamb Frye and Kron, 2003; Sanchez and Kron, 2008). This led to an amended circumscription of the subfamilies (Sanchez and Kron, 2008), whereby Eriogonoideae was expanded to include the woody genera in Polygonaceae. Additional work with a more thorough sampling of the woody, tropical genera (Sanchez and Kron, 2009; Burke et al., 2010) have increased our understanding of relationships at the tribal level. The classification

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proposed here will reflect these new data, and produce a taxonomic treatment based on natural groups.

Taxonomic history—

Early workers recognized *Eriogonum* and allies (historically subfamily Eriogonoideae) as distinctive from the rest of Polygonaceae. Michaux (1803) distinguished *Eriogonum* by a lack of ocrea and presence of an involucre subtending the inflorescence. In his 1836 treatment, Bentham recognized 40 species of *Chorizanthe, Eriogonum*, and *Mucronea* as a separate tribe, Eriogoneae Dumort., but argued for their inclusion in Polygonaceae (rather than Amaranthaceae Juss.) based on inflorescence structure and fruit morphology. *Eriogonum* and allies were recognized by subsequent workers either at the rank of tribe or subfamily, and will hereafter be referred to as tribe Eriogoneae.

In one of the first comprehensive treatments for the family, Endlicher (1837) recognized three tribes: Eriogoneae, "Polygoneae verae" and "Polygoneae spuriae." The latter taxon included *Antigonon* Endl. and *Brunnichia* Banks ex Gaertn. based on the presence of a long funiculus and an inverted ovule which becomes erect at maturity. The morphology of the funiculus was adopted by Meisner (1856) as a diagnostic character in his treatment, although he also used ocrea morphology. He recognized four subfamilies: Eriogonoideae (for which Bentham wrote the treatment), Polygonoideae, Brunnichioideae Meisn., and Symmerioideae Meisn. Brunnichioideae had the same circumscription as Endlicher's Polygoneae spuriae, and included *Antigonon* and *Brunnichia* based on the presence of a long funiculus, ocrea reduced to a circular scar, and a habit of cirrose lianas. The monotypic subfamily Symmerioideae was segregated based on its pyramidal achenes and lack of ocrea. *Symmeria* Benth. has an unusual disjunct distribution, occurring in South America and western Africa.

Later workers (e.g. Bentham and Hooker, 1880; Dammer, 1893) did not adopt Meisner's subfamilial classification, and none of them recognized more than three subfamilies. The diagnostic characters which were used at the subfamilial or tribal level varied. These included tepal number, endosperm type, habit, and ocrea morphology. One recognized subfamily was always Eriogonoideae (sensu Meisner), and its circumscription was not altered until Sanchez and Kron (2008).

Gross's 1913 treatment was the first to incorporate morphological and anatomical characters. He recognized three subfamilies: Eriogonoideae, Polygonoideae and Coccoloboideae Luerss. (which included the woody, tropical genera) based on tepal number, ocrea presence and endosperm type. In 1925, Jaretzky amended Gross's treatment merging Coccoloboideae in Polygonoideae. He distinguished Eriogonoideae and Polygonoideae by branching pattern, tepal number, and presence of ocrea. This circumscription was widely accepted (e.g., Haraldson, 1978; Brandbyge 1993), with only Roberty and Vautier (1964) as a recent exception.

The first molecular phylogeny for Polygonaceae (Lamb Frye and Kron, 2003, *rbcL* data), showed that the two-subfamily classification did not represent natural groups. Subsequent studies, with more thorough sampling of taxa and DNA characters, have corroborated this finding (Sanchez and Kron, 2008; Sanchez et al., 2009; Burke et al., 2010). Although Eriogoneae proved to be monophyletic, Polygonoideae were paraphyletic. These molecular studies support two large clades: a clade comprised of the woody, Neotropical genera paraphyletic to the Eriogoneae and a second clade comprising the rest of Polygonoideae (Fig. 3.1). Based on these data, Sanchez and Kron (2008) recommended that the circumscription of Eriogonoideae be expanded to include the woody, tropical genera previously in Polygonoideae. Two genera did not fall neatly into these two clades: *Afrobrunnichia* Hutch. & Dalziel and *Symmeria.* The position of *Afrobrunnichia* is ambiguous as it is placed either sister to Polygonaceae, sister to

Eriogonoideae, or with *Brunnichia + Antigonon,* depending on the gene region used to reconstruct relationships, though the relationships are never well-supported (Fig. 3.1). *Symmeria* consistently falls as sister to the rest of Polygonaceae, even with increased outgroup sampling in Plumbaginaceae Juss.
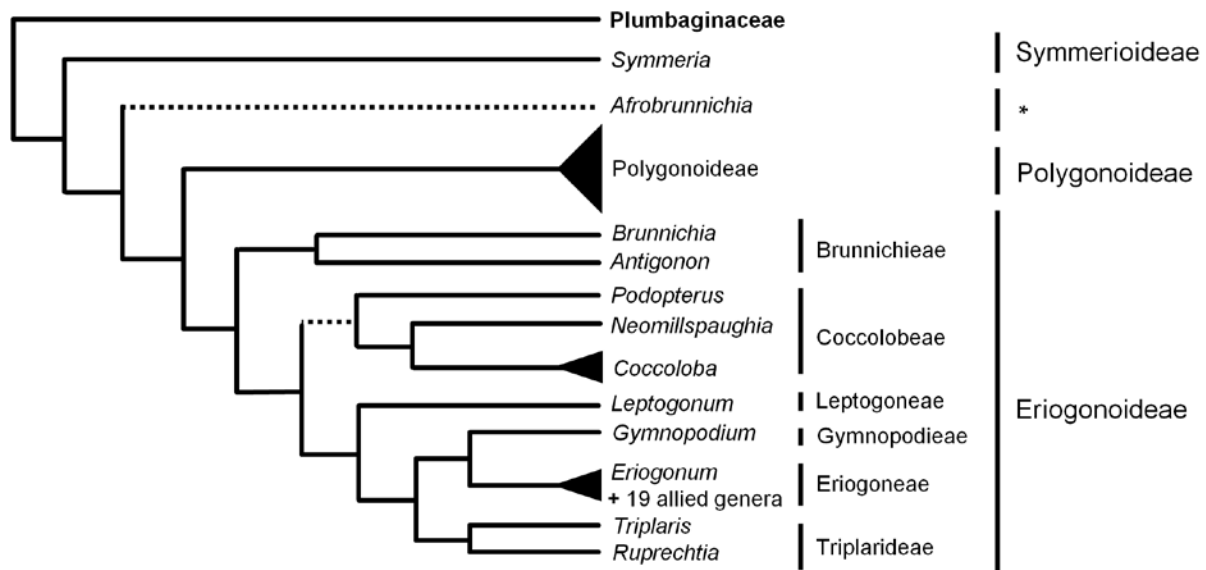

Figure 3.1. Summary cladogram of the phylogenetic relationships in Polygonaceae (based on Burke et al., 2010). Dashed branch lines indicate uncertainty in the phylogenetic placement of *Afrobrunnichia* and *Podopterus.* Tribal and subfamilial classifications are indicated on the right. *= incertae sedis.

The woody, tropical genera assigned to Coccoloboideae by Dammer (1893) and by Gross (1913) often were recognized as two tribes, Triplarideae C.A. Mey. and Coccolobeae Dumort., distinguished by tepal number and sexual system (Bentham and Hooker, 1880; Dammer, 1893; Gross, 1913; Jaretzky, 1925; Buchinger, 1957; Brandbyge, 1993). Dammer and Gross recognized these tribes within Coccoloboideae, while other workers placed them within Polygonoideae. Occasionally Brunnichieae C.A. Mey was also recognized as distinct based on habit, ocrea type and funiculus (Meyer, 1840).The tribal circumscription of Eriogonoideae

proposed here includes the four older tribes Brunnichieae, Coccolobeae, Eriogoneae, and Triplarideae, and two new tribes, Leptogoneae and Gymnopodieae (Table 3.1).

Proposed classification—

In view of recent phylogenetic studies (Lamb Frye and Kron, 2003; Sanchez and Kron, 2008, 2009; Sanchez et al., 2009; Burke et al., 2010), we propose here a revised subfamilial treatment, and a tribal treatment for Eriogonoideae; a revised tribal treatment of Polygonoideae has been published separately (Sanchez et al., 2011). Our treatment distinguishes natural groups supported by the extensive phylogenetic analyses of the past several years. When possible, our circumscriptions are also supported by putative morphological synapomorphies; in a few cases (Leptogoneae, Gymnopodieae) distinct tribes with many autapomorphies are recognized. To be conservative, we excluded *Afrobrunnichia* from subfamilial or tribal placement until there is better support for its phylogenetic affinities. Subfamilies and tribes are ordered below according to their position on the evolutionary tree (Fig. 3.1), from base to apex. For each tribal treatment, suites of diagnostic characters are in bold typeface. An overview of morphology and habit of subfamilies and tribes are summarized in Fig. 3.2.

TABLE 3.1 Comparison of recent (past 50 years) taxonomic treatments for Eriogonoideae.

Tribe	This Paper	Brandbyge 1993	Haraldson 1978
Brunnichieae	*Antigonon, Brunnichia*		
Coccolobeae	*Coccoloba, Neomillspaughia, Podopterus*	*Antigonon, Brunnichia* (incl. *Afrobrunnichia*), *Coccoloba, Muehlenbeckia* (incl. *Homalocladium* [F. Muell] L.H. Bailey), *Neomillspaughia, Podopterus*	*Antigonon, Brunnichia, Coccoloba, Fallopia, Harpagocarpus* Hutch. & Dandy, *Muehlenbeckia, Podopterus, Reynoutria*
Eriogoneae	*Acanthogonum, Chorizanthe, Dedeckera, Eriogonella, Eriogonum, Eucycla, Gilmania, Goodmania, Harfordia, Hollisteria, Lastarriaea, Mucronea, Nemacaulis, Pterogonum, Pterostegia, Sidotheca, Stenogonum*	(as subfamily) *Aristocapsa* Reveal & Hardham, *Centrostegia* Benth., *Chorizanthe, Dedeckera, Dodecahema* Reveal & Hardham, *Eriogonum, Gilmania, Goodmania, Harfordia, Hollisteria, Lastarriaea, Mucronea, Nemacaulis, Oxytheca* Nutt., *Pterostegia, Stenogonum, Systenotheca*	Not treated
Leptogoneae	*Leptogonum*		
Gymnopodieae	*Gymnopodium*		
Triplarideae	*Ruprechtia, Triplaris*	*Gymnopodium, Leptogonum, Ruprechtia, Symmeria, Triplaris*	*Gymnopodium, Leptogonum, Millspaughia* B.L. Rob., *Ruprechtia, Symmeria, Triplaris*

Figure 3.2. Images of tropical Polygonaceae genera clockwise from top left: A. *Symmeria paniculata* (Symmerioideae), habit and inflorescence (*Galvenez 6*, SPH). B. *Antigonon platypus* (Brunnichieae), habit and flower (*Burke 25*, BH). C. *Coccoloba barbadensis* (Coccolobeae), infructescence with fleshy, accrescent perianth (*Burke 65*, BH). D. *Gymnopodium floribundum* (Gymnopodieae), flower (*Burke 93*, BH). E. *Triplaris peruviana* (Triplarideae), infructescence with scarious, accrescent perianth (*Sanchez 171*, WFU). Credits: A: Igapó Team. B, C, D: Janelle Burke. E: Mauricio Gaviria.

TAXONOMIC TREATMENT

KEY TO SUBFAMILIES OF POLYGONACEAE

The presence of ocrea is a synapomorphy for Eriogonoideae + Polygonoideae (with a reversal in Eriogoneae). Ocrea morphology, along with plant habit, are used as characters to distinguish the subfamily Eriogonoideae from Polygonoideae.

1. Petiole dilated with wings enclosing shoot meristem; stamens 40–50; achene pyramidal
………………………………………………………………………………... 1. **Symmerioideae**

1. Petiole not dilated or wings not enclosing shoot meristem; stamens 3–15; achene lenticular, triquetrous or trigonous.

  2. Plants herbs or infrequently subshrubs with monopodial growth; ocrea tubular, hyaline, chartaceous, membranaceous or foliaceous, occasionally reduced on plants of arid or arctic habitats ……………………………………………………………………… 2. **Polygonoideae**

  2. Plants herbs, shrubs or trees with sympodial growth, or shrubs, trees or lianas with monopodial growth; ocrea usually obsolete or scarious, when foliaceous, either terminal, conical and early caducous (*Ruprechtia*, *Triplaris*), or only distally caducous (*Coccoloba*), rarely long and hyaline (*Podopterus cordifolius*) …………….……………….3. **Eriogonoideae**

1. **SYMMERIOIDEAE** Meisn. in A.P de Candolle & A.L.L.P. de Candolle, Prodr. 14: 4, 185. 1856
Plants shrubs, lianas or small trees; nodes not swollen. *Leaves* persistent, alternate; petiole present, winged, not articulated at base; blade simple. *Ocreae* absent. *Inflorescences* axillary; primary inflorescence monochasial; secondary inflorescence paniculate. *Involucres* absent. *Pedicels* slender, subtended by connate, tubular bracteoles. *Flowers* unisexual, estipitate;

perianth accrescent, white to yellow, unkeeled, without protuberances, not glandular; hypanthium short; tepals 6, dimorphic; nectary origin unknown; stamens 40–50; staminodes absent; filaments connate basally, flattened; gynoecium 3-carpellate; ovary 1-locular with basal vestigial partitions; ovule 1, orthotropous with basal placentation; styles 3, distinct; stigma broadly fimbriate. *Achenes* pyramidal, red, matte, not winged, enclosed by 3 inner tepals adnate to fruit wall; endosperm ruminate; embryo morphology unknown.

Symmerieae R. Hogg, Veg. Kingd.: 615. 1858.

　　　1 genus (*Symmeria*) / 1 sp.

　　　Description as for subfamily. Chromosome number unknown.

　　　Distribution: Amazon Basin (Bolivia, Brazil, Colombia, Ecuador, Guyana, Peru, Venezuela) and western Africa (Senegal, Guinea, Sierra Leone).

　　　Symmeria has repeatedly been placed as sister to the rest of Polygonaceae in phylogenetic analyses (Fig. 3.1; Sanchez et al., 2009; Burke et al., 2010); because of this we assign *Symmeria* to its own subfamily. This is not without precedence as Meisner (1856) recognized Symmerioideae based on the absence of ocrea and a pyramidal achene with adherent tepals. Instead of ocrea, *S. paniculata* Benth. has expanded petiole bases that enclose the developing shoot meristem. Given the phylogenetic placement of *Symmeria* on the tree, this may represent the intermediate or ancestral ocrea condition for the family. This taxon also has basal partitions in the ovary, suggesting the 1-loculate condition in most of the family (*Coccoloba* being the only exception) is derived from a 3-loculate ancestor. The trans-Atlantic disjunction exhibited by this species is unique in the family; new collections of African *Symmeria* are needed to verify the distribution and determine whether there is one or two species.

2. **POLYGONOIDEAE** Eaton, Bot. Dict., ed. 4: 30. 1836

Plants annual or perennial herbs or shrubs; nodes usually swollen. *Leaves* deciduous,

occasionally persistent, alternate; petiole present (absent), not winged, articulated basally or not;

blade simple, rarely lobed. *Ocreae* present (greatly reduced in some species of *Atraphaxis* L.,

Calligonum L. and *Koenigia* L.), persistent, often distally deciduous or splitting, hyaline,

membranaceous or chartaceous, rarely scarious. *Inflorescences* axillary or terminal; primary

inflorescence monochasial; secondary inflorescence spicate, racemose, paniculate or capitate;

Involucres absent. *Pedicels* filiform to winged, subtended by hyaline or membranaceous connate

bracteoles ("ocreolae"). *Flowers* bisexual, occasionally unisexual, often stipitate; perianth

persistent or accrescent in fruit, often white to pink, occasionally green, yellow, red, or purple,

keeled in *Fallopia* Adans. and *Reynoutria* Houtt., sometimes tuberculate (*Rumex*), occasionally

glandular or glandular- punctate; hypanthium short or well-developed; tepals (2–) 5–6 ,

monomorphic or dimorphic; nectaries, when present, perigonal, discoid, or of papillae, trichomes

or globose appendages; stamens (1–) 6–9; staminodes absent; filaments usually distinct,

sometimes connate basally into tube, filiform, flattened or dilated; gynoecium (2–) 3 (–4)-

carpellate; ovary 1-locular, without basal partitions; ovule 1, orthotropous with basal

placentation; styles 3, distinct or rarely connate proximally; stigma usually capitate, occasionally

peltate, fimbriate, penicillate or reduced. *Achenes* trigonous or lenticular, yellow, brown or black,

lustrous or matte, winged or not, sometimes enclosed by perianth, perianth rarely adnate to fruit

wall (*Muehlenbeckia* Meisn., *Persicaria*); endosperm not ruminate; embryo straight or curved.

See Sanchez et al. (2011) for a revised tribal classification for this subfamily.

3. **ERIOGONOIDEAE** Arn., Botany: 126. 1832

Plants annual, biennial or perennial herbs, shrubs, trees, or lianas; nodes swollen or not. *Leaves* deciduous or persistent, alternate (whorled in *Goodmania* Reveal and Ertter); petiole present, rarely winged (*Antigonon*) or absent, not articulated basally; blade simple, rarely undulate, lobed or awn-tipped. *Ocreae* present (except in Eriogoneae)*,* persistent, distally deciduous or early caducous, leaving circular scar when caducous, hyaline, scarious, membranaceous or foliaceous. *Inflorescences* axillary or terminal; primary inflorescence monochasial or dichasial; secondary inflorescence spicate, racemose, paniculate, umbellate or capitate. *Involucres* when present (Eriogoneae) composed of whorls or a spiral of free or fused bracts. *Pedicels* filiform to winged, subtended by 2 linear or connate ovate or tubular bracteoles, these hyaline, membranaceous or foliaceous. *Flowers* unisexual or bisexual; often stipitate; perianth accrescent (rarely persistent and non-accrescent), mostly white to yellow but variously green, pink, maroon or purple, keeled in *Podopterus* Bonpl and *Neomillspaughia* S.F. Blake*,* awned in *Chorizanthe* Benth. and *Lastarriaea* Rémy*,* occasionally glandular, the glands sessile or stipitate, not punctate; hypanthium short or well-developed; tepals 5 or 6, monomorphic or dimorphic; nectary perigonal, discoid, or of papillae; stamens 8–9 (3, 6 or 9 in Eriogoneae); staminodes occasionally present (*Coccoloba*, *Ruprechtia* C.A. Mey, *Triplaris* Loefl.); filaments distinct or connate basally into a ring or tube, rarely with appendages (*Antigonon*), often dilated, also filiform, flattened, or subulate (*Coccoloba*); gynoecium 3(–4)-carpellate; ovary 1-locular, sometimes with vestigial basal partitions (*Coccoloba*, *Triplaris*); ovule 1, orthotropous (anatropous in Brunnichieae) with basal placentation (free-central in Brunnichieae); styles 3, distinct; stigma capitate or occasionally peltate or decurrent (Triplarideae). *Achenes* trigonous or globose, rarely lenticular, red, yellow, brown, gray or black, lustrous or matte, rarely winged, enclosed by perianth, perianth rarely adnate to fruit wall (*Coccoloba*); endosperm ruminate or not; embryo straight or

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curved.

KEY TO TRIBES OF ERIOGONOIDEAE

1. Ocrea absent; inflorescences subtended by an involucre of 1–3 or 6 bracts, or rarely lacking

(*Gilmania*); pedicels occasionally subtended by two linear bracteoles; plants annual, biennial

or perennial herbs, subshrubs or shrubs …………..………………………… **6**. **Eriogoneae**

1. Ocrea present or reduced to a circular scar; inflorescences lacking an involucre; pedicels

subtended by one spathiform or two connate, tubular bracteoles; plants shrubs, trees or lianas.

2. Tepals 5; stamens 8, connate or adnate to perianth.

3. Plants lianas; inflorescence axes modified as tendrils ……………….. **1**. **Brunnichieae**

3. Plants usually shrubs or trees, or if lianas then inflorescence axes not modified as tendrils

……… ……………………………………………………………… **2**. **Coccolobeae**

2. Tepals 6; stamens 3 or 9, adnate to perianth or free, not connate.

4. Flowers unisexual; tepal lobes accrescent and alate ……………………….. **4**. **Triplarideae**

4. Flowers bisexual; tepal lobes accrescent or not, but then never alate.

5. Perianth not accrescent; stamens 3, adnate to perianth; endemic to Hispaniola ………...

…………………………………………………………………… **3. Leptogoneae**

5. Perianth accrescent; stamens 9, free; southern Mexico south to Guatemala …………...

……………………………………………………………………**5**. **Gymnopodieae**

1. **Brunnichieae** C.A. Mey. in Mém. Acad. Imp. Sci. Saint.-Pétersbourg, ser. 6, Sci. Math.,

Seconde Pt. Sci. Nat. 6(2): 150. 1840

2 genera (*Antigonon*, *Brunnichia*) / 5 spp.

Plants **suffrutescent lianas**, synoecious. *Stems* with internodes solid. *Ocreae* 1–2 mm,

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sheathing, scarious, frequently caducous or deciduous. *Leaves* usually lacking winged petioles, if present, not enclosing developing meristem. *Inflorescences* not subtended by an involucres; **apex of axes modified into tendrils.** *Flowers* bisexual; perianth accrescent; tepals 5; stamens 8; filaments connate (*Antigonon*) or adnate to perianth (*Brunnichia*), flattened or dilated. *Achenes* trigonous, smooth, enclosed by membranaceous tepals (*Antigonon*) or a coriaceous hypanthium (*Brunnichia*); endosperm ruminate or uniform. Chromosome number: $n = 20, 24$ (Jaretzky, 1828; Rao, 1936; Lewis et al., 1962).

Distribution: Southeastern United States south through Mexico to Costa Rica.

The character of habit (suffrutescent, tendril-bearing lianas) clearly distinguishes *Antigonon* and *Brunnichia* from the rest of Eriogonoideae. This is consistent and highly supported by molecular data (Sanchez and Kron, 2009; Sanchez et al., 2009; Burke et al. 2010). Meisner (1856) recognized the group at the rank of subfamily, emphasizing the almost obsolete ocrea and long, basal funiculus. While the ocrea are not more than 1–2 mm in length, they are not truly obsolete, but instead deciduous.

2. **Coccolobeae** Dumort., Anal. Fam. Pl.: 18. 1829.

3 genera (*Coccoloba*, *Neomillspaughia*, *Podopterus*) / 130–150 spp.

Plants **shrubs, lianas** or **small trees**, synoecious or polygamo-dioecious. *Stems* with internodes solid or hollow. *Ocreae* 2–40 mm, sheathing or conical (rarely spatulate), hyaline, scarious, membranaceous or foliaceous, caducous or only distally caducous with age. *Leaves* without winged petioles. *Inflorescences* not subtended by an involucres; apex of axes not modified into tendrils. *Flowers* unisexual or bisexual; perianth accrescent; tepals 5; stamens 8; **filaments connate,** dilated or **subulate**. *Achenes* bluntly trigonous to globose, smooth, **enclosed**

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by membranous tepals (*Podopterus* and *Neomillspaughia*), or by a **fleshy hypanthium** (*Coccoloba*); endosperm ruminate or uniform. Chromosome number: *n* = 11 (*n* = 66 in *C. uvifera*). (Graham and Wood, 1965)

Distribution: Southeastern U.S., Mexico, Central America, South America, Caribbean and Hawaii

The relationship of *Neomillspaughia* as sister to *Coccoloba* is well-supported by phylogenetic analyses (Sanchez et al., 2009; Burke et al., 2010), but the position of *Podopterus* is more tenuous. The results shown here (Fig. 3.1) do not depict *Podopterus* as part of a monophyletic group with *Neomillspaughia* + *Coccoloba.* However, other analyses with chloroplast intergenic spacers data and different sampling (Burke, unpublished), or under maximum likelihood analysis (Sanchez et al., 2009), support the placement of *Podopterus* in a clade with *Neomillspaughia* + *Coccoloba*. Although the molecular data are equivocal, *Podopterus* shows strong morphological affinities to *Neomillspaughia* and *Coccoloba*, such as shrubby habit and five tepals; we therefore place *Podopterus* in Coccolobeae. The inner tepals of *Podopterus* are accrescent and membranaceous in fruit, as are those of *Neomillspaughia.*

3. **Leptogoneae** Jan. Burke & Adr. Sanchez, **trib. nov.**, based on [cohort] *Leptogonaneae*
Roberty and Vautier in Boissiera 10: 67. 1964. **–**Type: *Leptogonum* Benth.
1 genus (*Leptogonum*) / 1 sp.
Plants small trees, synoecious. *Stems* with internodes solid. *Ocreae* 2–3 mm, sheathing, scarious, early caducous. *Leaves* without winged petioles. *Inflorescences* not subtended by an involucres; apex of axes not modified into tendrils. *Flowers* bisexual; **perianth not accrescent;** tepals 6; **stamens 3**; filaments adnate to perianth, flattened. *Achene* bluntly trigonous, smooth,

enclosed by a persistent perianth; endosperm uniform. Chromosome number unknown.

Distribution: Hispaniola, on serpentine or limestone soils

Leptogonum is unique in the subfamily in lacking accrescent tepals in fruit, the reduction to three stamens, and the leaves clustered at stem apices. Because *Leptogonum* is a relatively isolated genus, we recognize it as its own tribe. It is sister to the rest of the six-tepaled clade in Eriogonoideae, albeit with low bootstrap support (Fig. 3.1; Burke et al., 2010). Although this relationship is tenuous, no characters suggest an affinity of *Leptogonum* to any other tribe, while the occurrence of six tepals supports its current position on the molecular tree.

Three species have been described, although the most recent treatment of the genus (Brandbyge, 1990) recognized only one with two varieties. This is a stark contrast to *Coccoloba,* which also occurs in the West Indies but is species-rich (ca. 79 species in the Caribbean alone). Brandbyge postulated that the lack of evolutionary success of *Leptogonum*, as inferred from number of species, could be due to lack of dispersal vectors for its fruits. *Coccoloba* fruits are surrounded by a fleshy perianth and are buoyant, whereas the achenes of *Leptogonum* lack accessory tissue.

4. **Triplarideae** C.A. Mey. in Mém. Acad. Imp. Sci. Saint-Pétersbourg, ser. 6, Sci. Math.,

Seconde Pt. Sci. Nat. 6(2): 147. 1840.

2 genera (*Ruprechtia*, *Triplaris*) / ca. 55 spp.

Plants small to large trees or occasionally lianas, **dioecious**. *Stems* with internodes solid or hollow. *Ocreae* 0.1–32 cm, **conical or sheathing**, scarious, chartaceous or foliaceous, **early caducous**. *Leaves* without winged petioles. *Inflorescences* not subtended by an involucres; apex of axes not modified into tendrils. *Flowers* **unisexual**; perianth accrescent; tepals 6; stamens 6;

filaments adnate to perianth, filiform or flattened. ***Achenes*** trigonous, **often 3-lobed**, enclosed by a membranaceous hypanthium or tepals; endosperm ruminate or uniform. Chromosome number: *n* = 7, 11, 14. (Jaretzky, 1928; Cocucci, 1961)

Distribution: Southern Mexico, Central America, South America.

The affinity of *Triplaris* with *Ruprechtia* is strong, though generic circumscription of each genus needs attention. This tribe can be recognized as dioecious trees with spathiform ocreae (short and scarious in *Ruprechtia*) often enclosing the developing shoot and leaf, and an achenes with three deep sulci. The morphology of the ocrea in *Triplaris* is similar to stipules found in other families (e.g., Moraceae) as the ocrea is conical and early caducous. These genera are also known for their associations with ants which live in the hollow stems in all species of *Triplaris* and some species of *Ruprechtia* (e.g., *R. cruegeri* Lindau). The association of ants living in hollow stems has also been documented for *Coccoloba* (*C. schiedeana* Lindau, fide Standley and Steyermark, 1946).

Generic circumscription of these genera is in flux. Recent phylogenetic analyses suggest *Ruprechtia* is not monophyletic (Fig. 2 in Burke et al., 2010), since *R. triflora* Griseb. is sister to the rest of the Triplarideae clade. This species is distinctive, and can be easily distinguished by the presence of brachyblasts (Pendry, 2004). Other authors have suggested that species with less fusion of the perianth are primitive, and have given rise to the other genera (e.g., the segregate *Enneatypus* Herzog, fide Roberty and Vautier, 1964). Based on work in progress (A. Sanchez and K. Kron), new segregate genera will likely be recognized in this tribe.

5. **Gymnopodieae** Jan. Burke & Adr. Sanchez, **trib. nov.** – Type: *Gymnopodium* Rolfe –

Frutices vel arbores. Involucrum nullum. Flores hermaphroditi, gynoecio cum 3 sulcis

longitudinalibus. Stamina 9, libera.

1 genus (*Gymnopodium*) / 1 sp.

Plants **shrubs** or **small trees**, synoecious. *Stems* with internodes solid. *Ocreae* 1–2 mm, sheathing and scarious or wanting, caducous. *Leaves* without winged petioles. *Inflorescences* not subtended by an involucre; apex of axes not modified into tendrils. *Flowers* bisexual; perianth accrescent; tepals 6; **stamens 9**; **filaments free, filiform**. *Achenes* trigonous, lobed, with 3 longitudinal sulci, enclosed by membranaceous tepals; endosperm type unknown. Chromosome number unknown.

Distribution: Isthmus of Tehuantepec and Yucatán Peninsula: Belize, Mexico (Campeche, Chiapas, Oaxaca, Quintana Roo and Yucatán) and Guatemala (Petén).

Gymnopodium grows as a shrub or small tree on limestone soils on the Yucatán Peninsula in Mexico, Belize and Guatemala. *Gymnopodium* and Eriogoneae form a monophyletic group with strong support (Sanchez et al., 2009; Burke et al., 2010), and hence could be proposed as one tribe. Since Eriogoneae differ from *Gymnopodium* in so many characters (sympodial growth, involucre) we recognize Gymnopodieae as a distinct tribe. Three species have been recognized within *Gymnopodium* (Blake, 1921), but these distinctions were based on leaf shape and pubescence, which varies depending on occurrence in sun or shade (Burke, pers. obs.). Because of the plasticity of previous characters, we follow Ortiz (1994) and recognize one polymorphic species in this tribe.

6. **Eriogoneae** Dumort., Anal. Fam. Pl.: 17. 1829.

About 17 genera (*Acanthogonum* Torr., *Chorizanthe*, *Dedeckera* Reveal & J.T. Howell, *Eriogonella* Goodman, *Eriogonum*, *Eucycla* Nutt., *Gilmania* Coville, *Goodmania*, *Harfordia*

Greene & Perry, *Hollisteria* S. Watson, *Lastarriaea* J. Rémy, *Mucronea* Benth., *Nemacaulis* Nutt., *Pterogonum* H. Gross, *Pterostegia* Fisch. & C.A. Mey., *Sidotheca* Reveal, *Stenogonum* Nutt.; fide Kempton, 2010) / ca. 325 spp.

Plants annual, biennial or perennial herbs, subshrubs or shrubs, synoecious or polygamo-dioecious, rarely dioecious. *Stems* with internodes solid or hollow. ***Ocreae* absent**. *Leaves* without winged petioles. *Inflorescences* subtended by **involucres** (except *Gilmania*); apex of axes not modified into tendrils. *Flowers* bisexual or infrequently unisexual; perianth usually accrescent; tepals 6; stamens (3, 6) 9; filaments free, connate or adnate to perianth, filiform. *Achenes* bluntly trigonous to globose, smooth (rarely winged), slightly enclosed by membranous tepals or by a coriaceous hypanthium (*Lastarriaea* and *Chorizanthe*); endosperm not ruminate. Chromosome number: $n = 9$, 11–12, 14, 16–22, (38–) 40–44. (Stokes and Stebbins, 1955; Ertter, 1980; Hardham, 1989; Reveal and Hardham, 1989; Freeman and Reveal, 2005)

Distribution: Western, southern and southeastern North America, from Alaska to central Mexico, and South America (Chile and western Argentina).

Most taxonomic or floral treatments (Haraldson, 1978; Brandbyge, 1993; Freeman and Reveal, 2005) recognize Eriogoneae as a subfamily. The Eriogoneae form a diverse assemblage of species which have radiated in western North America and in southern South America. This tribe is always recovered as monophyletic with strong support (Sanchez and Kron, 2008; Sanchez et al., 2009; Burke et al., 2010). There are also many morphological synapomorphies, such as the presence of a tubular involucre or a complex of free and whorled involucral bracts, and sympodial growth (Brandbyge, 1993; Freeman and Reveal, 2005). Molecular studies have shown that many of the generic circumscriptions are not monophyletic (Kempton, 2010) and the above tentative summary of genera reflects the reduction of genera from 20 to about 17, many with markedly different from previous circumscriptions. Generic circumscriptions will be

revised based on a comprehensive molecular study of the tribe.

CONCLUSIONS

Our study revises the infrafamilial classification within Polygonaceae to reflect our improved understanding of natural groups. We recognize three subfamilies in Polygonaceae and amend Eriogonoideae and Polygonoideae with revised circumscriptions based on phylogenetic data. We also resurrect Symmerioideae based on the consistent phylogenetic position of *Symmeria* as sister to the rest of Polygonaceae (Sanchez et al., 2009; Burke et al., 2010). Finally, we propose a novel tribal classification for Eriogonoideae, with six recognized tribes and the creation of two new tribes: Leptogoneae and Gymnopodieae. This study provides a global reference point for evolutionary relationships within Polygonaceae.

ACKNOWLEDGMENTS

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CHAPTER 4

MONOGRAPH OF *ANTIGONON* (POLYGONACEAE)

JANELLE M. BURKE

Abstract. *Antigonon* (Eriogonoideae: Polygonaceae) is a genus of four species of suffrutescent vines. The native range extends from western Mexico south to Nicaragua, mostly occurring along the western and eastern coastal plains and thickets, though plants are commonly found in disturbed or ruderal areas elsewhere. Three of the four species are cultivated as ornamentals, and one, *Antigonon leptopus*, has become invasive across the tropics. Phylogenetic analyses with two chloroplast intergenic spacers (*psaI-accD*, *psbA-trnH*) and one nuclear region (*LFY* 2nd intron) were conducted to investigate species relationships. The two species with a more southern distribution, *A. amabile* and *A. cordatum*, are most closely related and sister to clade consisting of *A. platypus* and *A. leptopus.* Hybrid forms between *A. platypus* and *A. leptopus* have been identified in Mexico where the respective species ranges overlap. Species circumscription and nomenclature has been contentious in this small genus, and both are clarified here. A new subspecies, **Antigonon leptopus subsp. coccinuem,** occurring in Baja California Sur and the Sonoran desert, is proposed.

Keywords— Antigonon, Flora of Mexico, monograph, Polygonaceae

Antigonon Endl. is a genus of four species native to Mexico and Central America. Species of *Antigonon* climb via branched tendrils that terminate the inflorescence axes, and persist vegetatively by producing numerous tuberous roots. They are valued as ornamentals for their aesthetic value and nectar production (Duke, 1960; Ortíz 1994; Pichardo and Vibrans, 2009). The flowers are quite attractive and showy, with white, peach or pink perianth colors. Each flower only lasts two days, although an entire inflorescence axis can remain in bloom for at least 11 days (Raju et al., 2001). Of the four species of *Antigonon,* only *A. platypus* Hook. & Arn. has not been seen or documented as a cultivated ornamental. *Antigonon leptopus* Hook. & Arn. is so widely cultivated it has now become a pest across the tropics, and is invasive on various tropical islands (Burke and DiTommaso, in press).

The native range of the genus extends from western Baja California south to Nicaragua, or possibly Costa Rica (Duke, 1960). In the native range, plants are common on coastal plains and in thickets. However, all species also share a propensity to be successful colonizers; a common habitat of these plants is disturbed or ruderal areas (Pichardo and Vibrans, 2009). In Mexico, species of *Antigonon* are most commonly found along the western or eastern coasts; individuals are rarely found in the central states or in areas above 1,000 m. Because of their value as ornamentals within the native range, anthropogenic movement has made the determination of species' native ranges more difficult. Presumed native ranges of the four species overlap to some extent; specifically the distribution of *A. leptopus* overlaps with those of *A. platypus* and *A. cordatum* M. Martens & Galeotti in Mexico.

Antigonon, and its sister genus *Brunnichia* Banks ex Gaertn., are both in the tribe Brunnichieae (sensu Burke and Sanchez, in press). Although both are vines climbing by tendrils with an accrescent perianth, the genera are not easily confused and the generic limits of *Antigonon* are clearly defined. The distribution of *Brunnichia* is restricted to the southeastern

United States, and the perianth is coriaceous in fruit (Graham and Wood, 1965), whereas *Antigonon* are tropical vines, with all perianth segments accrescent and chartaceous in fruit.

The most contentious taxonomic issue in *Antigonon* is species delimitation. There have been one to eight species recognized by different taxonomists (Graham and Wood,1965; Brandbyge, 1988; Brandbyge, 1993), although three to five species has been the common treatment (Standley and Steyermark, 1946; Duke, 1960; Ewing, 1982). Most workers placed some species in synonymy with *A. leptopus* (Duke, 1960; Aymard and Howard, 2004). In his treatment of Polygonaceae, Brandbyge (1993) stated that in *Antigonon* "the described species are poorly defined and a taxonomic revision is needed".

One goal of this monograph was to resolve the taxonomic issues with species circumscription and nomenclature. These issues are especially relevant to distinguish *A. leptopus*, the most invasive species, from its congeners where they co-occur. This monograph also provides keys and distribution maps, clarifies the nomenclature, and puts forward a phylogenetic hypotheses inferred from multiple genomes. Diagnostic characters used in this treatment to distinguish species within *Antigonon* include: perianth length-to-width ratio in fruit, shape of the perianth base in fruit, achene shape, flower color and shape of the leaf petiole. Using these criteria, I recognize four species in the genus. *Antigonon leptopus* is the most morphologically variable and geographically widespread species. In contrast, *Antigonon amabile* W. Bull*, A. cordatum* and *A. platypus* are relatively narrowly distributed and morphologically uniform.

TAXONOMIC HISTORY

Antigonon was first described by Endlicher in 1837, when he placed it the tribe 'Polygonae spuriae' alongside *Brunnichia*, but did not assign any species to the genus. About a

year later Hooker and Arnott, from the collections of Captain Beechey's voyage, described the first two species: *A. leptopus*, the type species, and *A. platypus*, in a footnote in the same publication. Five years later, two additional species of *Antigonon*, *A. cordatum* and *A. cinerascens,* were simultaneously described by M. Martens and H. Galeotti (1843). Subsequently, the names *A. insigne* Mast., *A. amabile* and *A. macrocarpum* Britton & Small were described based on cultivated specimens of *Antigonon.* The white or green-colored species, *A. flavescens* (= *A. platypus*), was redescribed by S. Watson in 1887. In total, 11 species names have been proposed within *Antigonon.* Nomenclatural issues are discussed under each taxonomic species, or the names have been excluded.

Although species synonymy in *Antigonon* has been dynamic, there have been few issues with generic circumscription. Only two species currently placed within *Antigonon* were previously described in another genus: *Polygonum grandiflorum* Bertol. and *Polygonum scandens* L. sensu Sessé & Moc.

The name '*Antigonon*' has been 'corrected' over the years by various workers, based either on perceived errors in orthography or legitimacy. Stuntz (1913) argued that *Antigonon* is a later homonym of *Antigona* Vell. (Flacourtiaceae, now in synonymy with *Casearia* Jacq.), and hence proposed a new name for the genus, *Corculum* Stuntz, including the new combination *C. leptopus* (Hook. & Arn.) Stuntz. The names *Antigonon* and *Antigona* have a different spelling, and likely have a different etymology. *Antigona* was named for the Greek heroine Antigone (Andrews, 1872), whereas *Antigonon* (Greek: anti knees)(Brown, 1954) most likely refers to the zig-zag appearance of the stem growth, though this etymology is uncertain. The name is sometimes changed to *Antigonum* (e.g. Koch, 1871), probably to conform to the common etymology and orthography of other Polygonaceae genera, such as *Polygonum* L. (Greek: many knees) or *Eriogonum* Michx. (Greek: wooly knees)(Brown, 1954), though either ending is a

common transliteration from a neuter Greek noun (Stern, 2004).

MORPHOLOGY

Habit and node architecture—

 Antigonon are perennial vines climbing by tendrils. Stems are distinctly pentagonal in cross section. It is often documented that the tendrils are modified from the apex of the inflorescence axis (Standley and Steyermark, 1946; Duke, 1960), however they can also originate from sterile axillary growth. Nodes of *Antigonon* are multilacunar with five gaps (Freid, 2000), and can be associated with more than one axillary bud. When two axillary buds are present, one produces a vegetative axis and the other will either mature to form an axillary tendril or an inflorescence axis. An alternative explanation is two axillary buds are always present, but one is occasionally suppressed (Graham and Wood, 1965). In *Antigonon leptopus* subsp. *coccineum*, three axillary buds per node have been seen (Fig. 4.1).

 Stems of *Antigonon* produce true wood, with secondary xylem and phloem. In addition, several cambial variants are seen, including formation of successive cambia in older stems, and intraxylary phloem (Carlquist, 2003). There is also marked variation in vessel diameter, with ranges from 10 to 145 μm, generally falling to a bimodal distribution of size categories (i.e. small or large). This wide variation in vessel size is apparent even within one vascular bundle (Carlquist, 2003).

 The vines perennate through the formation of numerous tuberous roots, often concentrated around a central root crown. In *A. leptopus*, vegetative spread can occur through the formation of above-ground runners.
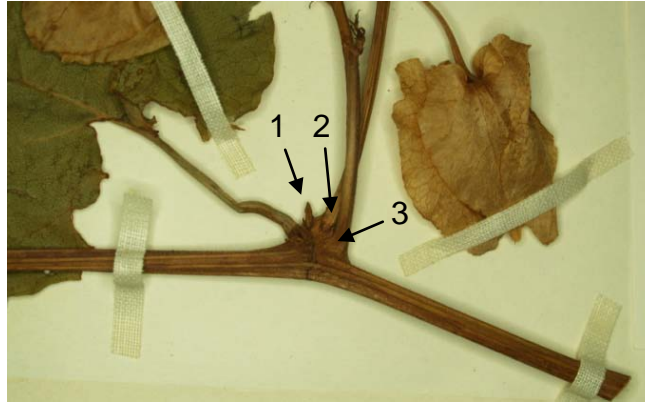
Figure 4.1. Detail of node of *Antigonon leptopus* subsp. *coccineum* (*Carter 2067*, US). Note common origin of leaf base, two axillary branches, and an additional axillary bud (arrows).

Ocrea—

The ocrea, a characteristic feature for Polygonaceae, are quite small in *Antigonon* compared to other genera of tropical Eriogonoideae such as *Coccoloba* P. Brown or *Triplaris* Loefl. Early workers hypothesized that the ocreae were absent (e.g. Meisner, 1856) since only a circular scar is seen at the node in mature growth. The ocrea are scarious and usually extremely short (< 1 mm), and are continuous with the petiole base (Freid, 2000). They are usually deciduous, though in two species, *A. platypus* and *A. leptopus*, the ocreae can be longer and more conspicuous, occasionally persisting in mature growth.

Figure 4.2. Comparative morphology of two *Antigonon* species: *A. amabile* and *A. cordatum*. A–D: *Antigonon amabile*, A. Flower buds and perianth in flower (*Steyermark 49495*, F), B. Perianth in fruit (*Archer 433*, US), C. Achene (*Correll 49300*, NY), D. Mature leaf (*Donnell Smith 4922*, F), E–H: *Antigonon cordatum*, E. Flower buds and perianth in flower (*Dressler & Jones 167*, MO), F. Perianth in fruit (*Matuda 17322*, NY), G. Achene (*Dorantes 360*, MO), H. Mature leaf (*Ucan 4352*, NY). Scale bar = 1 cm.
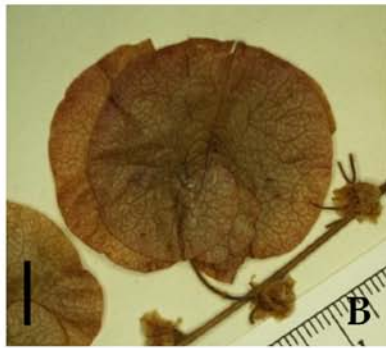
Figure 4.3. Comparative morphology of two *Antigonon* species: *A. platypus* and *A. leptopus*. A–D: *Antigonon platypus*, A. Flower buds and perianth in flower (*Elorsa 2705*, NY), B. Perianth in fruit (*Hinton 6869*, US), C. Achene (*Hinton 6869*, US), D. Mature leaf (*Elorsa 2705*, NY), E–H: *Antigonon leptopus*, E. Flower buds and perianth in flower (*Nee 32786*, NY), F. Perianth in fruit (*Balogh 1046*, US), G. Achene (*Felger 12044*, MO), H. Mature leaf (*Nee 32786*, NY).

Scale bar = 1 cm.
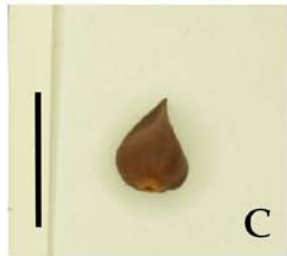
Leaves—

Leaf shape and size is quite variable across the genus (Fig. 4.2d, h; Fig. 4.3d, h). Leaves are always simple and alternate, with festooned brochidodromous venation. Shape of the leaf base can be deeply or shallowly cordate, or truncate. The apex is always attenuate, either acuminate or acute, and frequently also mucronate. In general, leaf shape is not a good taxonomic character; although the majority of individuals within a species may have a similar leaf shape, there are many exceptions. Variation is phenotypically plastic as leaves change shape and size depending on sun exposure.

Leaf petioles are almost always twisted around the stem, with all leaves oriented to one side of the stem, probably as a phototropic response. In addition, the proximal portion of the petiole is swollen into a pulvinus, which may add support to the leaf blade, though its exact function is not known. In two species, *A. cordatum* and *A. platypus*, the leaf petiole is winged, with the lamina decurrent along the petiole. Since these species are not most closely related, it is not a synapomorphy, but instead is a reliable diagnostic character to delimit each species from its sister species. Anatomically, petioles of *Antigonon*, along with its sister genus *Brunnichia*, have an endodermoid layer and tannaniferous idioblasts (Freid, 2000).

Inflorescence—

The primary inflorescence structure is a partial scorpioid cyme (pleiothyrse sensu Gross, 1913; Brandbyge and Øllgard, 1984) with one to six flowers. The flowers are tightly clustered on a short peduncle and the primary inflorescence structure has occasionally been described as fascicled (Standley and Steyermark, 1946; Duke, 1960; Graham and Wood, 1965), though technically incorrect. The primary cymose units are in turn borne on an elongate secondary inflorescence axis. The distance between the primary inflorescence units on the secondary

inflorescence axis varies from 0.5 to 2 cm, and is not a reliable taxonomic character to delimit species. The terminus of the secondary inflorescence axis is always modified into a branched tendril.

Flower—

Perianth aestivation in *Antigonon* is quincuncial, but its expression is quite variable across species (Fig. 4.2a, e; Fig. 4.3a, e). In *A. cordatum*, the edges of the tepal lobes are so closely adpressed that they appear valvate in bud, even though the margins of the tepals do in fact overlap in a quincuncial pattern. The other three species have exposed perianth margins, and the margins of *A. amabile* are characteristically undulate.

Each pedicel is subtended by two fused hyaline bracteoles, which surround the base. The bracteoles ('ochreolae' sensu Duke, 1960) have two distinct apices, except in *A. amabile* where the margin and apex are erose. Bracetoles of *A. amabile* are conspicuous, whereas the bracteoles in the other species are inconspicuous. The pedicel is persistent, and forms an articulation with the distal stipe (Freeman and Reveal, 2005), a stalk-like, elongate base of the perianth tube/ hypanthium.

The flower plan consists of five perianth segments, fused into a short hypanthium along with the base of the staminal column. There are eight stamens, arranged in one whorl; they can be connate in a short ring or an extended column. Occasional aberrations of merosity are found, most frequently in *A. amabile* and *A. leptopus* subsp. *coccineum*, where six perianth segments and nine stamens are sometimes observed. This slight expansion may also be apparent in the gynoecium where the carpel number is sometimes four, giving rise to a tetraquetrous achene. This is the first time a 4-merous gynoecium has been reported in Polygonaceae outside of *Calligonum* (Brandbyge, 1993).

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All species of *Antigonon* exhibit opaque, stipitate glands on the inner portion of the flowers. In the two species, *A. leptopus* and *A. platypus*, the glands are found on the staminal column, especially on the free portion of the filaments. In *A. amabile* and *A. cordatum*, the glands are on the adaxial surface of the tepals, clustered around the central portion of each segment. The function of these glands is not known, though they are probably not nectariferous. Nectar is produced at the base of the ovary, and pools within the staminal ring.

Fruit—

The fruit of species of *Antigonon* is an achene, as in other Polygonaceae (Fig. 4.2c, g; Fig. 4.3c, g). In *Antigonon*, this is almost always 3-sided and sulcate, but can be terete and almost bulbous at the base (*A. leptopus*, *A. platypus*). The pericarp can be thickly chartaceous to more indurate. The seed takes up most of the volume of the locule, and is not fused to the pericarp. At maturity, the achene is enclosed by the five accrescent, chartaceous tepal lobes (Fig. 4.2b, f; Fig. 4.3b, f). The achene, persistent perianth and persistent stipe are dispersed together as one diaspore.

REPRODUCTIVE BIOLOGY

Flowers of *Antigonon* persist for two days and are protandrous. In fact, the entire plant have synchronized flowering at one sexual stage, reducing the chances of geitogamy, although this system may be 'leaky' and with only the majority of flowers at the same stage (Raju et al., 2001). This is a 'synchronous dichogamy' sexual system sensu Lloyd and Webb (1986). The most common pollinator observed in Mexico are bees, but hummingbirds, sun birds, flies, butterflies and wasps have also been observed pollinating *Antigonon* flowers (Burke, pers. observation; Raju et al., 2001). Nectar is probably the reward for these pollinators, as *Antigonon*

leptopus flowers produce 1–1.5 µl of nectar with 26 –28% sugar content (Raju et al., 2001).

Antigonon leptopus has a high germination rate: up to 80% of commercially available seeds germinate, and 70% of seeds from invasive populations. On average, the germination rate for *A. leptopus* from native, invasive or commercial seed sources is 44%, with the other species half of that rate, or less (Ewing, 1982).

CHROMOSOME NUMBERS

Workers attempting chromosome counts of *A. leptopus* have not reached a consensus. Jaretzky (1928) counted a variable number of chromosomes, but stated there were never more than $2n = 40$. In contrast, Rao (1936) reported $2n = 48$ in counts from pollen of *A. leptopus* from India. Counts range from $2n = 40$–48 (Graham and Wood, 1965) or $2n = 14$ (Subramanian, 1980), though there was no way to determine the accuracy of the species identification for the low count. There are no recorded counts from other *Antigonon* species. As the sister genus *Brunnichia* is also $2n = 48$ (Freeman and Reveal, 2005), it is assumed genome duplication has occurred before speciation within *Antigonon*, and all species are polyploid.

HABITAT AND DISTRIBUTION

Species of *Antigonon* thrive in thickets (Standley and Steyermark, 1946; 'lochmophilous' Duke, 1960) distributed along the Atlantic and Pacific coasts of Mexico and Central America. Plants will flower year-round if enough moisture is present (Ewing, 1982; Raju et al., 2001). Some species, *A. leptopus* and *A. cordatum*, are also found in tropical dry forest ('selva baja caducifolia'). Most populations occur near sea level, and are rarely found above 1,000 m. However most species are successful colonizers and are frequently found in a variety of habitats: ruderal areas, secondary forests, matorral, deserts and agricultural fields. The vines are

commonly cultivated within Mexico, and hence are also frequently found in gardens or abandoned homesteads.

Antigonon amabile and *Antigonon leptopus* have been widely cultivated outside of Central America. *Antigonon amabile* is common on many Caribbean islands, as well in Colombia and Venezuela. In these areas, it often thrives as a garden escape. *Antigonon leptopus* is also cultivated in the Caribbean and in South America, but its anthropogenic dispersal is much more widespread: this species now occurs throughout the tropics where it has become an invasive species (see Burke and DiTommaso, in press).

SPECIES CONCEPT

A phylogenetic species concept (sensu Nixon and Wheeler, 1990) was employed, whereby species were delimited based on a unique combination of diagnostic characters. Phylogenetic trees, based on molecular data, were used to help inform species delimitation and relatedness. However, reciprocal monophyly was not used as a criterion for delimiting species. Subspecies were defined based on slight morphological differences that were correlated with geographic distribution. These morphological differences often occurred in different combinations in a given individual, and are hence not diagnosable at the species level, and are therefore presumed to represent natural variation with one interbreeding species.

PHYLOGENY

Large-scale phylogenetic studies in the Polygonaceae affirmed the phylogenetic placement of *Antigonon* within the tribe Eriogonoideae, sister to *Brunnichia* with strong statistical support (Sanchez and Kron, 2009; Burke et al., 2010). These studies also supported the monophyly of *Antigonon*. Because relationships between the species of *Antigonon* have not been

investigated, I undertook a phylogenetic study, using molecular data from both the plastid and nuclear genomes.

Materials and Methods—

Sampling — Thirty-seven samples of *Antigonon* were included in the study, encompassing the four morphological species, subspecies, and putative hybrids. The majority of samples were taken from my personal collections (Appendix 4.1), along with field observations. Three field trips to Mexico were completed, encompassing the following areas: Guerrero, Michoacán, Oaxaca, Veracruz and the Yucatán peninsula. Several collections from Guerrero and Oaxaca states included morphological intermediates between *A. leptopus* and *A. platypus*. Therefore, molecular sampling for *A. leptopus* and *A. platypus* was more intensive to test species boundaries and compare placement of morphological intermediates. For *A. amabile* and *A. leptopus*, sampling included individuals growing outside the native range: one sample of *A. amabile* from Venezuela and 11 samples of *A. leptopus* from the Yucatán peninsula, the Caribbean, South America and the United States (Appendix 4.1). The only species in the sister genus *Brunnichia*, *Brunnichia ovata* (Walter) Shinners, was used as an outgroup.

Molecular Data Collection—Total genomic DNA was extracted from silica-dried leaf material using the Qiagen DNeasy Mini Plant Kit (Qiagen, Valencia, California, US). Two samples were extracted from herbarium specimens (*Pinzl 8469*, *Veliz 15414*, Appendix 4.1). This was accomplished by first manually grinding tissue with a mortar and pestle, then incubating for 18 h at 42°C with 600 µL of an SDS-based buffer and 30 µL of proteinase K, before continuing with the protocol for the DNeasy kit, with a final elution of 100 µL.

Plastid DNA sequence data were generated using primers for *psaI-accD* (Shaw et al., 2007) and *psbA-trnH* from (Shaw et al., 2005). PCR conditions were 25 µL volume reaction with

5 μL flexi buffer, 2 μL MgCl$_2$, 1 μL each primer [10μM], 0.13 μL *Taq* polymerase. Products for

the region *psaI-accD* were amplified following 'slow and cold' PCR cycling program

recommended by Shaw et al. (2005). The region *psbA-trnH* was amplified with the following

PCR program: 94°C initial denaturation, followed by 40 cycles of 94°C denaturation for 30 s,

58°C primer annealing for 1 min, and 72°C primer extension for 1 min 30 sec, with a final 10

min extension period at 72°C.

Primers for 2nd intron of *LFY* were designed specific to the Eriogonoideae, to amplify ca.

750 bp region. Primers were LFY1R (CCT GCC GAC ATA NTG GCG CAT CTT GGG CTT)

and LFY3F (TGC AAG GGG TAA GAA GAA CGG CCT TGA). Products were amplified

using phusion polymerase, with PCR conditions of 25 μL volume reaction with 5 μL phusion

high fidelity buffer, 0.8 μL each primer [10μM], 1 μL dNTP mix [10 μM each], 0.1 μL

polymerase and 1 μL template DNA. PCR cycling program had varied annealing temperature,

with 1 min initial denaturation at 98°C, followed by 20 cycles of 98°C denaturation for 10 s,

64°C annealing for 30 s, and 72°C extension for 2 min. This was followed by 20 cycles of 98°C

denaturation for 10 s, 64°C annealing, decreasing 0.5°C each cycle, and 72°C extension for 2

min, ending with 7 min final extension at 72°C.

One accession from each species of *Antigonon* was selected for cloning. Cloning

conditions were done following the TOPO-TA cloning kit (Life Technologies, Carlsbad, CA)

instructions. Four colonies were chosen per amplicon for sequencing. Only one specimen was

heterozygous, and then only at three base pairs. Because not enough heterozygosity existed to

design allele-specific primers, amplicons from *LFY* were directly sequenced. Heterozygosity was

observed by double-base calls, and only occurred in three accessions. In these instances, the

character was scored as ambiguous for the two nucleotides.

PCR products were run on a 1% agarose gel stained with EtBr. All plastid amplicons were cleaned with enzymes Exonuclease I and Antarctic Phosphotase (New England BioLabs, Ipswich, Massachusetts) to remove residual PCR primers before adding one sequencing primer. Cleaned products were sequenced at the Cornell Biotechnology Resource Center on an Applied Biosystems (Foster City, California) 3730 DNA analyzer.

Data analysis—Sequences were aligned using MUSCLE (Edgar, 2004), and further adjusted by hand. Tails on either end of the aligned sequences were trimmed to exclude amplified primer sequence. Indels were not coded as characters for this analysis. The two chloroplast matrices were analyzed separately, and then concatenated and analyzed simultaneously. The aligned matrices were analyzed under a parsimony criterion using WINCLADA (Nixon, 2002), using the options TBR and xmult with 10 starting trees and 10 search replicates per search with 1000 replicates. Support values were calculated with a statistical bootstrap. Parametric bootstraps were conducted in TNT (Goloboff et al., 2008) with 10 starting trees and 10 search replicates for 1000 replicates. Maximum likelihood analyses were conducted for the plastid regions using Garli (Zwickl, 2006). The most likely model of molecular evolution was estimated using jModeltest (Posada, 2008). The model GTR+I+G was selected as most optimal for the combined plastid dataset. Data were analyzed with twice as many 'attachmentspertaxon' as taxa in the dataset, with two search replicates. Nonparametric bootstrap values were calculated in Garli using the same search criteria for 200 replicates.

Phylogenetic networks were produced from *LFY* sequences for *A. leptopus* and *A. platypus.* The first analytic method used was statistical parsimony, as implemented in TCS (Clement et al., 2000). Ambiguous base pair calls and gaps were coded as missing and connections were set at 95% cut-off. Analyses with SplitsTree ver. 4 (Huson and Bryant, 2006) were done under a split decomposition criterion, with a Jukes-Cantor correction for distances.

These analysis was conducted both with and without the morphological intermediates between *A. leptopus* and *A. platypus.*

Results—

Analyses of the data suggest one main subgeneric division between a clade grouping *A. amabile* and *A. cordatum* (clade A), and a clade of *A. leptopus* and *A. platypus* (clade B, Fig. 4.4). The results are consistent with morphological similarities among the taxa. *Antigonon amabile, A. leptopus* and *A. platypus* were not reciprocally monophyletic.

Despite the high variability in the intergenic regions used, there is a lack of genetic divergence among accessions of *A. leptopus* and *A. platypus*. The five sampled populations of *A. platypus,* from Michoacán and Oaxaca, Mexico do not form a clade on the tree. Instead, accessions of *A. leptopus* and *A. platypus* from the same region in Oaxaca (clade C) form a clade.

Phylogenetic analyses of *LFY* sequences supported the subgeneric division within the genus, but supplied no resolution between accessions of *A. leptopus* and *A. platypus* (Fig. 4.5a). Phylogenetic network analyses were more informative. The TCS network showed divergent genetic profiles for *A. leptopus* and *A. platypus*, with the exception of *A. leptopus x platypus Burke 24*, an intermediate between the two profiles, and *A. leptopus Burke 23*, which grouped with the *A. platypus* haplotypes (Fig. 4.5b). Many loops were formed among the *A. leptopus* haplotypes. When the morphological intermediate *Burke 24* was removed, most of these loops disappeared, and the two species segregated as two distinct genetic groups, without overlap (results not shown). The same result was found with SplitsTree: the distance of accession *Burke 24* was in between *A. leptopus* and *A. platypus* portions of the network, but became clearly segregated with fewer interconnections when the morphological intermediate was removed (results not shown).

Figure 4.4. Phylogram from maximum likelihood analysis of combined plastid data matrix (*psbA-trnH* and *psaI-accD*). Parsimony support values are above branches, maximum likelihood values are below branches. Clades A and B represent two major clades recovered from the analysis, each constituting two species. Clade C is a clade recovered of two species all collected in close proximity in Oaxaca, Mexico.
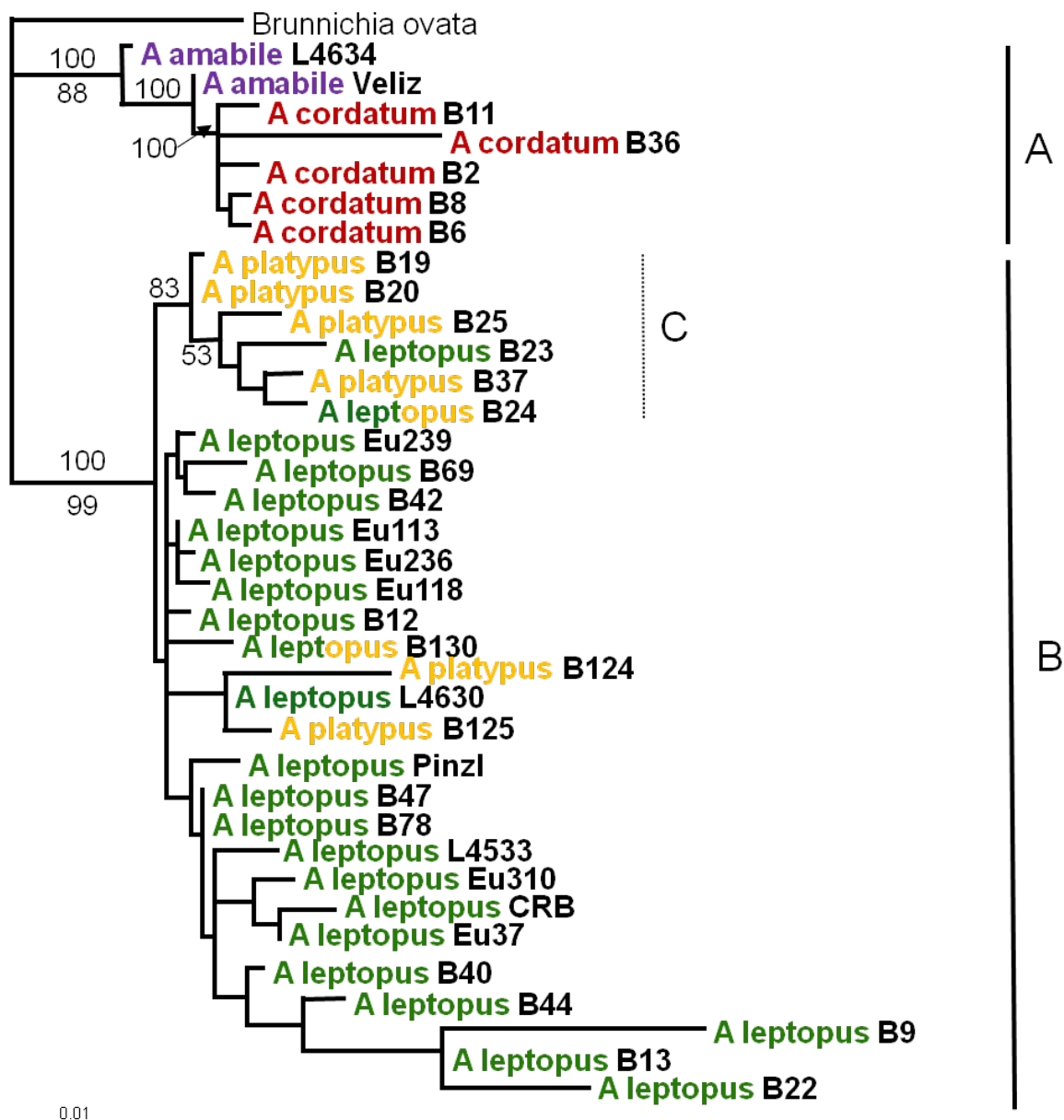
Figure 4.5. Results from phylogenetic and network analyses of *LFY* sequences. A. Consensus tree from parsimony analysis of *LFY* sequences. B. Structure of haplotype network from TCS, with all *A. leptopus, A. platypus* and hybrids included. Identical haplotypes were combined, oval size represents number of accessions. *= *A. leptopus Burke 23* was included with these *A. platypus* haplotypes**.**

A

B

⬤ =	A. platypus
⬤ =	A. leptopus
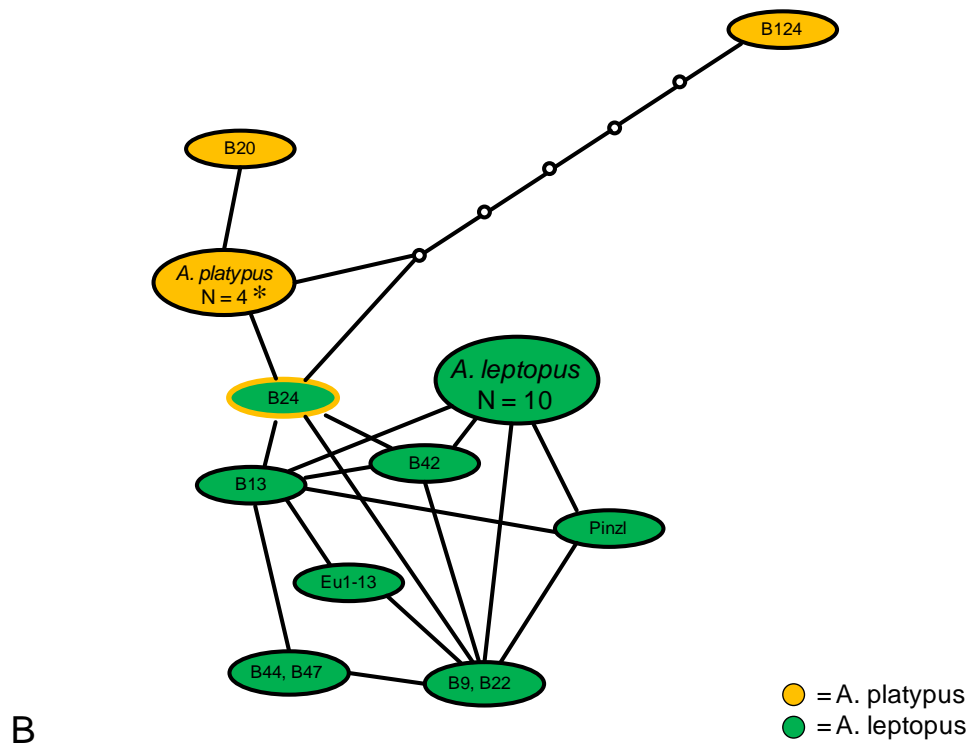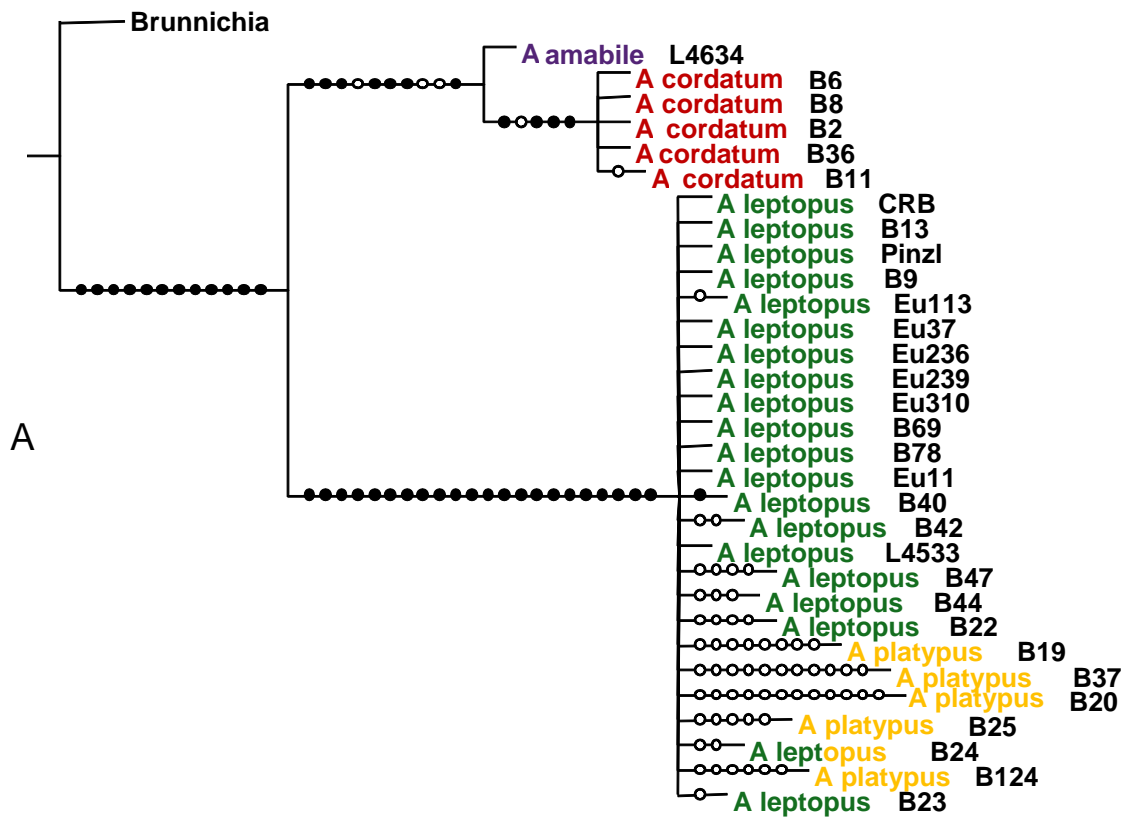
Discussion—

A generic division into clades A and B is concordant with geographic distributions and several morphological characters. *Antigonon amabile* and *A. cordatum* share a more southern distribution. In addition, both species have floral stipitate glands only on the inner surface of the tepals, and the stamens are fused into a ring. In contrast, *A. leptopus* and *A. platypus* share a more northern distribution, mostly restricted to Mexico. They share the character of floral stipitate glands only on the filaments, and the stamens are fused into a column.

Neither *A. platypus* nor *A. leptopus* is a monophyletic species; instead samples from both are intermixed. Since these species are genetically similar, and share some overlapping ranges, they could be treated as one polymorphic species. The presence of morphological intermediates, plants with pink flowers and winged petioles, also suggest there is introgression between these two species. The ability of the two species to hybridize has been confirmed by crossing experiments by Ewing (1982) who produced viable F1 hybrids between *A. platypus* and *A. leptopus.* She did not observe flower morphology, but she did observe that the F1 crosses had a winged petiole.

Although the evidence of introgression and chloroplast haplotype phylogeny suggest one polymorphic species, I have decided to treat these entities as separate species based on two lines of evidence: (1) suites of diagnostic morphological differences between *A. leptopus* and *A. platypus* and (2) divergent nuclear allelic profiles. In addition, the structure observed in the chloroplast haplotype phylogeny may be attributable to historical phylogeographic patterns instead of phylogenetic.

The nuclear marker used for this study showed a different trend in genetic separation between *A. leptopus* and *A. platypus.* Interpreting allelic variation in a network framework, we see two distinct genetic profiles. The morphologically intermediate specimen sampled shares the

genetic profile of both species, suggesting introgression or recombination. Presence of recombination within this nuclear region was not tested explicitly because the region did not have enough variation. The other two species in the genus can also be distinguished based on morphological characters. No morphological intermediates have been seen between *A. amabile* and *A. cordatum.*

The plastid haplotype phylogeny appears to coincide with geographic distribution of accessions. There is evidence for this in the well-supported clade C (Fig. 4.4), which consists of individuals from both species collected in close proximity in Oaxaca. This pattern is not surprising; plastid sequences are often used to track phylogeographic patterns (Schaal et al., 1998). Due to their small effective population size of the genome and uniparental inheritance (Birky, 1995; Templeton et al., 1995), plastid markers usually track historical patterns rather than recent genetic exchange.

In conclusion, the phylogenetic study has elucidated species relationships that are largely concordant with gross morphological differences between species and geographic distribution. Data from both plastid and nuclear genomes, as well as morphology, have helped to inform species delimitation and presence of introgression between *A. platypus* and *A. leptopus.*

MATERIALS AND METHODS

Material from herbaria BH, F, MO, NY, TEX/LL, and US were used for morphological study and to determine species distributions. The type specimens for all valid names in *Antigonon* were examined, either in person or by inspection of a digital image. Measurements of flowers and fruits from dried specimens were first boiled in water with 2% detergent and then dissected and measured. At least 20 specimens were measured per taxon, chosen to encompass morphological diversity and distribution. Complete exsiccatae were not generated; instead one

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exemplar specimen was selected for each locality at the municipality level (i.e. county in the United States, municipio in Mexico).

TAXONOMIC TREATMENT

ANTIGONON Endl., Gen. Pl. 310. 1837. —TYPE: *Antigonon leptopus* Hook. & Arn.

Corculum Stuntz, Bull. Bur. Pl. Industr. U.S.D.A. 282: 86. 1913, *nom. superfl.* —TYPE: *Corculum leptopus* (Hook. & Arn.) Stuntz

Plants herbaceous or suffrutescent, capreolate vines; roots fibrous, often tuberous. Stems pentagonal (terete) in cross section, pubescent or glabrate; indument, when present, of multicellular trichomes, their vacuoles often tinted brown, red or magenta; axillary branches leafy or modified as tendrils or inflorescence axes, 1–3 per geniculate node, when >1then, one axillary branch leafy and others inflorescence axis or tendril. Ocrea cylindrical or reduced to line of cilia, scarious, deciduous (proximally persistent). Leaves alternate, simple, petiolate; petiole terete or flanked by decurrent leaf lamina and winged, twisted, modified as a pulvinus proximally or absent; lamina cordate, lanceolate, ovate, sagittate or deltoid, puberulent to densely pannose, basally truncate to deeply cordate, apically acute, acuminate or cuspidate, and usually mucronate with entire to rugose margin; venation festooned brochidodromous; vernation revolute. Secondary inflorescence axes terminal or axillary racemes, usually terminating in branched tendril; primary inflorescence of 3–8 flowers arranged in a dense cyme, appearing fascicled due to short peduncle; axis subtended by 1 bract, sometimes also by an unbranched tendril; bract sessile, subulate or clasping, hyaline, apically mucronate, acuminate or cirrose. Pedicel terete, articulate with floral stipe, minutely pilose to velutinous, persistent, subtended by 2 fused bracteoles, these sheathing the pedicel; bracteoles cylindrical and bifid, hyaline,

persistent, translucent, peach, pink or brown, apically mucronate, acuminate or cirrose, marginally erose or entire. Flower bisexual, aestivation quincuncial (appearing valvate) with an entire, undulate or crumpled in bud; stipe long, narrow, often winged distally, trichomes longer than on pedicel, accrescent. Perianth connate and forming an hypanthium proximally, eglandular or occasionally with opaque, stipitate glands, accrescent; tepals 5(–6), outer 3 broader than the inner 2, marginally minutely ciliate. Stamens (7–)8(–9), glabrous or with opaque, stipitate glands; filaments in one whorl, equal or of 2 lengths, connate into fleshy ring or column forming a nectar cup, basally flattened or dilated, often intercalated with dentate appendages; anthers dorsifixed, introrse, versatile; pollen subprolate, tricolporate, white or yellow. Gynoecium 3(–4) carpellate; ovary 1-celled, trigonous (tetragonous) with basal placentation; ovule 1, borne on a long funiculus, anatropous and pendulous at anthesis, then orthotropous as it matures; styles 3, arcuate on first day of anthesis then erect, often connate proximally into a short (ca. 0.5 mm) beak; stigma peltate and bilobed. Diaspore consisting of accrescent perianth, included achene, accrescent stipe and persistent filaments; perianth as described above except chartaceous; achene trigonous, triquetrous or subglobose, apically attenuate, triangular in cross section, dull or lustrous. Seed 1, subglobose to trigonous, rivulose, apically acute; endosperm oily and granular, ruminate, white; embryo central or slightly excentric, radical superior, cotyledons oblong. Chromosome number $2n = 40, 44, 48$.

KEY TO THE SPECIES OF *ANTIGONON*

1. Floral glands on inner surface of tepals; stamens connate into a ring < ⅓ filament length; outermost tepal in fruit as long as broad. ………………………………………………… 2

    2. Leaf indument densely pubescent on abaxial surface; petiole terete; aestivation quincuncial; perianth light pink or peach …………………………………………*Antigonon amabile*

2. Leaf indument variable, rarely densely pubescent abaxially; petiole winged; aestivation seemingly valvate; perianth light to dark pink………………………… *Antigonon cordatum*

1. Floral glands on staminal column or lacking; stamens connate into a column > ⅓ of filament length; outermost tepal in fruit longer than broad. …………………………………………3

   3. Perianth white, light green or yellow, 4–9 mm long; petiole winged.

   ………………………………………………………………… *Antigonon platypus*

   3. Perianth pink to red, occasionally white, 6–14.5 mm long; petiole terete. …………………

   …………………………………………………………………*Antigonon leptopus*

1. ANTIGONON AMABILE W. Bull., Cat. New Beautiful Rare Plants William Bull. 1 Apr 1871. *Antigonon amabile* K. Koch, Wochenschr. Vereines Beford. Gartenbaues Konigl. Preuss. Staaten 14(17): 131. 29 Apr 1871, *nom. illeg.* ―TYPE: COLOMBIA. [Distrito Capital]: Bogota, [sin dat.], *Shuttleworth s.n.* (neotype, designated here for both names: K- scanned image!, barcode K000585039). Fig. 4.6.

Antigonon insigne Mast., Gard. Chron., n.s. 7: 780. 1877. ―TYPE: VENEZUELA. [Distrito Federal]: Caracas, Nov 1871, *Ernst 1*, (lectotype, designated here: K- scanned image!, barcode K000585040)

Antigonon macrocarpum Britton & Small, Sci. Surv. Porto Rico & Virgin Islands 266. 1924. ―TYPE: COSTA RICA. Livingston, 16 May 1918, *W.W. & H.E. Rowlee 28* (holotype: NY!; isotype: US!).

Plant climbing to 5 (–15) m, indument densely pilose to velutinous on young axes, pilose on older axes, trichomes 0.2–0.3 mm long, brown. Stems 1.6–3.3 mm diameter; pentagonal to nearly terete in cross section, tawny-brown to magenta-brown; axillary tendrils 5.5–15 cm. Ocrea

0.4–0.9 mm long. Petiole 0.5–2.1 cm, not winged, densely pilose (moderately pilose); lamina 3.5–10.6 cm long, 3.2–6.2(–10) cm wide (L:W ratio 0.9–2.2), ovate or cordate, basally cordate (truncate), not decurrent along petiole, apically acute or cuspidate (round), mucronate, marginally entire or sinuous (rugose), ciliate, adaxially dull green, sparsely hispid or trichomes present only on primary and secondary veins, abaxially cinereous, velutinous, trichomes along veins and margin, usually with additional pannose pubescence on blade, these trichomes long, slightly curled, white. Secondary inflorescence axes 5.5–28 cm long; primary inflorescences 8–35 mm apart, often subtended by unbranched tendril, composed of (3–)4–5(–8) flowers; bract 2.7–5.0 mm long, ovate, apically acuminate or mucronate. Pedicel 2–6.3(–9.5) mm at anthesis, pilose to velutinous; bracteole translucent to peach, apically acute (mucronate), marginally erose. Flower aestivation quincuncial, with a crumpled perianth margin crumpled; stipe 2.3–12.2 mm at anthesis, terete or winged to 2 mm, densely pilose to velutinous. Perianth 7.7–15.3 mm long, peach to pale pink, adaxially glandular, glands denser proximally; hypanthium 0.8–4.7 mm (ca. 15-25% of perianth length); outermost tepal 7.4–13.8 mm long, 7.4–14.1 mm wide, ovate to orbicular, basally shallowly cordate to cordate, apically round or mucronate; innermost tepal 6.3–11.4 mm long, 3–8.2 mm wide, oblong to ovate. Stamens glabrous, or rarely with sporadic stipitate glands; filaments equal in length, 2.7–5 mm long, pink, connate in a ring 0.5–1.0 mm, without dentate appendages; anthers 1.0 mm long, brown or black, drying red. Gynoecium pink or brown; ovary 1.7–3.3 mm; style 1.9–2.2 mm; stigma ca. 0.5 mm, pink, brown or black. Diaspore stipe 7.1–12 mm; perianth rosy pink to green, outermost tepal 19.5–35.8 mm long, 18.3–36.6 mm wide (L:W ratio 0.9–1.15), orbicular (ovate), basally reniform, innermost tepal 14.3–22 mm long, 5.5–12.6 mm wide, elliptical or ovate; achene 7.1–12 mm, bluntly triquetrous (tetraquetrous), tan to light brown, apically 3-alate, basally triangular (nearly terete), pericarp indurate. Seed 4.3–7.0 mm, subglobose, brown or black.

Figure 4.6. Antigonon amabile. A. Leaf. B. Inflorescence axis. C. Flower without perianth. D. Perianth in fruit, both inner and outer tepals. E. Anthers. Illustration accompanying Master's description of *Antigonon insigne* (Masters, 1877, p. 789)*,* drawn from a plant grown by William Bull in London from seed collected in Colombia.
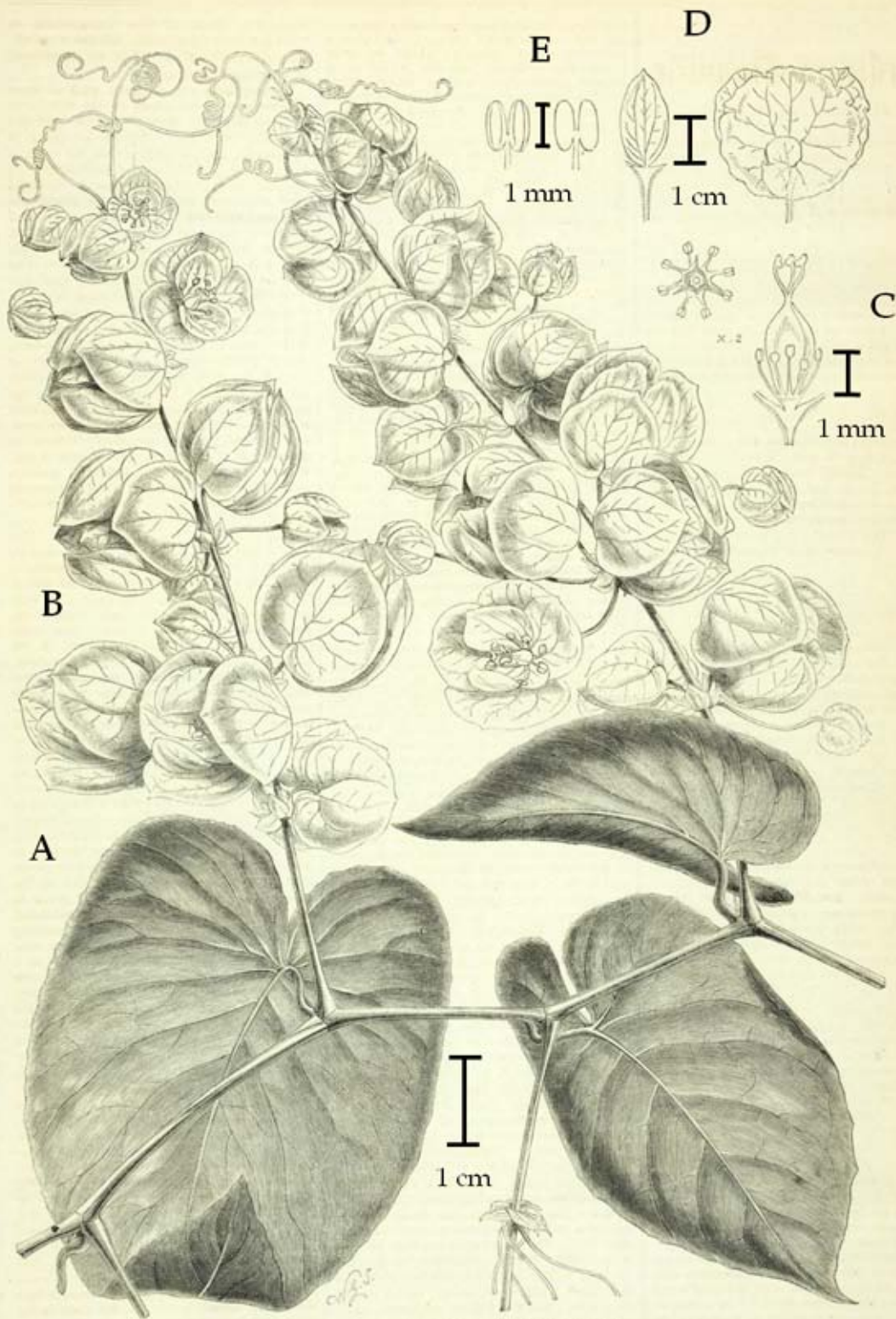
FIG. 126.—MR. BULL'S ANTIGONON INSIGNE (SEE P. 780).

Phenology— Flowering year round, especially when cultivated. In native range, mostly Oct.-Dec. Fruiting all year, mostly in Nov.-Dec.

Local name and uses—"Bellísima": Costa Rica, Colombia, Ecuador, Honduras, Nicaragua, Peru. "Cadeña de amor": Ecuador. "Colación": El Salvador. "Confitillo": Honduras. "Lluvia": Bolivia. Cultivated as an ornamental for its showy flowers, and a large persistent perianth surrounding the achene, also planted to attract bees for honey production.
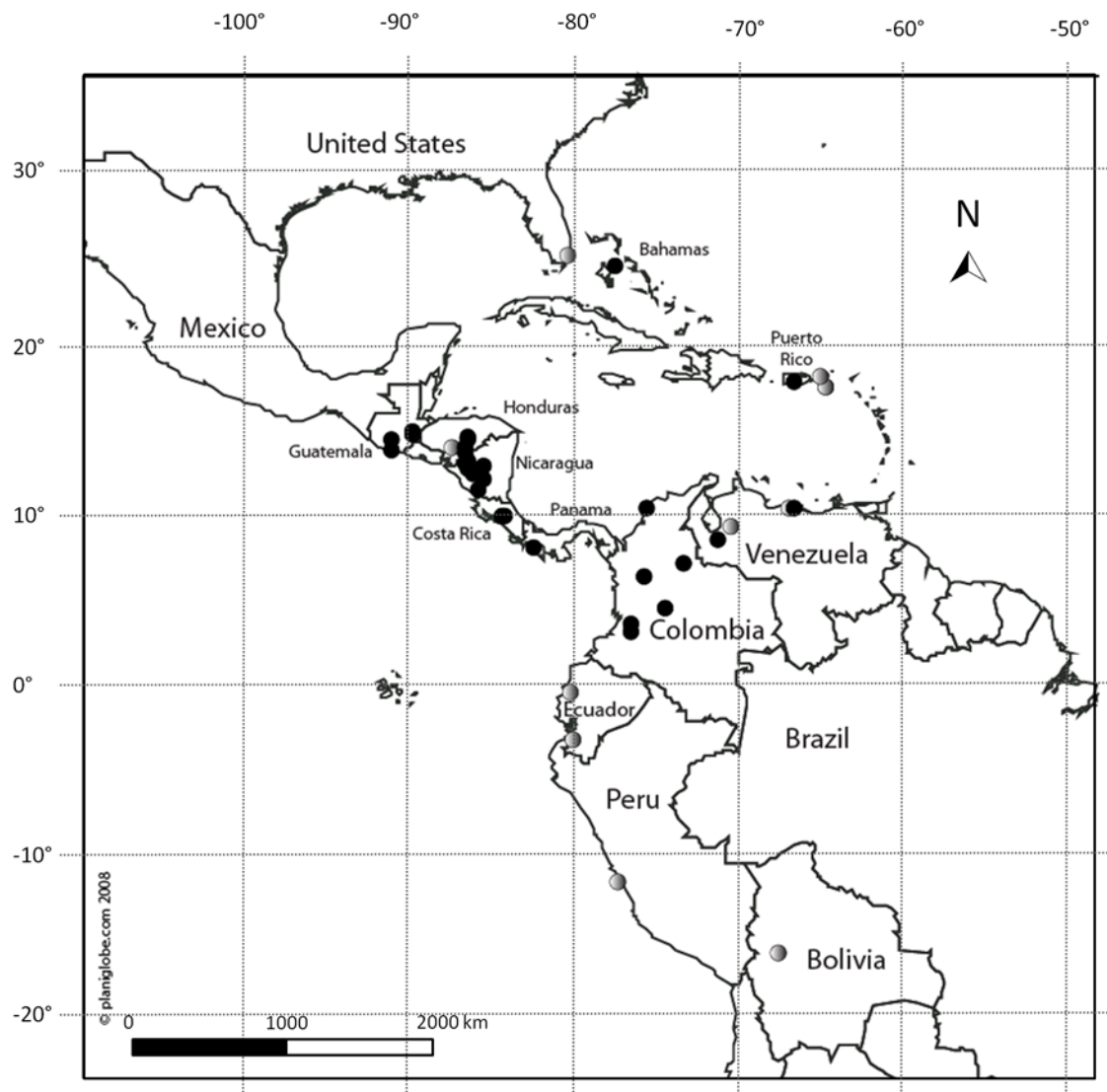

Figure 4.7. Geographic distribution of *Antigonon amabile.* Spontaneous collections have filled circle (●), cultivated collections have a gray gradient filled circle (○).

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Distribution—Native distribution along the Pacific slopes and plains of Central America: Guatemala (Esquintla, Zacana), Honduras (El Paraíso, Francisco Morazan, Olancho), Nicaragua (Boaca, Chontales, Estelí, Leon, Matagalpa, Nueva Sengovia); cultivated in the native range and also in the Bahamas, Bolivia, Brazil, Colombia, Costa Rica, Ecuador, Panamá, Peru, Puerto Rico, St. Croix, St. Thomas, United States of America, Venezuela (Fig. 4.7); mostly in moist thickets, also secondary forests, pastures; 100–1800 m.

Discussion— Flowers of *Antigonon amabile* can be distinguished from other species by the crumpled appearance of tepals in bud and its black anthers (red when dried). The velutinous-pannose hairs on the abaxial leaf surface are also diagnostic and gives the blade a velvety feel.

William Bull, a horticulturalist in London, validly published *Antigonon amabile* in his seed catalogue on 1 Apr 1871. The same species (as *Antigonum amabile*) was described a mere four weeks later by K. Koch (1871) based on same cultivated material and hence his name is a later homonym. Bull did not reference any specimens in his protologue and no original material is known to exist. To select a neotype, material was investigated that most likely came from the original seed source cultivated by Bull, namely an E. Shuttleworth collection, as Shuttleworth collected for Bull in Colombia (Masters, 1877). A specimen at K gathered by Shuttleworth in Bogota, Colombia probably is the voucher for the seeds cultivated by Bull in London. Thus this sheet is now designated as the neotype of *A. amabile.*

Antigonon amabile was previously referred to as *A. guatimalense* in herbarium collections, but has now been placed in synonymy with *A. cordatum.* See nomenclatural discussion under *A. cordatum.*

Based on label data, the native range for this species of *Antigonon amabile* is most likely restricted to Central America, with populations in the Caribbean and South America being the result of cultivation or localized naturalization. In particular, almost all specimens from

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Caribbean Islands were either collected in a town or at an abandoned homestead. Colombia is the only questionable area that may be an extension of the native range; some specimens have been collected far from any homestead.

Although this may be the most attractive species of *Antigonon,* it is not known to have been cultivated outside of the New World (Egypt is a possible exception, *Gillis 9909* [MO]). The vine is often found in disturbed places where it can form dense cover over other vegetation. The specimen cultivated at the Jardín Botánico de Caracas was introduced over 100 years ago, and now covers the canopies of several trees (pers. observation). Cultivated plants have often been assigned to *A. macrocarpum,* here placed in synonymy with *A. amabile*. It is suspected the species was cultivated for its large fruits and showy, persistent perianth, as they can have enlarged ovaries with four carpels (*Britton & Marble 1493* [NY], *Rueda 12197* [MO]), a characteristic rarely seen elsewhere in the genus.

Representative Specimens Examined—**Spontaneous.**

BAHAMAS. New Providence, Nassau, corner of Village Rd. & Shirley St., 15 Dec 1977, *Correll 49300a* (NY).

COLOMBIA. Antioquia: Bello, 13 Jul 1930, *Archer 433* (US). Bolívar: Cartageña, [sin dat.], *Schott 1* (F, NY). Cauca: Quilichao, May 1904, *Jameson s.n.* (US). Cundinamarca: a la salida de Fusagasugá, 12 Apr 1946, *Duque-Jaramillo 3195* (NY). Santander: 8 km from Bucaramanga on road to Santander, 16 Jul 1968, *Barkley 38C302* (TEX). Valle del Cauca: plana del Valle del Cauca, entre Gorgona y Cabuyal, 2 Jun 1943, *Cuatrecasas 14482* (F).

COSTA RICA. San José: San José, Mar 1894, *Donnell Smith 4922* (F, US); Río de Oro, Santa Ana, 31 Jan 1966, *Jiménez 3650* (F).

GUATEMALA. Chiquimula: Mpio. Chiquimula, transect La Hondonada, 6 Oct 2003,

Veliz 14514 (MO). Escuintla: Mpio. San José, San José, 27 Jan 1906, *Kellerman 6666* (F, US). Sacatepéquez: Mpio. Alotenango, Capetillo, Mar 1892, *Donnell Smith 2483* (US). Zacapa: Mpio. Río Hondo, trail between Río Hondo and waterfall, Sierra de las Minas, 10 Oct 1939, *Steyermark 29495* (F); Mpio. Zacapa, near divide on road between Zacapa and Chiquimula, 9 Oct 1940, *Standley 73805* (F).

HONDURAS. El Paraíso: Mpio. Danlí, Valle de Jamastrán, NO de Chichicaste, 14 Dec 1958, *Williams & Molina 8800* (F, US). Olancho: Valle Catacamas, cerca de El Plomo, 19 Nov 1963, *Molina 13299* (F, NY, TEX); Mpio. Juticalpa, alrededores de Casas Viejas, 6 km NO de Juticalpa, 13 Apr 1985, *Alvardo Flores 155* (NY).

NICARAGUA. Boaca: Mpio. San Lorenzo, Puente Las Pitas, 4km S de la desviación a Camoapa, sobre carretera Chontales-Managua, 5 Aug 1984, *Hernández & Stevens 624* (NY); Mpio. Teustepe, mountains near Cacao, 14 Nov 1946, *Williams & Molina 10962* (F, MO, NY). Chontales: Cerro La Bateca at Hacienda Veracruz, 8 km S of Coapa, *Nee 28285* (NY). Estelí: Mpio. Estelí, along Estelí river, 5 km from Estelí town, 3 Nov 1968, *Molina 23048* (F, MO, NY); Reserva Natural Miraflora, Comunidad La Naranja de Fátima, 25 Nov 1999, *Rueda 12197* (MO); 5-7 km E of Estelí, 26 Nov 1973, *Williams & Molina 42463* (F, US); Mpio. La Trinidad, km marker 121 on hwy 1, 27 km S of Estelí, 1 km NW of Matagalpa/Estelí border, 1 Sep 1983, *Miller & Nee 1480* (NY, TEX). Matagalpa: Mpio. Ciudad Darío, Route 1, K73, Casas Viejas, 23 Dec 1968, *Hamblett 1039* (F, NY); Mpio. Río Blanco, along road between Waswalí Abajo and Waswalí Arriba, 24 May 1982, *Stevens 20302* (NY). Nueva Segovia: ca. 6.2 km N of N edge of Ocotal, Quebrada El Nancital, 7 Aug 1977, *Stevens 3072* (NY). Rivas: Ometepe island, Oct 1869, *Levy 142* (P).

PANAMA. Chiriquí: [08°00'00"N, 82°20'00"W], 4 Jul 1966, *Tyson et al. 4236* (MO).

PUERTO RICO. Mpio. Ponce, Ponce, Villa Suecia, 4 Feb 1932, *Britton & Britton 9895*

(NY)

U.S. VIRGIN ISLANDS. St. Croix: Bassin [Christiansted], 18 Nov 1895, *Ricksecker 88*
(F, MO, NY, US).

VENEZUELA. Mérida: Mpio. La Punta, Dist. Liberator, a la salida hacia La Parroquia,
14 Mar 1972, *Lopez-Palacios 2762* (US). Miranda: Mpio. Zamora, Guatire, 5 Nov 1984,
Llamozas 4 (MO).

Cultivated.

BOLIVIA. La Paz: Prov. Sur Yungas, trail Chulumani to Ocobaya, cult. in Ranch
Tecempaya, 12 Dec 1935, *Mexia 4290* (MO).

ECUADOR. El Oro: al lado de la carretera, frente una casa, 24 Nov 1976, *Albert de
Escobar 934* (MO, TEX). Manabí: entre La Salina y Chone, 26 Jul 1945, *Acosta Solís 10611* (F).

HONDURAS. Morazán: vicinity of Tegucigalpa, bo. Concordia, 7 Oct 1949, *Standley
24127* (F, US).

PERU. Callao: patio of Colegio Americano, 22 May 1967, *Robertson & Austin 2* (MO).

UNITED STATES OF AMERICA. Florida: Dade Co., Fairchild Tropical Botanic
Garden, 24 Oct 1970, *Gillis 9909* (MO).

U.S. VIRGIN ISLANDS. St. Croix: Bassin [Christiansted], 8 Jan 1897, *Ricksecker 16* (F,
MO, P, US). St. Thomas: Charlotte Amalie, 11 Feb 1913, *Britton & Marble 1493* (NY).

VENEZUELA. Dto. Federal: Jardín Bótanico de Caracas, 27 Jan 2006, *Luckow et al.
4634* (BH, VEN). Trujillo: Trujillo, patio of Gran Hotel, 2 Apr 1944, *Steyermark 55853* (F).

2. ANTIGONON CORDATUM M. Martens & Galeotti, Bull. Acad. Roy. Sci. Bruxelles x: 354. 1843.

—TYPE: MEXICO. Veracruz: Guaspaltepec, Jun 1840, *Galeotti 463* (lectotype, designated

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here: BR- scanned image! barcode 528781; isolectotypes: P!, US!, W- scanned image!). Fig. 4.8.

Antigonon guatimalense Meisn., Prodr. (DC.) 14(1): 184. 1856. *Antigonon grandiflorum* B.L. Rob., Proc. Amer. Acad. Arts 44(21): 613. 1909., *nom. superfl. Polygonum grandiflorum* Bertol., Fl. Guatimal. 12-13. 1840., *nom. illeg.,* non Willd. ―TYPE: GUATEMALA. [Escuintla]: Escuintla, 1837, *Velazquez s.n.* (holotype: BOLO- scanned image!).

Polygonum scandens [L.] sensu Sessé & Moc., Pl. Nov. Hisp. 61. 1888.

Plant climbing to 10 m, indument pilose on younger axes, puberlent on older axes, trichomes 0.1–0.3 mm long, white, beige or red-tinged. Stems 1.9–3.6 mm diameter, pentagonal to nearly terete in cross section, brown, red or green; axillary tendrils 4–13 cm. Ocrea 0.4–2 mm long or reduced to line of cilia. Petiole 0.4–4 cm, winged (½–) ¾- entire length, pilose (puberlent); lamina 2.7–10.6 cm long, 2.0–9.3 cm wide (L:W ratio 1.0–1.9), cordate or ovate (deltoid), basally shallowly to deeply cordate (truncate), decurrent along petiole, apically acute or cuspidate (rounded), mucronate, marginally sinuous or rugose (entire), minutely ciliate, adaxially green to dark green, puberlent to sparsely hispid (velutinous), abaxially light green, hispid or pilose along primary veins, without notable pubescence on lamina, trichomes short, stiff, white or brown. Secondary inflorescence axes 5—22 cm long, primary inflorescences 3.8–24.5 mm apart, not subtended by tendril , composed of (2–)3–5(–6) flowers; bract 1.5–3.2 mm long, subulate, apically acuminate. Pedicel 2.0–8.8 mm at anthesis, minutely pilose to moderately pilose; bracteole translucent to dull brown, apically acuminate to long-acuminate, marginally entire. Flower aestivation quincuncial, but seemingly valvate with entire perianth margin; stipe 4.0–13.2 mm at anthesis, terete or winged to 3 mm, sparsely pilose to moderately pilose. Perianth 6.5–12.3 mm long, pale pink to dark pink, adaxially glandular, glands denser proximally;

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hypanthium 0.6–1.8 mm (ca. 7-18% of perianth length); outermost tepal 5.8–10.5 mm long, 3.8–9.0 mm wide, ovate, basally cordate, apically acute or mucronate; innermost tepal 5.4–9.9 mm long, 2.4–4.7 mm wide, oblong or elliptical. Stamens glabrous, rarely with sporadic stipitate glands); filaments all equal length, 2.6–5 mm long, pink, connate in a ring 0.4–0.8 mm, without dentate appendages; anthers 0.8–1.0 mm, white or yellow. Gynoecium pink; ovary 1.9–3.5 mm; style 1.5–2.2 mm; stigma ca. 0.4–0.6 mm, dark purple or red. Diaspore stipe 7.7–16.4 mm; perianth light green to pink, outermost tepal 19.0–27.1 mm long, 13.2–27.7 mm wide (L:W ratio 0.85–1.1), orbicular, basally deeply cordate to reniform, innermost tepal 12.1–18.9 mm long, 4.9–8.8 mm wide, oblong or elliptical; achene 8.9–12.5 mm, triquetrous, tan to brown, apically 3-alate, basally bluntly triangular or terete, pericarp indurate. Seed 3.2–7.0 mm, subglobose, dark brown or black (red).

Phenology— Flowering year round, especially Jul.–Nov; fruiting Aug.-Dec.

Local name and uses—"Coamecate": Guerrero and Veracruz, Mexico. "Colación": El Salvador. "Confite": Chiapas, Mexico and El Salvador. "Coralillo": Guatemala. "Rosa morada": Veracruz, Mexico. "San Diego": Yucatan, Mexico. "Santa Rosa": Veracruz, Mexico. Cultivated in Mexico as an ornamental and also to attract bees for honey production.

*Distribution—*Along the Pacific and Atlantic plains of Mexico and Central America: El Salvador (Ahuachapán, Sonsonate, Usulután), Guatemala (El Progresso, Escuintla, Huehuetenango, Jutiapa, Santa Rosa, Suchitepéquez, Zacapa), Honduras (Comayagua, Cortés, Santa Bárbara), Mexico (Chiapas, Guerrero, Michoacán, Oaxaca, Tabasco, Veracruz, Yucatán) (Fig. 4.9); tropical deciduous forest, common in disturbed secondary forest and thickets; 0–1400 m.

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Figure 4.8. Antigonon cordatum. A. Leaf. B. Inflorescence axis. C. Flower. D. Perianth in fruit. E. Achene. Illustration from Ewing (1982), habit drawn from *Calzeada 15* (MEX), open flowers from *Smith 1997* (GH), fruit from *Dorantes 360* (MEX), and large leaf from *Boege 2650* (MEX). Reproduced with permission.
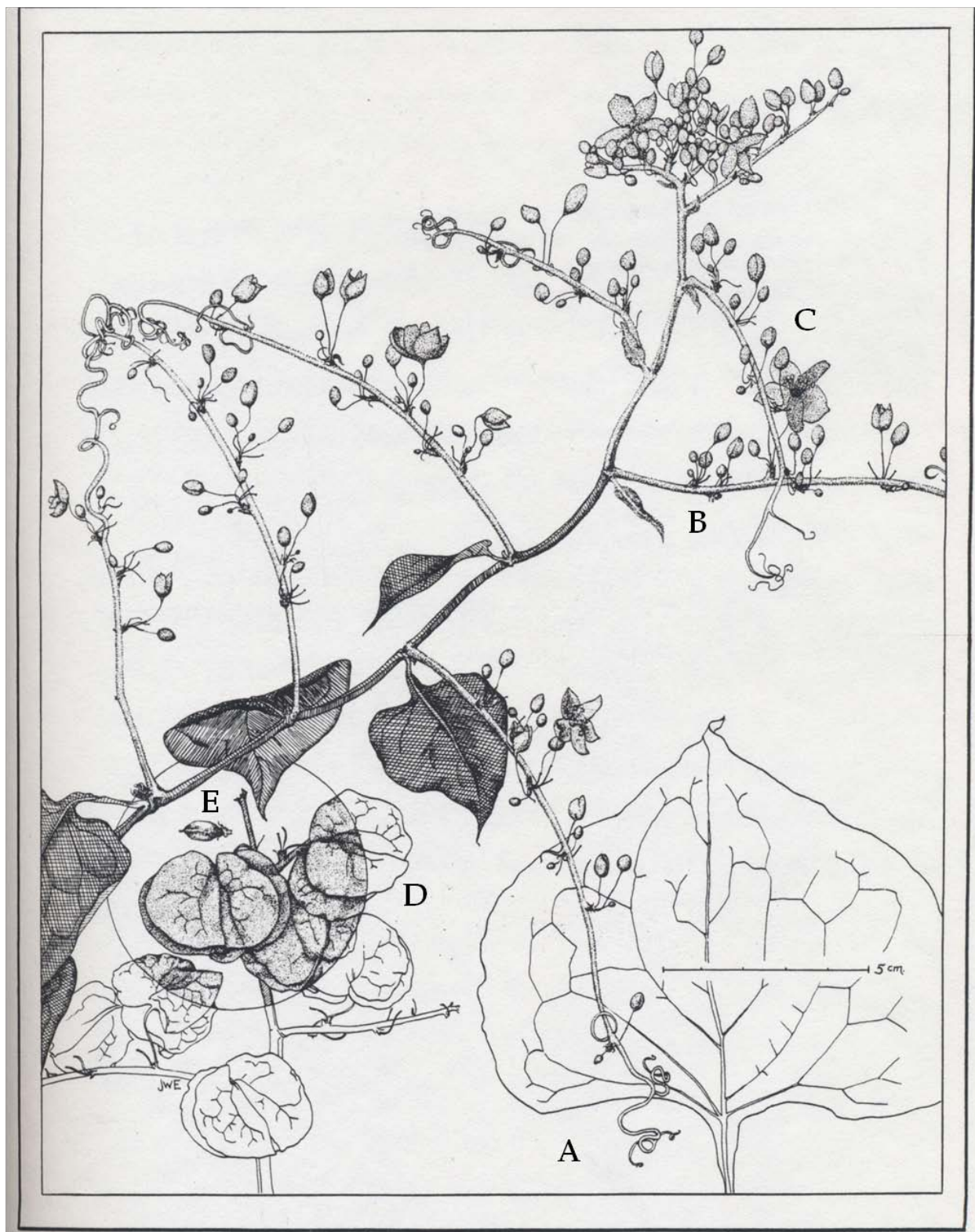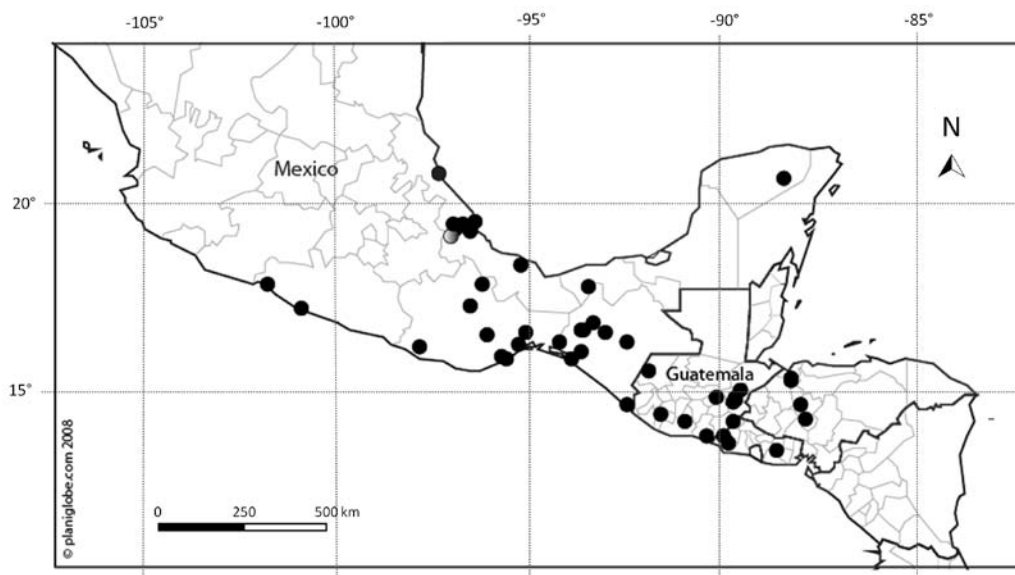
Figure 4.9. Geographic distribution of *Antigonon cordatum.* Spontaneous collections have filled circle (●), cultivated collection has a gray gradient filled circle (◐).

Discussion— Antigonon cordatum can be readily distinguished from other *Antigonon* species based on the wide, cordate leaves with winged petioles, and the aestivation. In bud, the tepal margins are tightly adpressed, so the aestivation appears valvate. Flower color is another distinctive character for *A. platypus*: in general the flowers are darker pink than *A. amabile.* On the first day of anthesis, when the flowers are male-receptive, the tepals are dark pink, on the second day, when the flowers are female-receptive, the tepals are pale pink. This change in flower color has only been observed in *A. cordatum* and some collections of *A. leptopus* in Veracruz.

Unlike *A. leptopus* and *A. amabile*, *A. cordatum* has not often been cultivated outside of the native range; although within Mexico, people often have the vines in their yards or gardens, either for ornamentation or to attract bees.

Nomenclatural confusion in this species stems from an article by Martens and Galeotti (1843) in which they described two *Antigonon* species simultaneously: *A. cordatum* and *A.*

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cinerascens. For each they cited a specific specimen, gave a description and a brief discussion with locality data. Unfortunately in this article the descriptions (and later application) were switched and the names do not match the type specimens. Hence the name *A. cinerascens* has previously been applied to this taxonomic species, but upon examination of the types, it has become clear that this name is in synonymy with *A. leptopus,* and *A. cordatum* is the correct name for this species.

Meisner (1856) proposed *A. guatimalense* as a new combination for *Polygonum grandiflorum* Bertol., a later homonym and thus not legitimate. Many of Bertoloni's exsiccatae were thought to have been destroyed at the Bologna herbarium (BOLO) during World War II, but many types are extant, including that for *P. grandiflorum* (Cristofolini et al., 1987). Regrettably the type of *P. grandiflorum* does match the traditional application of the name, and thus *A. guatimalense* is now a synonymy of *A. cordatum.*

***Representative Specimens Examined—* Spontaneous.**

EL SALVADOR. Ahuachapán: [13°55'09"N, 89°50'55.5"W], 1923, *Padilla 499* (US). Usulután: El Triunfo, Jan 1893, *Donnell Smith 5063* (F, US). Sonsonate: Mpio. Izalco, near Izalco, 19 Mar 1922, *Standley 22177* (NY, US); Mpio. Nahuizalco, Nahuizalco, 20 Feb 1898, *Hartman 123* (F, NY, TEX).

GUATEMALA. Chiquimula: Valley of Río Chiquimula, 1.5 mi NE of Chiquimula, 21 Oct 1939, *Steyermark 30180* (F). El Progreso: km post 43 from Guatemala on CA-9, 8 Apr 1970, *Harmon & Dwyer 3476* (US). Escuintla: [14°18'3.5"N, 90°48'44.3"W], 14 Mar 1890, *Donnell Smith 1997* (US). Huehuetenango: Between Santa Ana Huista and woods of Rancho Lucas, Sierra de los Cuchumatanes, 26 Aug 1942, *Steyermark 51323* (F). Jutiapa: Laguna de Güija, Apr 1894, *Donnell Smith 6351* (F, US). Santa Rosa: Region of Capulín, S of Los Cerritos, road to

Alhumado, 7 Dec 1940, *Standley 79648* (F). Suchitepéquez: Mazatenango, Jan 1894, *Donnell Smith 6374* (F, NY, TEX). Zacapa: between km 40 & 45 on road to Zacapa, 21 Oct 1994, *Castillo 2282* (NY-2); Gualán, Feb 1912, *Cockerell 76* (US); near divide on road between Zacapa and Chiquimula, 9 Oct 1940, *Standley 73842* (F).

HONDURAS. Comayagua: Comayagua Valley, 10 Aug 1948, *Williams & Molina 14676* (F-2); Mpio. Meámbar, Meámbar, 17 Jul 1933, *Edwards 629* (F, US). Cortés: Along the stream El Encanto, Montaña La Cumbre, 5 Dec 1950, *Molina 3574* (F, US). Santa Bárbara: Río Bermejo, San Pedro Sula, Feb 1888, *Donnell Smith 5432* (F, US-2).

MEXICO. Chiapas: Mpio. Acala, Río Grijalva, 20 k north of Acala, 30 Jul 1981, *Breedlove 51898* (TEX); Mpio. Chicoasén, Mirador, 10 km SW of Chicoasén, 17 Sep 1988, *Reyes-Garcia 958* (MO); Mpio. Cintalapa, km 24 on hwy Mexico 190, between Rizo de Oro-Tapanatepec, 1 Aug 2002, *Alvarado 236* (MO); Mpio. Ocozocoautla, 500 m S of Rancho El Palmar, or 7 km W of Ocozocoautla, along hwy Mexico 190, 18 Jul 1990, *Reyes-Garcia 1969* (MO); between San Ricardo and Ocozucuatla, *Nelson 2979* (F, US); Mpio. Las Rosas, NE slope of Valley of Chiapas, 4 km NW of Las Rosas, 8 Aug 1965, *Mori 1032* (F, US); Mpio. Tapachula, los llanos Tapachula, near beach, 12 Dec 1948, *Matuda 18520* (F); Mpio. Tonalá, Arista, 20 Dec 1947, *Matuda 17322* (F, NY); Mpio. Villacorzo, 4.5 km W of Sierra Moreno, 10 Jul 2004, *Calonico 25480* (MO). Guerrero: Mpio. Tecpán de Galeana, San Luis de la Loma, Nov 1937, *Hinton et al. 10870* (F, NY, US); Mpio. La Unión, Carretera Ixtapa-Playa Azul, 3 km SE de la desviación a La Unión, 23 Oct 1977, *Ladd et al. 280* (F). Oaxaca: Dto. Ixtlán, near Comaltepec, Jul 1894, *Nelson 924* (US); Dto. Jamiltepec, El Churro del Santo, 12 Oct 1921, *Conzatti 4438* (US); Dto. Juchián, Asunción Ixtaltepec, 21 Nov 1998, *Perez-Garcia 1371* (MO); Dto. Tehuantepec, km 339 of hwy from Salina Cruz-Huatulco, 15 Aug 2007, *Burke 34 & Pale* (BH); road to San Pedro Huamelula, winding through hills off main hwy 200, 15 Aug 2007, *Burke 36*

& Pale (BH); 3 km sobre el camino a San Mateo del Mar, 27 Nov 1986, *Garcia et al. 2806* (MO, NY); Dto. Tuxtepec, Chiltepec, summer 1940, *Martinez-Calderon 238* (TEX, US); Dto. Yautepec, Yautepec, km 122 of hwy Oaxaca-Tehuantepec, 24 Sep 2001, *Sales 3997* (TEX). Tabasco: Mpio. Huimanguillo, Rancho El Limón, 6 km from the intersection with the railroad, Dec 1983, *Ventura 20844* (NY). Veracruz: Mpio. Actopan, Estación biologica El Morro de la Mancha, 8 Aug 2007, *Burke et al. 3* (BH); Mpio. La Antigua, Loma Iguana, 26 Aug 1987, *Zamora 574* (NY); Mpio. Chicoasén, 3 km from Chichoasén, 8 Aug 2007, *Burke et al. 7* (BH); Mpio. Coatepec, Carretera Jalcomulco-Tuzamapan, 9 Aug 2007, *Burke 15 & Avendaño* (BH); Mpio. Emiliano Zapata, Dos Ríos, Cerro Gordo, 12 Oct 1970, *Ventura 2582* (F), 8 Oct 1971, *Dorantes 360* (F, MO-2); Mpio. Paso de Ovejas, near Paso Mariano, hwy 140 to Veracruz, 9 Aug 2007, *Burke 11 & Avendaño* (BH); Mpio. San Andrés Tuxtla, Laguna Encantada, 27 Jul 1973, *Gomez-Pompa 5107* (NY, TEX), 24 Aug 1953, *Dressler & Jones 167* (F, MO, NY, US); Mpio. Xalapa, Volcancillo, 4 km SW de Rafael Ramirez, 26 Sep 1972, *Dorantes et al. 1648* (F). Yucatán: between Pixoy and Valladolid, 14 Nov 1985, *Ucan 4352* (NY, TEX).

Cultivated.

MEXICO. Veracruz: Mpio. Huatusco, side of road from Huatusco-Xalapa, 17 Aug 2007, *Burke 46 & Pale* (BH).

3. ANTIGONON PLATYPUS Hook. & Arn., Bot. Beechey Voy. 309. 1838. —TYPE: MEXICO. Oaxaca: Tlacolola, Aug 1834, *Andrieux 117* (holotype: K!; isotype: P!). Fig. 4.10.

Antigonon flavescens S. Watson, Proc. Amer. Acad. Arts 22: 446. 1887. —TYPE: MEXICO. Jalisco: Chalapa, among hills, *Palmer 722* (holotype: GH!, isotypes: BM, K!, MO!, NY!, P!, US!)

Plant climbing to 2 m, indument puberlent to pilose on younger axes, glabrate to puberlent on older axes, trichomes 0.1–0.3 mm long, white or brown. Stems 1.6–3.6 mm diameter, pentagonal to bluntly pentagonal in cross section, greenish-brown to brown; axillary tendrils 3.1–13.5 cm. Ocrea 0.5–2.9 mm long. Petiole 0.8–3.4 (–6.2) cm, winged ½–¾ (entire) length, puberlent to pilose; lamina 3.3–20.5 cm long, 1.5–12.7 cm wide (L:W ratio 1.0–2.3), deltoid or cordate (ovate), basally cordate or truncate, decurrent along petiole, apically acute or acuminate and mucronate, marginally entire or sinuous (rugose), occasionally ciliate, adaxially green, puberlent or sparsely hispid, often with salt-secreting glands, abaxially green or light green, pilose along main veins (pilose or velutinous on lamina), trichomes 0.1–0.2 mm, stiff, white. Secondary inflorescence axes 4—15 cm long, primary inflorescences 3.7–15.5 mm apart, rarely subtended by tendril, composed of (1–)2–4 (–6) flowers; bract 1.3–3.1 mm long, subulate, apically acuminate to long-acuminate and cirrose. Pedicel 0.8–3.1(–4.4) mm at anthesis, minutely pilose; bracteole translucent, apically acuminate to long-acuminate (cirrose), marginally entire. Flower aestivation quincuncial with entire (undulate) perianth margin; stipe 1.0–5.3 mm at anthesis, winged to 1.5 mm, minutely pilose to moderately pilose. Perianth 4.1–8.2(–9.3) mm long, white or light green, adaxially not glandular; hypanthium 0.3–1.1 mm (ca. 5-15% of perianth length); outermost tepal 3.5–8.2(–9) mm long, 2.0–7.0 mm wide, ovate to orbicular, basally cordate, apically acute and mucronate; innermost tepal 3.4–7.0 mm long, 1.2–2.5(–3) mm wide, lanceolate or elliptical. Stamens covered with stipitate glands, especially on filaments; filaments equal or 2 different lengths within each flower, 1.5–3.8 mm long, white, pink, or green (purple), connate in a column 0.6–1.9 mm, with dentate appendages; anthers 0.5–0.7 mm long, yellow. Gynoecium green or pink, drying purple; ovary 0.8–2.1 mm; style ca. 0.6–1.5 mm; stigma 0.3–0.5 mm, pink or yellow. Diaspore stipe 2.0–7.3 mm; perianth white, green or brown, outermost

tepal 8.6–16.6 mm long, 3.9–14 mm wide (L:W ratio 1.1–2.3), elliptical or ovate, basally cordate (reniform), innermost tepal 8.9–12.3 mm long, 2.2–4.5 mm wide, lanceolate (conchate, linear); achene 7.6–9.3 mm, trigonous, light brown to brown, apically triangular, basally terete, pericarp papery. Seed 3–6 mm, subglobose, brown or black.

Phenology— Can flower year round, mostly Aug.-Oct. Fruiting mostly in Oct.-Nov.

Local name and uses—"Coamecatl": Chiapas, Mexico. **"**Mata cuyo": Oaxaca, Mexico. "San Miguelito": Jalisco, Mexico. No documented uses.

Distribution— Native distribution along the Pacific and Atlantic slopes and plains of Mexico and Guatemala: Guatemala (Chiquimula), Mexico (Chiapas, Colima, Guerrero, Jalisco, México, Michoacán, Oaxaca, Querétaro, Veracruz)(Fig. 4.11); mostly thickets in coastal plain, also secondary forest and tropical deciduous forest; 0–1250 m.

Discussion— Antigonon platypus can be distinguished from the other *Antigonon* species primarily based on its white flowers and dilated petiole. Although there is a white-flowered morph of *A. leptopus* common in cultivation, these plants do not have a dilated petiole as in *A. platypus.* This species is a low growing, common plant along the Pacific coast of Mexico, though likely less common now due to habitat destruction for coconut plantations.

Figure 4.10. Antigonon platypus A. Leaf. B. Inflorescence axis. C. Flower. D. Perianth in fruit. E. Achene. Illustration from Ewing (1982), based on living specimens grown by her at Indiana University from seed collected in Oaxaca, Mexico. Reproduced with permission.
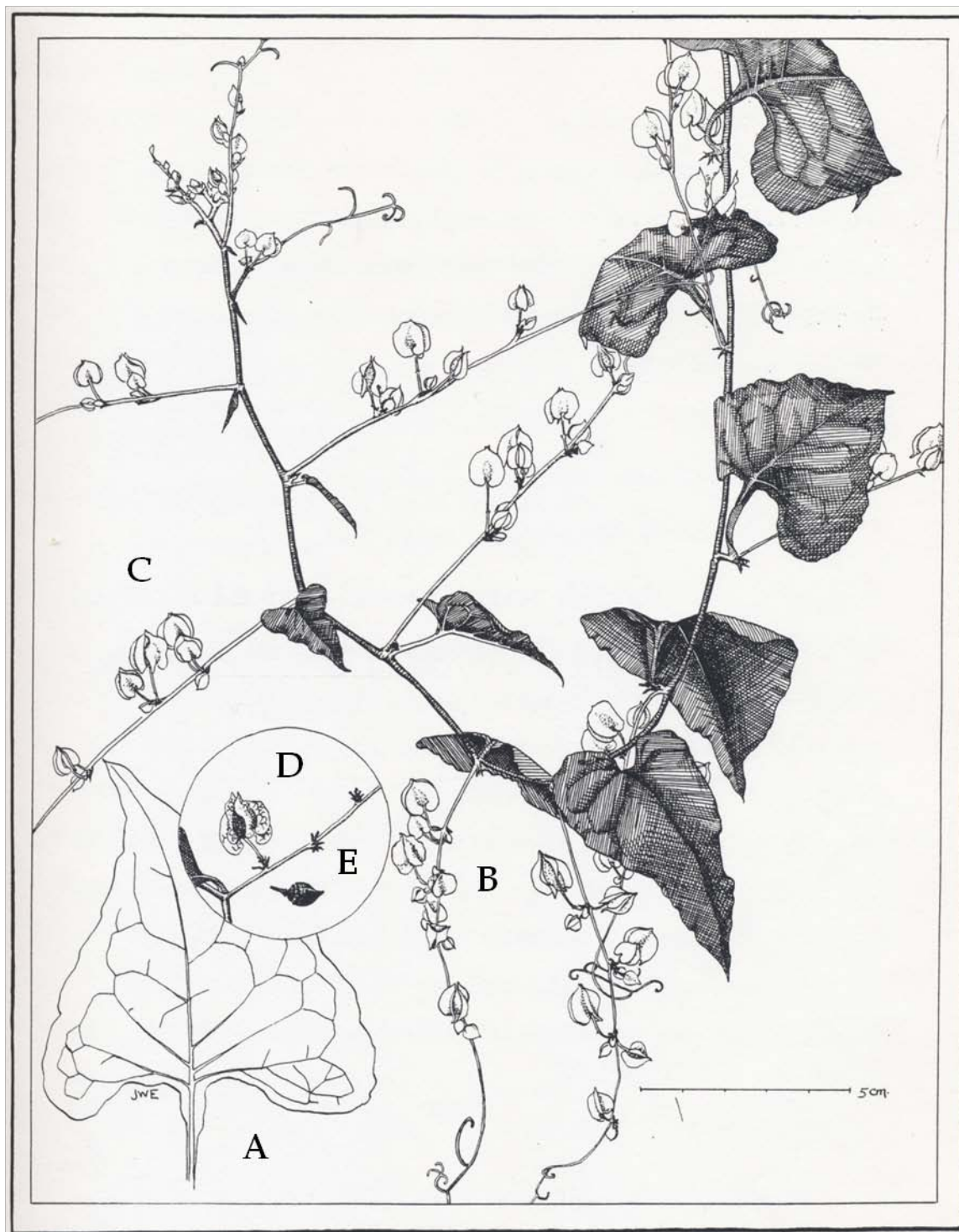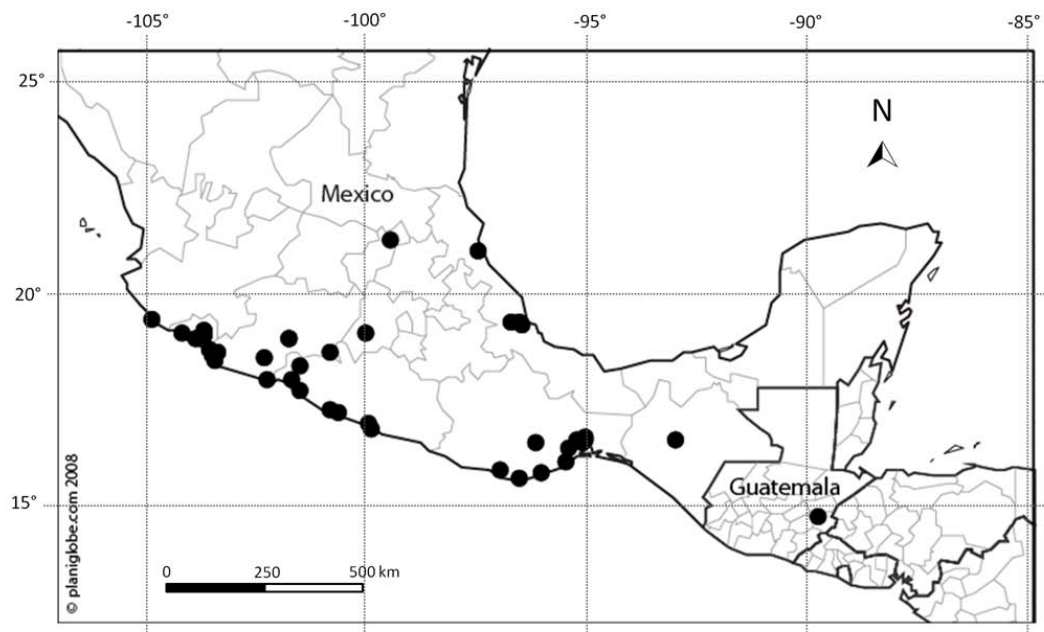
Figure 4.11. Geographic distribution of *Antigonon platypus.* Spontaneous collections have filled circle (●). No collections were cultivated.

Antigonon platypus was described by Hooker & Arnott (Hooker et al., 1838) in a footnote for *A. leptopus,* but has not been applied as a species name, likely due to the equivocation of the wording. They state that there are probably three entities from the collections of Andrieux and from Captain Beechey's Voyage, but are not sure if *A. platypus* is a good species, even though they provide the diagnosable character of winged petiole base or 'footstalk' (hence *leptopus* 'narrow foot' and *platypus* 'wide foot') to distinguish the two. Following the criteria of Article 34.1 of the ICBN (McNeill et al., 2006), I interpret Hooker and Arnott as expressing doubt to the taxonomic status of *A. platypus,* but nonetheless accept it, and is thus validly published.

Representative Specimens Examined— **Spontaneous.**

GUATEMALA. Chiquimula: 1.5 mi NE of Chiquimula, *Steyermark 30103* (F).

MEXICO. Chiapas: Mpio. Acala, Río Grijalva, 10 km S of Highway 190, along the road

to Acala, *Laughlin 2645* (F). Colima: Mpio. Manzanillo, como a 50 m del Ejido Nuevo

Cuyutlan, *Vigueras 20* (NY); Mpio. Tecomán, 5-10 mi N of Tecomán along highway, *Thompson*

& Fields 322 (TEX); Mpio. Armería, Armería, *Moldenke 1723* (TEX); Mpio. Colima, 7 mi S of

Colima, *Johnson 38473* (MO). Guerrero: Mpio. San Miguel Totolapan, in San Luis de la Loma,

Burke 131 (BH); Mpio. Acapulco de Juárez, between Acapulco and Pie de la Cuesta,

MacDaniels 218 (F); road to Yetla, off of coastal road from Zihuatanejo-Acapulco, *Burke 133*

(BH); Mpio. Zihuatanejo de Azueta, 3 km al NW del desvio a El Camalote, *Soto et al. 5925*

(MO, NY); Mpio. La Unión de Isidoro Montes de Oca, 14 km al N de La Unión, carretera a

Coahuayutla, *Soto et al. 6045* (MO, NY); Mpio. Atoyac de Álvarez, Atoyac, *Hinton 10938* (NY,

US); Mpio. Tecpán de Galeana, terracería a Sta. María y La Hacienda, 3-6 km N de Tecpán,

Koch et al. 79273 (NY). Jalisco: Mpio. La Huerta, Cuitzmala, Cerro Costero, *Castillo et al. 5243*

(TEX). Mexico: Mpio. Temascaltepec, Temascaltepec, *Hinton 4726* (US). Michoacan: Mpio.

Lázaro Cárdenas, Playa Azul, in town, *Burke 128* (BH); Mpio. Aquila, 11 km from turn-off to

Osutla, *Burke 124* (BH); near San Telmo, Hwy 200, *Burke 123* (BH); Las Brisas, *Guerrero 1318*

(TEX); Mpio. La Huacana, en la carretera La Huacana, en los márgenes de la presa Zicuiran,

Soto et al. 1600 (MO, NY); corner of la Presa Zicuiran, close to La Huacana, *Rzedowski 37400*

(MO); Mpio. Tumbiscatío, 1 km to the SW of the intersection of Tumbiscatío, hwy Nueva Italia-

Playa Azul, *Soto 3585* (MO); Mpio. Huetamo, en Cuitzeo, *Soto et al. 4310* (MO, NY); Mpio.

Coahuayana, on the hwy Cuatro Caminos-Playa Azul, intersecion with Coahuayana, *Soto et al.*

4487 (MO, NY). Oaxaca: Dto. Juchitán, Road to La Mata, off of hwy Matias Romero-Salina

Cruz, *Burke 19* (BH), *Burke 20* (BH); Ixtaltepec, on road to Ixtepec, outside town, *Burke 25*

(BH); Dto. Tehuantepec, St. Domingo Chihuitan, on road from Ixtepec, *Burke 26* (BH); Puente

Morrizal, close to Morro Mazatlan, *Burke 32* (BH); Mpio. San Pedro Huamelula, San Isidro

Chacalapa, 2 km N de la desviación de la carretera costera, *Salas 2556* (NY); Cerro Guiengola,

11 km NW of Tehuantepec, *Campos 3755* (MO); Dto. Pochutla, Barra de la Cruz, off of Hwy

200, *Burke 27* (BH); Puerto Angel, a few km W of town, *Burke 39* (BH); Dto. Yautepec, Mpio.

San Carlos Yautepec, 6.4 km to the SE of el Camarón, hwy to Tehuantepec, *Torres 12579* (MO).

Querétaro: Mpio. Jalpan, S of Tanchanaquito, Las Adjuntas de Los Ríos, *Lopez 762* (TEX).

Veracruz: Mpio. Alto Lucero, alrededores de Laguna Verde, *Dorantes et al. 5236* (F); Mpio.

Emiliano Zapata, E. Zapata Carrizal a orillas del Río Conejo, *Ortíz 1037* (MO); Mpio. Paso de

Ovejas, Paso de Ovejas-Paso de Mula, *Rosas 636* (F); Mpio. Puente Nacional, Puente Nacional,

cerca del Puente, *Ventura 2642* (NY, US).

4. ANTIGONON LEPTOPUS Hook. & Arn., Bot. Beechey Voy. 308-309, pl. 69. 1838. *Corculum*

   leptopus (Hook. & Arn.) Stuntz, Bull. Bur. Pl. Industr. U.S.D.A. 282: 86. 1913. ―TYPE:

   MEXICO. Nayarit: Tepic., 1825-1828, *Lay & Collie s.n.* (lectotype: *Hook. & Arn. pl. 69*). Fig.

   4.12.

Antigonon cinerascens M. Martens & Galeotti, Bull. Acad. Roy. Sci. Bruxelles x: 354. 1843.

   ―TYPE: MEXICO. [Nayarit]: San Blas, Feb 1840, *Galeotti 462* (holotype: BR- scanned

   image! barcode 528784, isotypes: P!, W- scanned image!)

Plant climbing to 1.5– 5(–15) m, indument glabrate to pilose on younger axes, glabrate to pilose

on older axes, trichomes 0.1–0.3 mm long, white, tan or brown. Stems 1.5–3.3 mm diameter,

pentagonal in cross section, reddish-brown, brown or tan; axillary tendrils 4.0–17 cm. Ocrea

0.5―5.0 mm long. Petiole 0.6–3.1 (–5.2) cm, not winged, hispid to moderately pilose (densely

pilose); lamina 3.3–11.5(–15.5) cm long, 2.5–8.1(–10) cm wide (L:W ratio 0.9–2.3), usually

cordate, also lanceolate, ovate, sagittate or deltoid, basally cordate, not decurrent along petiole,

apically acute or acuminate, mucronate, margin sinuous or rugose, ciliate, adaxially green or

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dark green, puberlent or hispid, occasionally with salt-secreting glands, abaxially green (light green, cinereous), glabrate to densely pilose, trichomes 0.1 mm and stiff or 0.2-0.3 mm and lax, white or brown. Secondary inflorescence axes 5.6–18 cm long, primary inflorescences 4.5–18 mm apart, not subtended by tendril, composed of (1–)2–4(–5) flowers; bract 0.9–3.5 mm long, subulate, apically acuminate (cirrose). Pedicel 1.2–4.1 mm at anthesis, minutely pilose to densely pilose; bracteole translucent or pink, apically acuminate to long-acuminate, marginally entire. Flower aestivation quincuncial with entire (undulate) perianth margin; stipe 2.3–6.5(–11.4) mm at anthesis, terete or winged to 1.5 mm, minutely pilose to moderately pilose. Perianth 6.4–11.1(–14.5) mm long, pink or magenta (white), adaxially not glandular; hypanthium 0.4–2.0 mm (ca. 5-11.5% of perianth length); outermost tepal 5.5–10.6(–12.6) mm long, (2.6–)3.3–8.3 mm wide, ovate to orbicular, basally cordate, apically round, acute or mucronate; innermost tepal 4.7–9.8 mm long, (1.3–)2–3.9(–6.2) mm wide, oblong, elliptical or ovate. Stamens covered with stipitate glands, especially on filaments; filaments 2 different lengths within each flower, 2.4–4.8 mm long, pink, connate in a column 0.7–2.4 mm, with dentate appendages; anthers 0.5–1.0 mm long, yellow (orange, red). Gynoecium green or pink, drying purple; ovary 0.8–2.3 mm; style ca. 1–2 mm; stigma 0.3– 0.6 mm, pink or yellow. Diaspore stipe 2.2–14.8 mm; perianth pink to magenta (green, brown); outermost tepal 11.4–19.2 mm long, 6.1–14.5 mm wide (L:W ratio 1.2–2.2), ovate (orbicular), base cordate, innermost tepal 9.6–15.0(–18.2) mm long, 2.6–6.2 mm wide, elliptical or lanceolate, conchate; achene 6.2–11.2 mm, subglobose to trigonous, light brown to brown, apically triangular, basally terete or bluntly 3-lobed, pericarp papery. Seed 3.4–8.4 mm, subglobose (trigonous), brown, black or red.

Figure 4.12. Antigonon leptopus. A. Leaf. B. Inflorescence axis. C. Flower with perianth. D. Staminal column. E. Anthers. F. Gynoecium. G. Perianth in fruit. H. Achene. I. Magnification of ocrea scar. Illustration accompanying Hooker and Arnott's description of *Antigonon leptopus* (pl. 69), also the lectotype.

TAB. LXIX.

E

1 mm

1 cm

C

B

I

F

1 mm

A

Antigonon leptopus.

G

1 cm

H

5 mm

D

1 mm

Swan Sc.
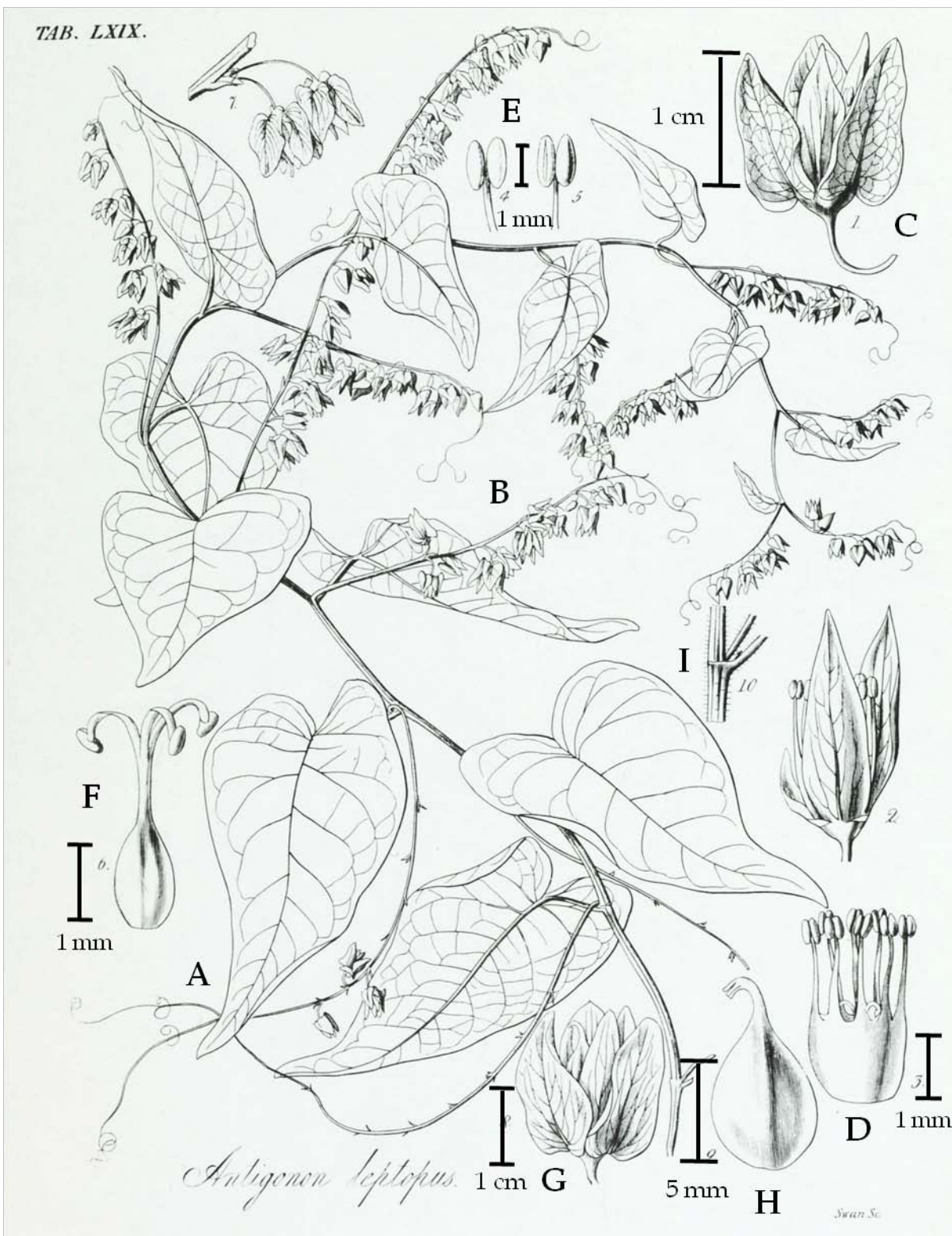
Phenology— Flowering year round, especially when cultivated. In native range, flowering year round. Mostly fruiting in the latter part of the year.

Local name and uses—"Bellísima": Costa Rica, Honduras, Oaxaca, Sonora, Nicaragua, Panama. "Coamecate": Michoacán. "Colación": El Salvador. "Confite": El Salvador. "Confitillo": Honduras. "Coral vine": Guatemala, Sonora. "Corona": Tamaulipas. "Coronilla": Baja California Sur, Sinaloa. "(Flor de) San Diego": Veracruz, Yucatán. "San Miguel(ito)": Baja California Sur, Nayarit, Sinaloa, Sonora. Cultivated as an ornamental for its showy flowers and vigorous growth. In Sonora it is also used as decoration in churches, and the leaves are smoked in cornhusks (*Pennington 21, 255* [TEX]). The tuberous roots are said to be eaten in Sinaloa (*Tays s.n.* [US]) and Guatemala (Standley and Steyermark, 1946).

*Distribution—*Although the current distribution of this species is vast, the native distribution of *A. leptopus* is limited to the Pacific and Atlantic coastal plains of Mexico (Baja California Sur, Colima, Jalisco, Nayarit, Oaxaca, Puebla, Sonora, Sinaloa, Tamaulipas and Veracruz). The Pacific distribution likely extends south through Jalisco, as the collections in Guerrero and Michoacán are more sporadic, and the plant is not commonly found in natural areas there. On the Atlantic coast, the northern range likely begins north in Tamaulipas, through Veracruz and south to Puebla and the Tomellín Canyon region of Oaxaca. This species is common as an ornamental and roadside weed in other Mexican states and throughout Central America: Costa Rica (San José), El Salvador (Ahuachapán, San Salvador), Mexico (Campeche, Chiapas, Chihuahua, Durango, Guerrero, México, Michoacán, Nuevo Leon, Querétaro, Quintana Roo, San Luis Potosí, Yucatán), Guatemala (Chiquimula, El Progreso, Izabal, Petén, Quetzaltenango, Retalhuleu, Sololá), Honduras (Atlántida, Colón, Comayagua, Cortés , Francisco Morazán , Olancho, Valle), Nicaragua (Granada, Leon, RAAS), Panamá (Canal Zone, Chiriquí , Herrera, Los Santos) (Fig. 4.13); mostly in secondary forest, but occurs in many

habitats, including tropical deciduous forest ('selva baja caducifolia'), matorral, temperate forest ('selva mediana'), tropical forest ('bosque humedo'), thickets and pastures; 0–1500 m.

In addition to the aforementioned regions, *A. leptopus* is common throughout the Caribbean, and has been introduced across the tropics where it is found in cultivation and as a weed (Fig. 4.14, see exsiccatae for detailed distribution).
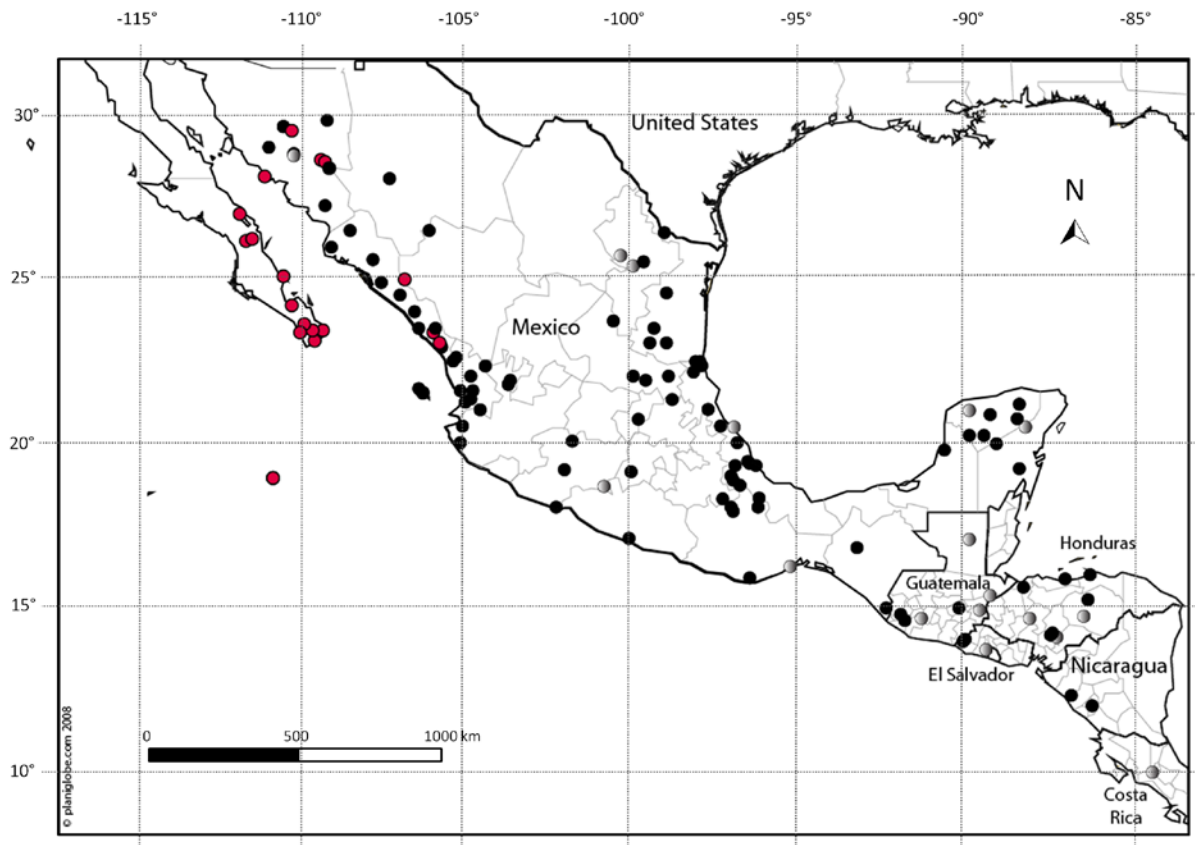

Figure 4.13. Geographic distribution of *Antigonon leptopus* in Mexico and Central America. *Antigonon leptopus* subsp. *leptopus* spontaneous collections have filled circle (●), cultivated collections have a gray gradient filled circle (◐). *Antigonon leptopus* subsp. *coccineum* spontaneous collections have pink filled circles (●).
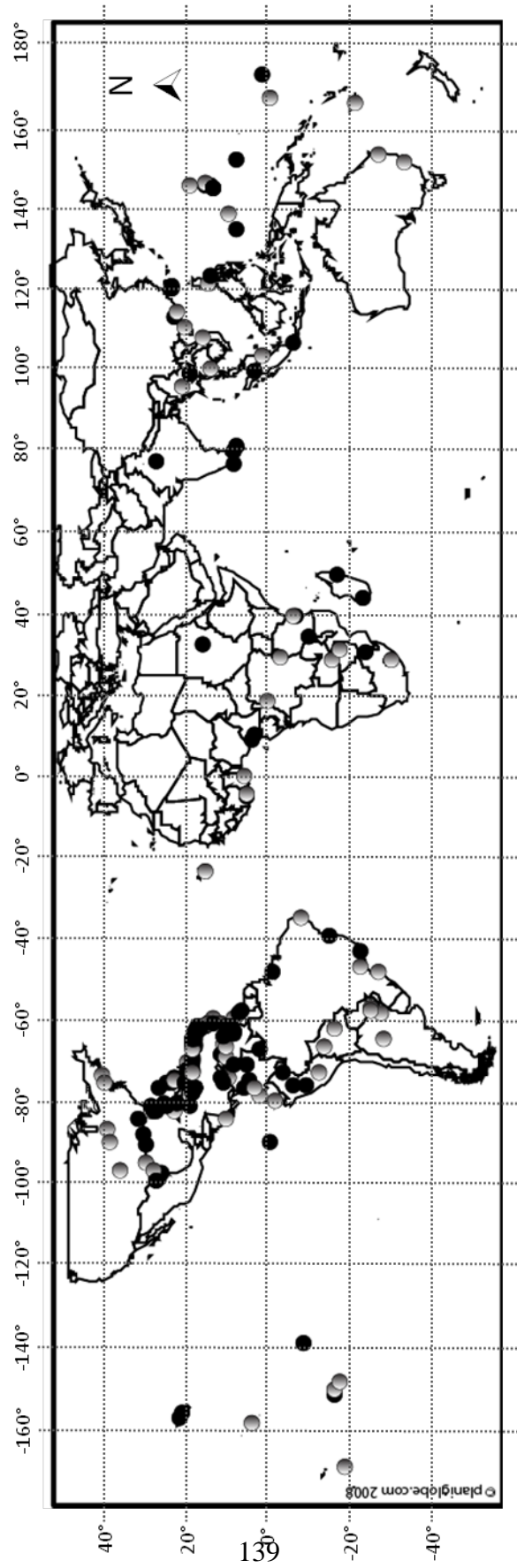
Figure 4.14. Global geographic distribution of *Antigonon leptopus,* excluding Mexico and Central America. *Antigonon leptopus* spontaneous collections have filled circle (●), cultivated collections have a gray gradient filled circle (◯).

Discussion—Antigonon leptopus is the most morphologically variable species in the genus. Flower color can be any shade of pink, and a white morph is common in cultivation. The leaves also have a quite variable shape, the petiole is usually terete, though can be winged (see hybrid discussion below). In general, *A. leptopus* can be distinguished from *A. platypus* by its pink flowers, terete petioles and cordate leaves. The flowers of *A. leptopus* can easily be distinguished from *A. amabile* or *A. cordatum* by the filaments which are formed into a column with dentate appendages instead of a shallow ring, and by the tepals which are much longer than wide in fruit.

Antigonon leptopus, though perhaps not the most attractive species in the genus, has been widely cultivated and naturalized across Mexico and Central America. The plant is prized for its vigorous growth, and its ability to flower year round with ample water availability. It grows in many habitats, but prefers sandy soils and does not tolerate shade. It has been introduced across the tropics, has subsequently become naturalized and now thrives as a weed, especially on tropical islands in the Caribbean and South Pacific.

KEY TO SUBSPECIES

1. Flowers white or pink, occasionally magenta; stems green, brown, tan or reddish brown, indumentum variable; habit variable, often high-climbing; bract subtending primary inflorescence apex acuminate, rarely cirrose; stipe length in fruit 2–9.5 mm; leaf abaxial surface glabrate to pilose on main and secondary veins, not leaf lamina; pantropical…………………………………………*Antigonon leptopus* subsp. *leptopus*

1. Flowers bright magenta to scarlet; stems deep reddish-brown or tan, densely pilose to velutinous, at least when young; habit low-growing or scrambling; bract subtending

primary inflorescence apex cirrose or acuminate; stipe length in fruit 6–15 mm; leaf abaxial surface glabrate to densely pilose, even on lamina, dull green; Baja California and adjacent islands, Sonoran desert…………… ………………*Antigonon leptopus* subsp. *coccineum*

ANTIGONON LEPTOPUS subsp. LEPTOPUS

Plant indument glabrate to densely pilose on younger axes. Stem reddish-brown, brown or tan. Ocrea 0.5–3.0 mm long. Petiole brown or dark brown (tan); lamina apically acute or acuminate, usually mucronate, abaxially hispid or pilose (glabrate), only on main veins, trichomes stiff (lax). Bract subtending primary inflorescence acuminate (cirrose) apically. Pedicel minutely pilose (moderately pilose). Perianth pink or magenta (white); hypanthium 0.4–1.35 mm (ca. 5-11.5% of perianth length). Diaspore stipe 2–9.5 mm; perianth pink (green, brown). Seed 3.4–6.0 mm, subglobose (trigonous), brown, black or red.

Representative Specimens Examined— **Spontaneous.**

ANTIGUA AND BARBUDA. Antigua: Parham, 26 Aug 1937, *Box 995* (US).

BAHAMAS. Cat Island: near Dumfries, 22 Oct 1967, *Byrne 372* (NY). Crooked Island: hills NE of Cabbage Hill, 22 Feb 1975, *Correll 44478* (F-2, NY). Central Abaco: Great Abaco, E side of Marsh Harbour, 16 Mar 1975, *Correll & Meyer 44716* (NY). Exuma: Hummingbird Cay, near cistern, Mar 1978, *Blair 4799* (MO, US).

BRAZIL. Bahia: Urucuca, Escola Media de Agropecuaria de Região Cacaueria Reserva "Gregorio Bondar", 20 May 1994, *Thomas et al. 10433* (NY). Pará: Belem, Mar 1929, *Dahlgren & Sella 566* (F). Rio de Janiero: Rio de Janiero, 20 Dec 1923, *Bailey & Bailey 267* (BH).

CAMEROON. South: area adjoining the Zenker Mansion, ca. 1 km SW of Bipindi, 15 Jan 1987, *Manning 1358* (MO).

CAYMAN ISLANDS (UK). Grand Cayman Island: Midland district, Bodden town, 2 Jun 1963, *Crosby 46* (TEX).

CHINA. Guangdong: Guangzhou, 29 Jun 1981, *Yip 365* (MO, NY).

COLOM BIA. Atlántico: Barranquilla, Puerto Colombia, 20 Apr 1974, *Plowman 3542* (US). Bolívar: Santa Catalina, Loma Las Puas, via Arroyo Grande a Las Canoas, 4 Feb 1987, *Cuadros 3290* (MO). Chocó: Quibdó, barrio Pan de Yuca, 24 Aug 1984, *Cordoba & Garcia 331* (MO). Casanare: Orocue, Río Meta, 3 Nov 1933, *Cuatrecasas 4418* (F). Cundinamarca: Poblado de Nariño, 15 Feb 1986, *Fernandez 5197 & Jaramillo* (MO). Magdalena: Río Manzanares, cerca de Santa Marta, 29 Dec 1948, *Giacometto 1058* (US).

CÔTE D'IVORE. Grand Lahou, sur le cordon lagunaire, 18 Oct 1986, *Gautier 505* (MO).

CUBA. Cienfuegos: Castillo de Jagua, 16 Sep 1895, *Combs 563* (F, MO, NY, US); Soledad, 3 Mar 1926, *Jack 4163* (US). Mayabeque: Canasi to Boca de Canasi, 18 Feb 1956, *Morton 10228* (US). Santiago de Cuba: Crucero de Firmeza, 9 Sep 1951, *Lopez 113* (US).

DOMINICA. St. Peter: between Coulibistri and Colihaut, 30 Jul 1964, *Wilbur et al. 8119* (F, MO, NY, TEX, US).

DOMINICAN REPUBLIC. La Romana: W side of Río Chavon, NW of Presa Chavon, 1.5 km N of La Romana-Presa Chavon road, 17 Nov 1980, *Mejia & Zanoni 9122* (MO, NY). Monte Cristi: Monción, *Valeur 255* (F, MO, NY, US). Peravia: Paso del Joba, 12 km NW of Bani, entry to La Monteria, 6 May 1981, *Mejia et al. 13237* (NY). Santo Domingo: Ciudad Trujillo, 1 mi W of city, 4 Nov 1945, *Allard 13038* (US).

ECUADOR. Galápagos: Santa Cruz Island, Graffer farm, 6 Mar 1960, *Leveque 33* (US).

EL SALVADOR. 13.5 mi E of Guatemala border, 1 Aug 1978, *Dziekanowski et al. 3211* (NY). Ahuachapán: 1923, *Padilla 571* (US).

EQUATORIAL GUINEA. Bioko Sur: Malabo, Luba, close to Finca Lawany, km 18, 27

Jul 1986, *Carvalho 2110* (NY).

FEDERATED STATES OF MICRONESIA. Chuuk: Truk-Moen [Weno], 20 Aug 1980, *Fosberg 60387* (US).

FRENCH POLYNESIA. Leeward Islands: Maupiti, E coast, Maupiti village, 23 Aug 1985, *Fosberg 64926* (US). Marquesas Islands: Ua Huka, Village of Vaipae'e, 30 Jun 1997, *Perlman 15867* (NY).

GUADELOUPE (FRANCE). Basse-Terre island: Gourbeyre, 1892, *Duss 2182* (F, NY, US).

GUAM. Sumay, 7 Apr 1936, *Bryan 1086* (NY, US); Pipeline Rd. in Chaot River Ravine, 26 Jun 1980, *Fosberg 59663* (US); Orote Peninsula, 18 Mar 1946, *Moore 331* (US); ranch near Finegayan, 29 Aug 1954, *Moran 4488* (US).

GUATEMALA. El Progreso: San Augustín Ac., 7 Jun 2003, *García et al. 667* (MO). Quetzaltenango: San Carlos Miramar, 19 Mar 1921, *Rojas 139* (US). Retalhuleu: Retalhuleu, 27 Feb 1939, *Standley 66776* (F).

GUAYANA. Demerara-Mahaiaca: Georgetown, S. Rumveldt Park, Houston Estate, 21 Sep 1986, *Pipoly et al. 8699* (NY, TEX, US). Mahaica-Berbice: Arbary River mouth and along canals, 28 Mar 1987, *Pipoly et al. 11254* (NY, TEX, US).

HAITI. Nippes: Miragoane , 20 Sep 1927, *Eyerdam 543* (US). Nord: Chaine Bonnet Leveque, next to the Palacio Sans Souci en Milot, 19 Nov 1982, *Zanoni et al. 24475* (MO, NY). Nord-Ouest: vicinity of Jean Rabel , 7 Feb 1929, *Leonard & Leonard 12753* (NY, US). Ouest: Plaine Cul-de-Sac, north bank of lake Etang /Trou Caiman, 27 Jan 1984, *Zanoni et al. 28758* (NY).

HONDURAS. Atlántida: La Ceiba, 1925, *van Severen 31* (US). Colón: Trujillo, banks of Río Cristales, 28 Dec 1980, *Saunders 757* (F, NY, TEX). Cortés: Parque infantil Río Piedras, 3

km al NW de San Pedro Sula, 27 Aug 1988, *Ortega 9* (F). Francisco Morazán: Colonia

Miramonte, 24 May 1985, *Rodriquez s.n.* (NY); Hatillo, 15 km NE of Tegucigalpa, 15 Feb 1985,

Sherman 163 (NY). Valle: alrededores de San Lorenzo, 28 Apr 1984, *Paredes 144* (NY).

INDIA. Kerala: Trivandrum, 16 Jan 1933, *Kurkiakose s.n.* (NY). Rajasthan: Bharatpur,

Aug 1953, *Koran s.n.* (US).

INDONESIA. Java: Depok, 1932, *Boenbel 51* (MO, NY). Sumatra: Air Joman, Asahan,

E of Serbangan, Jul 1935, *Boeea 8253* (NY, US).

JAMAICA. Cornwall Co.: St. James Parish, Montego Bay, 28 Mar 1920, *Maxon & Killip

1660* (F, US); St. Elizabeth Parish, Balaclava, 11 Mar 1927, *Orcutt 696* (MO). Middlesex Co.:

St. Catherine Parish, near Spanish Town, 30 Aug 1908, *Britton 3071* (NY). Surrey Co.: Kingston

Parish, Causeway bay near Kingston, Jan 1974, *Katsuro 54* (TEX); St. Andrew Parish, Halfway

Tree, 27 Jul 1939, *Philipson 505* (NY); St. Thomas Parish, between Easington and Llandewy, 24

Nov 1963, *Proctor 24240* (TEX).

KIRIBATI. Betio Island, 9 Mar 1968, *Adair 132* (US).

MADAGASCAR. Analanjirofo: along rte. 5 from Fenerive [Fenoarivo] to Maroantseta ,

28 Feb 1975, *Croat 32538* (MO). Atsimo-Andrefana: 8-16 km E of Tulear [Toliara] on road to

Tananarive [Antananarivo], 7 Feb 1975, *Croat 30983* (MO).

MEXICO. Campeche: Mpio. Campeche, China town center, 17 Apr 2008, *Burke et al. 89*

(BH, CICY); Mpio. Hopelchén, 2 km antes de llegar al límite de Yucatán, 29 Jul 1985, *Chan

5585* (F). Chiapas: Mpio. Tapachula, 20 de Noviembre, 30 Jul 1987, *Ventura & Lopez 4601*

(TEX); Mpio. Tuxtla Gutiérrez, en sitios de Tuxtla Gutierrez, 7 Oct 1971, *Breedlove 20024*

(TEX). Chihuahua: SW part of state, Aug 1885, *Palmer 46* (NY-2). Durango: Mpio. Pueblo

Nuevo, alrededores de Agua Caliente, ladera de cerro, 12 Oct 1983, *Fernandez 1947* (MO, NY).

Guerrero: Mpio. Coyuca de Benítez, W of Coyuca, on main road into town before bridge, 16

Aug 2008, *Burke et al. 132* (BH, MEXU). Jalisco: Mpio. Bolaños, Bolaños, 10 Sep 1897, *Rose 2848* (US); Mpio. Cabo Corrientes, 30 km S of Puerto Vallarta, Puente La Puerta, 6 Apr 1994, *Yanega 94579* (TEX); Mpio. Chapala, at base of Cerro de Tucuan, 10 Jul 1999, *Holmes 10278* (TEX-2); Mpio. Tomatlán, Playón de Mismaloya, cerca del estero, 11 Mar 1988, *Vigueras et al. 8* (NY); Mpio. Villa Guerrero, 41 km SW de Villa Guerrero, camino a Chimaltitlan, 18 Oct 1983, *Lott et al. 2017* (MO). México: Mpio. Tejupilco [Mpio. Temascaltepec], San Lucas del Maíz, 2 Feb 1933, *Hinton 3330* (NY). Michoacán: Mpio. La Huacana, off hwy Uruapan-Nueva Italia, road to El Huecho, 13 Aug 2008, *Burke et al. 110* (BH, MEXU); Mpio. Lázaro Cárdenas, Playa Azul, 15 Aug 2008, *Burke et al. 127* (BH, MEXU). Nayarit: Mpio. Acaponeta, near Acaponeta, 12 Apr 1910, *Rose et al. 14453* (NY); Mpio. Compostela, 20 mi W of Compostela, 26 Dec 1955, *Graber 13* (TEX); Juan Sánchez, 6 Apr 1897, *Nelson 4165* (US); Mpio. Jesús María, Cañón de Jesús María, ter. de Tepic, 4 Sep 1905, *Goldsmith 155* (F, MO, NY, US); Mpio. Ruiz, 4 km al E de El Venado, camino a San Miguel Zapote, 10 Sep 1985, *Tellez 9201* (MO); Mpio. San Blas, San Blas, 7 Apr 1980, *Balogh 1046* (US); Maria Madre Island, Tres Marías islands, 12 May 1897, *Maltby 108* (US-2); Maria Magdalena, Tres Marías islands, 27 May 1897, *Maltby 170* (NY); Mpio. Tecuala, Highway 15, 68 mi S of Mazatlán, 7 Feb 1960, *Carlson 3652* (F); Mpio. Tepic, Tepic, 22 Mar 1890, [collector unknown] (F #354713). Nuevo León: Los Ramones, camino a la hacienda El Carrizo al S de Los Ramones, [sin dat.], *Villarreal 7518* (TEX). Oaxaca: Dto. Cuicatlán, Cuicatlán, close to zócalo, 17 Aug 2007, *Burke 42 & Pale* (BH); Dto. Pochutla, N of Pochutla on hwy 175, 3 km N of gas station, 16 Aug 2007, *Burke 40 & Pale* (BH); Dto. Teotitlán, Tecomavaca, 17 Aug 2007, *Burke 44 & Pale* (BH); Dto. Tuxtepec, Chiltepec, 27 Mar 1967, *Martínez-Calderón 1337* (MO, TEX). Puebla: Mpio. San Jose Miahuatlán, tributarios del Río Calapa al S de San Jose Miahuatlán al E de carr. de cuota Tehuacan-Oaxaca, 4 Jul 1994, *Panero 4009* (NY, TEX). Querétaro: Mpio. Ezequiel Montes,

Ciervo a San Juan, 27 Aug 1905, *Altamirano 1749* (US). Quintana Roo: Mpio. Felipe Carillo Puerto, Felipe Carillo Puerto, 12 Apr 2008, *Burke et al. 69* (BH, CICY). San Luis Potosi: Mpio. Cuidad Valles, Valles, 17 Jun 1956, *Rzedowski 7782* (TEX); Mpio. Matahuala, Santa Cruz, ca. 1841, *Liebmann 699* (US-2); Mpio. Rioverde, Rioverde, Nov 1910, *Orcutt 6937* (TEX); Mpio. San Antonio, San Antonio, 7 Sep 1978, *Alcorn 1660* (TEX); Mpio. Tamazunchale, Tamazunchale, 14 Jul 1937, *Edwards 566* (F, MO, TEX). Sinaloa: Mpio. Ahome, Guadalupe, 18 Apr 1910, *Rose et al. 14721* (US); Mpio. Culiacán, 33 km NW of Culican, along rte. 15, 11 Jul 1966, *Cruden 1043* (TEX); Mpio. El Fuerte, Near Fuerte, 26 Mar 1910, *Rose et al. 13496* (NY, US); Mpio. Elota, 9 mi S of Elota, 24 Dec 1954, *Philbrick 395* (BH); Mpio. Escuinapa, Escuinapa, 17 Nov 1919, *Maltby 1281* (US); Mpio. Mazatlán, along hwy 15 de cuota, 19 km N of Mazatlán, 24 Aug 1995, *Snow 6618* (MO); Mpio. Mocorito, Mocorito, 27 Sep 1923, *Collins & Kempton 62* (US); Mpio. Navolato, Santa Fé (N of Villa Angel Flores), 1922, *Ortega 4692* (US); Mpio. San Ignacio, Los Labrados, 13 Oct 1926, *Mexia 915* (F, MO, NY, US). Sonora: Mpio. Carbó, wash between Carbó and Horcasitas, 17 Sep 1934, *Wiggins 7285* (F, US); Mpio. Granados, Granados, 18 Nov 1890, *Hartman 227* (NY, US); Mpio. Hermosillo, 16 mi S of Hermosillo on road to Guaymas, Sep 1941, *Wiggins & Rollins 202* (MO, NY, TEX, US); Mpio. La Colorada, Torres, 10 Jun 1897, *Maltby 178* (US); Mpio. Navojoa, Cerro Prieto, 15 km al NE de Navojoa, 2 Oct 1983, *Torres 3901* (MO); Mpio. San Miguel de Horcasitas, 18 mi SE of Carbó, 17 Sep 1934, *Shreve 6692* (MO); Mpio. Yécora, ca. 1.6 km NW of Curea, 12 Sep 1999, *Van Devender 99478* (TEX). Tamaulipas: Mpio. Altamira, Altamira, 21 Sep 1975, *Castillo 275* (TEX); Mpio. Jaumave, 80 mi S of Padilla on rte. 101, 6 Jun 1967, *Stuessy 804* (TEX); Mpio. Ocampo, El Progresso, 18 km NW of Ocampo, 23 Aug 1941, *Stanford et al. 1096* (NY); Mpio. San Carlos, 4 km al O de San Carlos en el camino al Diente, 16 May 1994, *Martínez & Martínez 2337* (TEX); Mpio. Tampico, Tampico, 28 Jul 1946, *Fisher 46195* (BH); Mpio. Victoria, cause

del Río San Marcos, 24 Sep 1985, *Jimenez 338* (MO); Mpio. Xicoténcatl, Rancho Calabazas, on Río Sabinas, across from Azteca, 3 mi W [actually east] of rte. 85, ca. 20 mi N of Ciudad Mante, 30 Mar 1975, *Harriman et al. 10837* (F). Veracruz: Mpio. Coetzala, limites con Omealca, 16 Jul 1976, *Vazquez 453* (F, NY); Mpio. Fortín, Fortín de las Flores, 12 Dec 1985, *Nee and Andrés 32105* (F, NY); Mpio. Misantla, Santa Cruz de Hidalgo, carr. Misantla-Martínez de la Torre, 26 Apr 1976, *Hernández et al 149* (F, NY); Mpio. Pánuco, Buenavista, tramo carretera Panuco-Tampico a 6 km de Panuco, 4 Aug 1986, *Gutiérrez 1951* (TEX); Mpio. Papantla, brecha González Ortega, 1 km antes de Plan de Palmar, 10 Nov 1981, *Cortés-Vázquez 32* (MO); Mpio. Paso de Ovejas, camino terracería La Vibora-Faisan, 1 km del Faisan, 29 Oct 1987, *González 134* (MO); Mpio. Plan del Río, Puente Nacional, 26 Dec 1971, *Dorantes 447* (MO); Mpio. Temapache, San Miguel, 1 km del Alamo, 29 Oct 1977, *Monroy et al. 102* (TEX); Mpio. Tezonapa, E de la colonia El Silvato, 28 Feb 1986, *Robles 362* (F); Mpio. Tlapacoyan, Tijeretilla, 31 May 1981, *Pedraza & Rodriguez 278* (F); Mpio. Totula, Mata Oscura, hwy 180, 9 Aug 2007, *Burke 9* (BH); Mpio. Tres Valles, Tres Valles, 14 Oct 1967, *Martínez 1522* (F, MO, NY, TEX); Mpio. Veracruz, Veracruz, 0.1 km adelante de Panteón de Santa Fé, 1 Jun 1988, *Zola & Luna 2688* (MO). Yucatán: Mpio. Kantunil, cerca a Kantunil, 10 Apr 2008, *Burke et al. 47* (BH, CICY); Mpio. Tekax, Tekax, [sin dat.], *Gaumer 2191* (F, MO, US); Mpio. Tizimin, Tizimin, sobre carr. a Valladolid, 22 Jan 1986, *Cabrera 10799* (NY); Mpio. Tzucacab, near border with Quintana Roo, 4 km SE of Kambuul, 13 Apr 2008, *Burke et al. 78* (BH, CICY); Mpio. Valladolid, Pixoy – Valladolid, 12 May 1985, *Ucan 3883* (F).

MONTSERRAT (UK). Coconut Hill, 27 Jan 1907, *Shafer 716* (F, NY, US).

NICARAGUA. Granada: Granada, 10 Feb 1903, *Baker 63* (MO, NY). León: Mpio. Nagarote, Nagarote, 18 Dec 1969, *Seymour 2377* (F, NY). RAAS: Corn Island, Mt. Pleasant, 8 Mar 1971, *Nelson & Seymour 4360* (F, NY).

NORTHERN MARIANA ISLANDS (USA). Rota Mun., behind W dock, 16 May 1966, *Evans 1966* (NY, US); Tinian Mun., Lake Hagoya, N end of island, 8 Jun 1946, *Fosberg 24794* (NY, US).

PALAU. Koror: Koror island, 16 Dec 1966, *Blackburn E29* (US).

PANAMA. Canal Zone [Colón]: along Gaillard hwy, 4 km SE of Gamboa, 30 Oct 1973, *Nee 7684* (US). Chiriquí: Boquete, 2 Aug 1969, *de Sánchez 1* (MO, NY). Herrera: Parita, Sarigua, 1 km de Puerto Limón, 11 Oct 1984, *Caballero & Sandoval 62* (F).

PERU. Huánuco: Tingo Maria, frente a Tingo Maria, izquierda Río Huallaga, 10 Oct 1959, *Ferreyra 13861* (US). Loreto: near Iquitos, 17 Jul 1929, *Williams 1529* (F). San Martín: Tarapoto, 10 Dec 1929, *Wiliams 5949* (F).

PHILIPPINES. Luzon Island: Camarines Prov., Nov 1914, *Valderrama 23423* (US).

PUERTO RICO (US). Mpio. Bayamon, Santurce, 31 Oct 1937, *Otero 181* (MO); Mpio. Camuy, Bo. Santiago, Rte. 488 next to Río Camuy, 2 Jul 1991, *Axelrod et al. 2594* (NY); Mpio. Cataño, Isla de Cabra, 29 Jul 1979, *Woodbury s.n.* (NY); Mpio. Coamo, Río Piedras, Las Piedras Chiquitas, Bo. Cuyón, at Rt. 717 km 2.1, 17 Jan 1993, *Axelrod 5586 & Sastre* (US); Mpio. Fajardo, Seven Seas, carr. 987, 4 Apr 1987, *Ortiz & Davila 26* (NY); Mpio. Guayanilla, along rte 335, 5 km S of Yauco, 20 Jun 1991, *Miller et al. 6499* (MO); Mpio. Vieques, Isla de Vieques, Las Marias, 5 Feb 1914, *Shafer 2706* (NY, US).

SAINT BARTHÉLEMY (FRANCE). Gustavia, 27 Nov 1937, *Questel 80* (NY).

SAINT EUSTATIUS (NETHERLANDS). Oranjestad, 10 Jun 2009, *Burke 1-17* (BH).

SAINT KITTS AND NEVIS. St. Kitts, Basseterre, 23 Aug 1932, *Johnson 1090* (NY).

SAINT VINCENT AND THE GRENADINES. St. Vincent, near Kingstown, 10 May 1947, *Morton 5735* (US).

SRI LANKA. Eastern: east side of Valachchenai bridge, on hwy A15, 20 Apr 1968,

Mueller-Dombois 680420-17 (US). North Western: 0.5 mi beyond Kalpitiya, 14 Nov 1970, *Fosberg & Jayasuria 52756* (MO, US).

SOUTH AFRICA. Limpopo: Transvaal, Legalameetse Nat. Res., Paris, near house Scott Branch, 2 Apr 1985, *Stalmans 524* (MO).

SUDAN. Khartoum, 26 Apr 1975, *D'Arcy 9155* (MO).

TAIWAN. Chiayi Hsien, Chuchi Hsiang, near Hsiangkuang Temple, 5 May 1994, *Lin 460* (MO); Tainan Co., Matou, 23 Oct 1988, *Tateishi & Kajita 25015* (MO).

TANZANIA. Dar es Salaam: Dar es Salaam, low sea cliffs along Kenyatta Dr., 21 Dec 1981, *Gereau 1546* (MO). Iringa: Ludewa, Lake Nyasa shore up to Lupingu, 31 Jan 1991, *Gereau & Kayombo 3795* (MO).

THAILAND. Chiang Mai: Chiang Mai, 4 Aug 2008, *Skema 436* (BH).

TRINIDAD AND TOBAGO. Trinidad: Moruga, 19 Mar 1921, *Britton & Broadway 2452* (NY, US).

UNITED STATES OF AMERICA. Alabama: Mobile Co., S side of Mobile along hwy, 22 Sep 1959, *Kral 37385* (US). Florida: Dade Co., Coral Gables, Old Cutler Rd and SW 168 St., 13 Mar 1994, *Loconte et al. 965* (NY); Hillsboro Co., near Temple Terrace, near Tampa, 7 Jul 1936, *Correll 5864* (NY); Monroe Co., Big Pine key, *Brumbach 9731* (NY); Orange Co., Goldenrod, along Semoran Rd., 24 Oct 1981, *Correll & Correll 52930* (NY); Pasco Co., along C-41 0.5 mi E of junction with I-75, 10 Jun 1984, *Hansen 9949* (TEX); Polk Co., near Mulberry, 12 Jun 1931, *McFarlin 5777* (TEX). Georgia: Dougherty Co., Albany, near railroad station, 5 Aug 1947, *Thorne 5865* (BH). Hawaii: Lanai, 15 Aug 1963, *Degener et al. 28542* (NY); Oahu, 2594 Round Top Dr., 27 Sep 1997, *Ray 1002 & Gibney* (NY). Louisiana: Terrebonne Parish, Houma, 20 Sep 1936, *Arceneaux 190* (BH). Texas: Cameron Co., Brownsville, Dec 1945, *Cory 51416* (NY); Duval Co., 1 mile NE of Realitos, between railroad and hwy 359, 30 May 1969,

Correll & Correll 37367 (TEX); Kleberg Co., NE part of Naval Air Station Kingsville, 19 Jul 2006, *Carr 24936* (TEX); Starr Co., NE bank of Rio Grande, ca 5 mi downstream from Falcon Dam, ca. 2.1 mi SW of jct. US Rte. 83 and F.M. 2098, 19 Apr 1994, *Carr 13597 and Elliott* (TEX); Webb Co., 2 miles SE of Laredo, 25 Apr 1965, *Guajardo 98* (TEX).

VENEZUELA. Amazonas: 20 km S of confluence of Rio Negro and Brazo Casiquiare , 21 Apr 1979, *Liesner 6848* (MO). Anzoátegui: Independencia, Río Orinoco, alrededores de Corrientoso, Sep 2003, *Diaz 6535* (MO). Bolívar: Ciudad Bolívar, 8 Jun 1931, *Holt & Blake 836* (NY, US); 75 km W of Upata, near El Pao on road to San Felix, 12 Jan 2007, *Luckow et al. 4533* (BH, VEN). Delta Amacuro: Lower Orinoco, Sacupana, May 1896, *Rusby & Squires 35* (F, MO, NY-2, US-2). Falcón: downtown Guamachito, 24 Jan 2007, *Luckow et al. 4630* (BH, VEN). Nueva Esparta: Isla Margarita, El Valle, Aug 1901, *Miller & Johnson 53* (F, MO-2, NY, US). Mérida: Mpio. La Punta, Dto. Liberator, a la La Parroquia, 14 Mar 1972, *López-Palacios 2763* (US). Monagas: between La Toscana and Chaguaramal, 11 Mar 1967, *Pursell et al. 8847* (NY, US).

U.S. VIRGIN ISLANDS. St. Croix: Diamond Ruby, 3 Dec 1925, *Thompson 1051* (NY). St. John: Caneel Bay, Dec 1940, *Woodworth 241* (F). St. Thomas: Villa Olga, 22 Sep 1962, *Croat 80* (MO).

Cultivated.

ARGENTINA. Corrientes: Dept. Mburucuyá, Estancia Santa Teresa, 6 Apr 1956, *Pedersen 3874* (US). Catamarca: Dept. Choya, Villa El Puerto, 27 Sep 1944, *Bruzzone 1527* (US).

AUSTRALIA. New South Wales: Sydney botanic garden, 17 Feb 1921, *Ferguson 17* (NY). Queensland: Brisbane botanic garden, 30 Apr 1931, *White 7629* (NY).

BAHAMAS. North Andros: Andros Island, Mastic Point, 2 Jun 1890, *Northrop 604* (F). Long Island: Clarence Town, 23 Jan 1973, *Cerbin 120* (NY).

BARBADOS. [13°10'00"N, 59° 31'60"W], 11 Nov, 1901, *Borell 122* (NY).

BOLIVIA. Beni: José Ballivián, espiritu en la zona de influencia Río Yacuma, 20 Apr 1980, *Beck 3484* (MO). Santa Cruz: Ñuflo de Chávez, 1 km E of San Javier, 2 Dec 1990, *Nee 40143* (MO, NY).

BRAZIL. Pernambuco: Recife, 21 Sep 1965, *Tavares 1412* (US). Santa Catarina: Florianopolis, 11 Dec 1961, *Klein 2870* (US). São Paulo: Campinas, Avenida Barão Itapura, 19 Feb 1936, *Santoro 385* (US).

BRITISH VIRGIN ISLANDS. Tortola: Pasea estate, 3 Dec 1965, *Darcy 235A* (MO).

BURUNDI. Bujumbura Mairie: Bujumbura, 23 Mar 1981, *Reekmans 9874* (MO).

CAPE VERDE. Ilha de Santiago: de Órgãos para Sta. Catarina, Ponte de Ferro dos Órgãos, 28 Dec 1955, *Barbosa 6115* (MO-2).

CHINA. Hainan: Yaichow, Jan 1933, *How & Chun 70023* (F, NY). Hong Kong: Sheung-shui, 5 May 1992, *Hu & But 20582* (MO).

COLOMBIA. Bolívar: Mpio. Mompox, Jardin Botanico "El Cuchubo", 19 Apr 1993, *Ramirez-Arango 4564* (MO). Nariño: Tumaco, 12 Jun 1950, *Espinosa 3005* (BH). Valle de Cauca: Cali, 15 Jun 1938, *Duque-Jaramillo 1791* (US).

COSTA RICA. San José: Cantón de Escazú, W side of Rte. 105, Santa Eduviges de Escazú, 27 May 1990, *Grayum 9856* (MO).

CÔTE D'IVORE. near Adiopodoumé, 17km W of Abidjan, in garden of Centre Neerlandais, 6 Apr 1962, *Leeuwenberg 3831* (MO).

CUBA. Havana: Santiago de las Vegas, 29 Sep 1904, *van Hermann 88* (F, NY).

DEMOCRATIC REPUBLIC OF CONGO. Équateur : Eala [near Mbandaka], Nov 1923,

Gossens 4506 (MO).

DOMINICA. St. Paul: 12th St. canefield, 6 Jul 1992, *Lee 15* (NY).

DOMINICAN REPUBLIC. Distrito Nacional: La Isabela, 5 Mar 1981, *Zanoni et al. 11619* (MO, NY). Puerto Plata: 6 km south of the Gran Parada, between Puerto Plata and Sosúa, in the old road to Santiago, village of Sabana de los Muertos, *Zanoni et al. 28160* (MO, NY).

ECUADOR. Guayas: Capeira, km 21 Guayaquil to Daule, 27 Sep 1981, *Dodson & Dodson 11562* (MO).

EL SALVADOR. San Salvador: Los Planes, S of San Salvador, 11 Jan 1946, *Carlson 38* (F).

FEDERATED STATES OF MICRONESIA. Yap: Yap Island, 4 Mar 1948, *Wong 552* (US).

FRENCH POLYNESIA. Leeward Islands: Raiatea, third valley s of Faaroa Bay, 17 Jan 1927, *Moore 549* (MO). Windward Islands: Tahiti, Pirae, Grand quarter, 5 Apr 1982, *Florence 2798* (NY, US).

GHANA. Greater Accra: Accra, 5 Aug 1971, *Enti 77* (MO).

GUATEMALA. Chiquimula: Mpio. Jocotán, near Menachor office, Nov 2001, *Kufer 271* (US). Izabal: vicinity of Quiriguá, 15 May 1922, *Standley 24327* (US). Petén: NW of El Remate, 20 May 1986, *Walker 1426* (MO). Sololá: Finca Mocá, Volcán Atitlán, 21 Jun 1942, *Steyermark 48064* (F).

GUAYANA. Barima-Waini: Waini Peninsula, Almond Beach, 3 Nov 2001, *Hollowell 715* (US).

HAITI. Artibonite: near Gros Morne, 18 Feb 1926, *Leonard 9888* (F, MO, US). Sud: Treme, 27 Jun 1980, *Peeters 80-14* (P).

HONDURAS. Comayagua: Near Siguatepeque, 29 Mar 1947, *Standley & Chacón 6645*

(F). Francisco Morazán: Campus of EAP, El Zamorano, 5 Feb 1987, *Molina 33980* (MO).

Olancho: Near Juticalpa, 5 Mar 1949, *Standley 17600* (F).

INDIA. Jharkhand: Chota Nagpur, Dist. Hazaribagh, Hazaribagh, Laidies Mission hedge,
21 Sep 1951, *Kerr s.n.* (BH).

INDONESIA. Sumatra: Asahan, 1918, *Bartlett & La Rue 420* (US).

KIRIBATI. Fanning Island, English Harbour, 2 Jul 1965, *Long 3498* (US).

MARTINIQUE (FRANCE). Saint-Pierre, 1878, *Duss 2093* (NY); Bellefontaine, 26 Dec
1940, *Stehle 4632* (US).

MEXICO. Michoacán: Mpio. Tuzantla, en Tuzantla, carr. Zitacuaro-Huetamo, 14 Mar
1982, *Soto 3808* (MO). Nuevo León: Mpio. Allende, along fence by roadside, 36 mi N of
Montemorelos, highway 85, 9 Aug 1972, *Dziekanowski et al 1705* (NY, US); Mpio. Monterrey,
El Bosque Motel in Monterrey, 4 Aug 1959, *Bell 16575 & Duke* (MO). Oaxaca: Dto.
Tehuantepec, Salina Cruz, Jun 1937, *Williams 9730* (F). Quintana Roo: Mpio. Tulum, road to
Chen Chen, village 8 km from Xuilub, 11 Aug 1989, *Mogensen 1079* (MO). Sonora: Mpio.
Alamos, Alamos, 16 Mar 1910, *Rose et al. 12962* (NY, US). Veracruz: Mpio. Tecolutla, along
Gulf of Mexico in Tecolutla, 19 Aug 1986, *Nee 32786* (MO, NY). Yucatán: Mpio. Mérida,
Mérida, 26 Nov 1980, *Calzada & Burgos 7248* (F).

MONTSERRAT (UK). Plymouth, botanic station, 1 Apr 1979, *Howard et al. 19228* (NY,
US).

MYANMAR. Mandalay: Mandalay, Nov 1950, *White 122* (US).

NAURU. Denigomodu, 29 Nov 1978, *Fosberg 58679* (US).

NEW CALEDONIA. [21°28'43.06"S, 165°40'45.56"E], 22 Oct 1950, *Guillaumin 7097*
(US).

NIUE. Alofi, 29 Jan 1940, *Yuncker 9960* (NY).

NORTHERN MARIANA ISLANDS (USA). Northern Island Mun., Agrihan, SW coast, village area, 2 Jul 1972, *Falanruw 2154* (US); Saipan, Tapotchau Mountain, ridge N of peak, 23 Feb 1950, *Fosberg 31765* (US).

PANAMA. Canal Zone [Panamá]: Balboa, Dec 1923, *Standley 28551* (US). Los Santos: Pocri, 14 Apr 1970, *Darcy 4203 & Croat (F).*

PARAGUAY. Central: in region lacus Ypacaray [Lago Ypacarai], Apr 1913, *Hassler 12564* (MO-2, NY, US). Dto. Capital: Asunción, 23 Apr 1978, *Schinini 15235* (F, MO).

PERU. Cusco: La Convención, Quillabamba, 14 Jul 1981, *Hoogte & Roersch 416* (F).

PHILIPPINES. Luzon Island: suburbs of Manila, 3 Aug 1983, *Deguchi et al 6328* (MO, NY).

PUERTO RICO. Mpio. Isabela, Isabela, 23 May 1957, *Sargent A63* (MO, US).

SINGAPORE. Greenhouse, 31 Jul 1967, *Shah 1257* (BH).

SOUTH AFRICA. Gauteng: Pretoria, Zoutpansberg, Davenham 740 farm, 29 Apr 1995, *Glen 3752* (MO).

TANZANIA. Zanzibar West: Magharibi, Dwefumu, 30 Nov 1999, *Fakih 572* (MO).

THAILAND. Bangkok: Bangkok, 4 Jun 1920, *Groff 5805* (NY). Chiang Mai: Chiang Mai coeducational center, 10 Aug 1976, *Anderson 3772* (MO).

TRINIDAD AND TOBAGO. Tobago: government house grounds, 8 Dec 1913, *Broadway 4777* (MO).

UNITED STATE OF AMERICA. Florida: Hernando Co., Brooksville, 11 May 1975, *Moldenke 29487* (TEX). Indiana: Putnam Co., Greencastle, DePauw University greenhouse, 5 Sep 1944, *Welch 8136* (NY). Missoui: St. Louis, botanic garden, 19 Oct 1914, *Thompson 43* (MO). New York: Bronx Co., New York botanical garden, 4 Jan 1904, *Muller s.n.* (NY). Oklahoma: Payne Co., Stillwater, OAMC greenhouse, 21 Jan 1947, *Ledbetter 102* (TEX).

Pennsylvania: Chester Co., Kennett square, Longwood gardens, 16 Jul 1964, *Peele 1403* (BH).

Texas: Harris Co., Houston, 3737 Bellaire Blvd, 10 Oct 1958, *Traverse 871* (TEX); Nueces Co.,

Mustang Island, 1 block N of drugstore, 17 Sep 1967, *Gillespie 96* (TEX).

VENEZUELA. Dto. Federal: Cerro Las Lluvias, Pariata, Maiquetía, 5 Jan 1981, *Barrios 10* (NY). Lara: Barquisimeto, 17 Sep 1968, *DeWolf 2041* (NY). Miranda: Baruta, sector Los

Naranjos, Urb. Las Mercedes, Calle Cristobal Rojas, 9 Dec 1984, *Machado 15* (MO).

VIETNAM. Da Nang: Tourane [Da Nang], Annam, 100 km S of Hue, May 1927,

Clemens & Clemens 3246 (MO, NY, US).

ZAMBIA. Northern: near Chilanga, Mt. Makelu research station, 18 Feb 1960, *Ruqus 2144* (BH).

ZIMBABWE. Harare, Elizabeth nursery, Mt. Hampden, 15 Apr 1975, *Biegel 4968* (BH).

ANTIGONON LEPTOPUS subsp. COCCINEUM Jan. Burke, **subsp. nov.** —TYPE: MEXICO. Baja California Sur: Mpio. La Paz, Miraflores, south of La Paz., Apr 1936, *Bailey 210* (holotype: BH!, isotype: F!).

Flores saturate rosei. Rami rosei pilosi. Lamina ovata profunde cordata subtus pilosa-subtomentosa.

Plant indument densely pilose to velutinous (glabrate) on younger axes. Stem reddish-brown or tan. Ocrea 1.7–5.0 mm long. Petiole tan or brown; lamina apically acuminate and mucronate, abaxially pilose to velutinous (glabrate, hispid), at least on main veins, trichomes lax (stiff). Bract subtending primary inflorescences acuminate or cirrose apically. Pedicel moderately to densely pilose. Perianth magenta or scarlet; hypanthium 0.8–2.0 mm (ca. 9-13.5% of perianth

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length). Diaspore stipe 6–15 mm; perianth deep pink to magenta. Seed 3.7–8.4 mm, subglobose, black (dark brown).

This newly-described subspecies is found in Baja California Sur and the Sonoran desert region of Mexico, on rocky or gravelly ground, 0–700 m. It is striking due to its deep pink or magenta flowers. The same color extends throughout the plant to the petioles and stems. The stems are often densely pubescent, as are the underside of the leaves. The plant is low-growing, frequently with more than one axillary bud per node, a character that occurs through the genus, but seen more frequently in this subspecies, perhaps linked to its scrambling habit.

The distribution of this subspecies is mostly restricted to Baja California Sur, however a few populations occur in Durango, Sinaloa and Sonora, as well as the Revilla Gigedo Islands. In the eastern portion of the range, this subspecies co-occurs with *A. leptopus* subsp. *leptopus.* It is not known to what extent the current distribution has been augmented by anthropogenic movement. There is evidence for *A. leptopus* subsp. *leptopus* cultivated in Sonora. Outside of Mexico, *A. leptopus* subsp. *coccineum* has been cultivated in Bolivia and possibly Hawaii.

Representative Specimens Examined— **Spontaneous.**

MEXICO. Baja California Sur: Mpio. Comundú, N of Comondú, small canyon, 26 Apr 1931, *Wiggins 5469* (F, NY, US); Mpio. La Paz, Miraflores, S of La Paz, 1 Apr 1936, *Bailey 210* (BH, F); Isla San Jose, 4 km from beach on W side of island, 13 Jan 1987, *Flores 445* (TEX); 5 mi SW of El Potrero, 31 Oct, 1905, *Nelson 7242 & Goldman* (NY); 15 mi S of Todos Santos, 24 Mar 1935, *Shreve 722* (MO, US); along Bahia de La Paz about 5 mi W of La Paz, 28 Mar 1974, *Taylor & Taylor 15748* (NY); Mpio. Loreto, W branch of Arroyo Hondo, N side of Cerro de la Giganta, 28 Nov 1947, *Carter et al. 2067* (F, MO, US); Mpio. Los Cabos, San José del Cabo,

Dec 1899, *Brandegee s.n.* (NY); Punta Los Frailes, 16 Feb 1940, *Dawson 1127* (US); Mpio.

Mulegé, inland from Concepción Bay, about 10 mi S of Coyote Cove, 2 Oct 1941, *Hammerly*

140 (MO). Colima: Mpio. Manzanillo, Revilla Gigedo Islands-Tres Marias Island, *Mason 1698*

(F); Revilla Gigedo islands-Cape San Lucas, *Mason 1861* (F). Durango: Mpio. Tamazula, La

Bajadas, 1921, *Ortega 4271* (US). Sinaloa: Mpio. Concordia, 15-20 km E of La Concordia above

Copala, 26 Oct 1973, *Breedlove 35667* (MO); Mpio. Rosario, 45 km S on hwy to Tepic from

Mazatlán, 13 May 1978, *Lane 2309* (TEX). Sonora: Mpio. Guaymas, Ensenada Grande, Bahía

San Pedro, 17 Jan 1965, *Felger 12044* (MO); Mpio. Onavas, road W of "Rancho El Palmar", ca.

20 km E of Onavas, 5 Apr 1991, *Joyal 1597* (TEX); Mpio. Soyopa, 6.3 km SE of Río Yaqui on

hwy 16, 24 May 1998, *Reina 98564* (NY, TEX); Mpio. Ures, Wash 5 mi E of Sacaton crossing

on road to Ures, 18 Sep 1934, *Wiggins 7301* (US).

Putative hybrids—

A number of putative hybrid populations between *A. leptopus* and *A. platypus* have been

identified in the Mexican states of Guerrero, Jalisco and Oaxaca (Fig. 4.15), based on

morphological intermediacy. Except for Guerrero, these populations occur where the southern

range of *A. leptopus* overlaps the northern range of *A. platypus.* Along the Pacific coast a number

of hybrid individuals were collected in Jalisco. These plants appear as *A. leptopus* in that they

have large, pink flowers, however they also have a winged petiole as in *A. platypus.* The

populations in Oaxaca exhibit a similar morphology. These plants occur in Tomellín canyon or

Tehuantepec, the southern Atlantic distribution of *A. leptopus.* Again, these plants have large,

pink flowers but exhibit the winged petiole of *A. platypus.* The putative hybrids collected in

Guerrero are different in that the overall gestalt of the plant is like *A. platypus,* except the flowers

are pink.

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These species are closely related, and thus introgression is not surprising (see phylogeny sections for discussion). The plants from Guerrero exhibit a combination of a winged petiole (*A. platypus*) and pink flowers (*A. leptopus*), characters which are usually mutually exclusive to the aforementioned species. This combination of morphological characters suggests either introgression between the two species, or this is a somatic mutation to a pink color form for this species. A similar somatic mutation to white flowers is seen in *A. leptopus.*
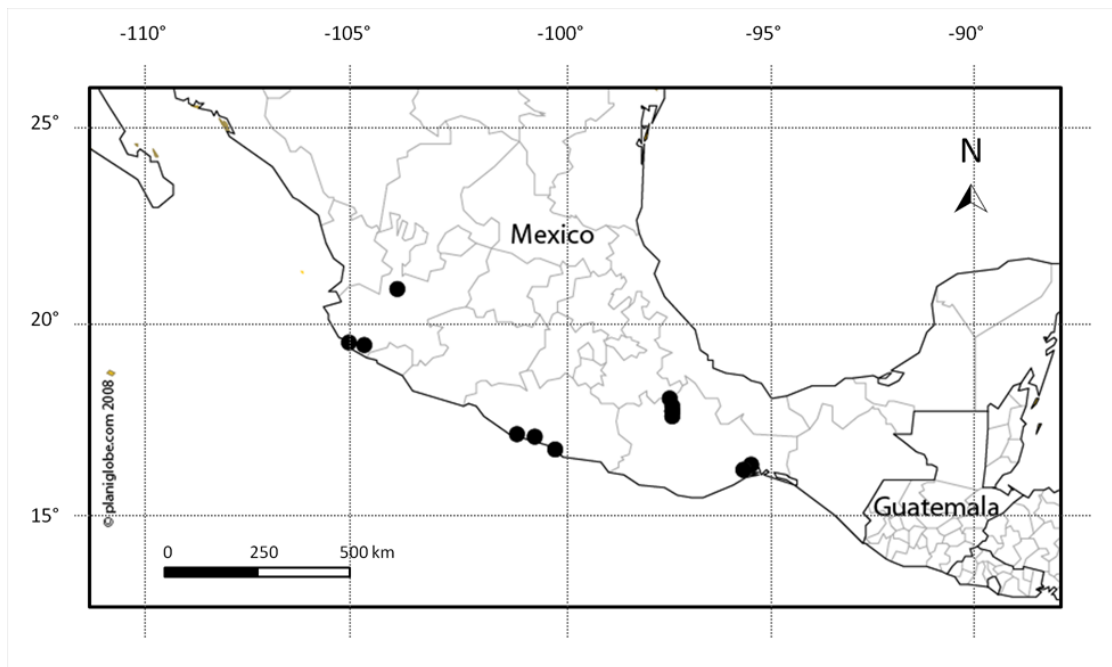

Figure 4.15. Geographic distribution of hybrids between *A. leptopus* and *A. platypus.*

Hybrid specimens examined—

MEXICO. Guerrero: Mpio. Acapulco de Juárez, Acapulco, Oct 1888, *Thiebaut 1058* (P); Mpio. Atoyac de Alvarez, Atoyac, 29 Aug 1939, *Hinton 14577* (US); Mpio. Técpan de Galeana, San Luis de la Loma, 16 Aug 2008, *Burke 130* (BH). Jalisco: barranca of Tequila, 2 Oct 1893, *Pringle 4570* (P, US); Mpio. La Huerta, hwy 200 ca. 12 km N of UNAM biology research station at Chamela, 12 Jan 1983, *Miller et al. 414* (MO); 3 km S of Chamela, rt 200 between Barra de Navidad and Puerto Vallarta, 5 Sep 1975, *Simpson 7044* (TEX-2). Oaxaca: Dto.

Cuicatlan, Cañón de Tomellin, 20 Jun 1908, *Conzatti 2204* (F); El Organal, Cañon de Tomellín, 31 May 1992, *Salinas 6921* (MO); Tomellín Canyon, 6 Jul 1897, *Pringle 6737* (F, MO, NY, US); Dto. Juchitan, Ixtaltepec, on road to Ixtepec, 14 Aug 2007, *Burke 24* (BH); Dto. Tehuantepec, 7 Dec 1970, *MacDougall s.n.* (NY-2); Dto. Teotitlán, Tehuacán, near Tecomavaca, 14 Jul 1961, *Smith et al. 3749* (F, US); 1 km E de la entrada al Tomellín, 4 Aug 1983, *Torres 3458* (MO).

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Antigonon viride S. Watson, Cat. Pl. Mexic. 305. 1897, *nom. nud.*

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APPENDIX

APPENDIX 4.1. Voucher information for specimens used in this study.

Species	Accessions no.	Locality	Specimen location
Antigonon amabile	Veliz 14514	Chiquimula, Guatemala	MO
Antigonon amabile	Luckow 4634	Caracas, Venezuela	BH, VEN
Antigonon cordatum	Burke 2	Veracruz, Mexico	BH
Antigonon cordatum	Burke 6	Veracruz, Mexico	BH
Antigonon cordatum	Burke 8	Veracruz, Mexico	BH
Antigonon cordatum	Burke 11	Veracruz, Mexico	BH
Antigonon cordatum	Burke 36	Oaxaca, Mexcio	BH
Antigonon leptopus	Broome s.n.	Miami, FL	BH
Antigonon leptopus	Burke 9	Veracruz, Mexico	BH
Antigonon leptopus	Burke 12	Veracruz, Mexico	BH
Antigonon leptopus	Burke 22	Oaxaca, Mexico	BH
Antigonon leptopus	Burke 23	Oaxaca, Mexico	BH
Antigonon leptopus	Burke 40	Oaxaca, Mexico	BH
Antigonon leptopus	Burke 42	Oaxaca, Mexico	BH
Antigonon leptopus	Burke 44	Oaxaca, Mexico	BH
Antigonon leptopus	Burke 47	Yucatán, Mexico	BH, CICY
Antigonon leptopus	Burke 69	Quintana Roo, Mexico	BH, CICY
Antigonon leptopus	Burke 78	Yucatán, Mexico	BH, CICY
Antigonon leptopus	Burke 1-13	St. Eustatius	BH
Antigonon leptopus	Burke 1-18	St. Eustatius	BH
Antigonon leptopus	Burke 2-36	St. Eustatius	BH
Antigonon leptopus	Burke 2-39	St. Eustatius	BH
Antigonon leptopus	Burke 3-7	St. Eustatius	BH
Antigonon leptopus	Burke 3-10	St. Eustatius	BH
Antigonon leptopus	Luckow 4533	Bolívar, Venezuela	BH, VEN
Antigonon leptopus	Luckow 4630	Falcón, Venezuela	BH, VEN
Antigonon leptopus subsp. *coccineum*	Pinzl 8469	Baja California Sur, Mexico	NY
Antigonon platypus	Burke 19	Oaxaca, Mexico	BH
Antigonon platypus	Burke 20	Oaxaca, Mexico	BH
Antigonon platypus	Burke 25	Oaxaca, Mexico	BH
Antigonon platypus	Burke 37	Oaxaca, Mexico	BH
Antigonon platypus	Burke 124	Michoacán, Mexico	BH, MEX
Antigonon platypus	Burke 125	Michoacán, Mexico	BH, MEX
Antigonon leptopus x platypus	Burke 24	Oaxaca, Mexico	BH
Antigonon leptopus x platypus	Burke 130	Guerrero, Mexico	BH, MEX
Brunnichia ovata	Alford 3851	Mississippi, USA	MSUS

CHAPTER 5

CORALLITA (*ANTIGONON LEPTOPUS*): INTENTIONAL INTRODUCTION OF A PLANT WITH DOCUMENTED INVASIVE CAPABILITY[3]

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Abstract. Corallita is a perennial vine, lauded as an ornamental for its vigorous growth, and plentiful pink flowers, and even its ability to smother unsightly landscapes. In the United States it thrives in horticultural zones 8 – 10, and is also successfully grown worldwide in tropical climes. When corallita is neglected, it can quickly grow over other vegetation, spreading beyond its area of introduction. Once established, it is difficult to eradicate since it produces many tuberous roots that can propagate vegetatively. Its fruits are buoyant, allowing for successful seed dispersal in water. The islands of Guam (South Pacific Ocean) and St. Eustatius (Caribbean Sea) represent two regions where corallita has become so pervasive it threatens local diversity. In Florida it is already classified as a Category II invasive. Our report reviews the literature and past studies of corallita in addition to adding new taxonomic and distribution information from herbarium specimens to clarify the identity and geographic range. It is recommended that introductions of this plant by the horticultural industry in both tropical and temperate regions be closely monitored to prevent spread. On tropical island nations, we advise against any new introductions.

Nomenclature: *Antigonon leptopus* Hook. & Arn., corallita, coral creeper, Mexican creeper, corallina, bellísima

Key words: ornamental; Polygonaceae; tropics; vine

Like many other members of the Polygonaceae [e.g., *Reynoutria japonica* Houtt.*, Emex spinosa* (L.) Campd.*, Persicaria perfoliata* (L.) H. Gross], *Antigonon leptopus* Hook. & Arn. (corallita) is documented as an invasive species of natural areas (Raju et al., 2001; Ernst and Ketner, 2007; Pichardo and Vibrans, 2009;). It climbs using tendrils, and persists vegetatively by producing numerous tubers (Pichardo and Vibrans, 2009). The flowers are visited by a myriad of pollinators (bees, flies, hummingbirds, butterflies), facilitating sexual reproduction outside of its natural range (Raju et al., 2001).

Corallita, native to Mexico, is cultivated as an ornamental for its showy flowers (Figure 5.1), and has been introduced across the tropics. It is a reported pest from the South Pacific to Africa and India (Raju et al., 2001). It is a roadside weed in its native Mexico (Howard, 2001; Pichardo and Vibrans, 2009), but it is on tropical islands where corallita has become most pervasive and problematic (Figure 5.2). On Christmas Island (Indian Ocean), corallita is reported as "…rampant on sea and inland cliffs and in previously mined areas …where it may be hampering the annual migration of crabs and interfering with natural regeneration" (Swarbrick and Hart, 2000). On St. Eustatius the vine is particularly pervasive, smothering whole areas of vegetation and killing the undergrowth (STENAPA, 2007). It has been estimated to cover 20%

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[3] Burke and DiTommaso. *In press*. *Invasive Plant Science and Management, Allen Press.*

of the island of St. Eustatius (Caribbean Sea) (STENAPA, 2007), and on Fiji (Pacific Ocean) and

Christmas Island (Indian Ocean) it is a documented threat to the local flora (Swarbrick and Hart,

2000; PIER, 2009). In the United States, it is hardy in horticultural zones 8 to 10 (Scheper, 2004)

and cultivated in Arizona, Florida, Hawaii, Louisiana, New Mexico, South Carolina and Texas

(Freeman and Reveal, 2005).

This invasion alert aims to summarize the current knowledge of the natural history and

invasive biology of corallita and call attention to its invasive potential.

NATURAL HISTORY, TAXONOMY AND DISTRIBUTION

Plant Traits—

Corallita is a perennial vine, climbing by tendrils at the end of the inflorescence axes. The

base of the plant can become slightly woody with age. Stems are pentagonal in cross section,

commonly 1 to 3 m long, though they can reach 9 to12 m in length (Scheper, 2004), and quickly

sprawl over surrounding vegetation. Leaves are alternate and usually 10 to 16 cm long. Leaf

shape is variable, but usually deltoid or cordate, the apex acute or acuminate (Figure 5.1E; Duke,

1960). An individual plant can propagate underground via roots, or spread above ground by the

production of stolons. Plants easily persist in the soil by producing tuberous roots (Figure 5.1D)

formed from an extensive root crown. Tuberous roots can range in size from < 0.5 g to 300 g

(Ernst and Ketner, 2007), but can reach 1.0 to 1.5 kg in size in older plants (Englberger, 2009).

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Figure 5.1. Images clockwise from top left: (A) Habit of *Antigonon leptopus* on roadside in St. Eustatius. (B) Detail of flower. (C) Seedling with cotyledons and first leaf. (D) Tuberous root produced from seedling. (E) Detail of inflorescence and leaf morphology. All photos by J. Burke.

The flowers of corallita are arranged in long, branching inflorescences, which are quite striking when hanging over a trellis or fence. The flowers are 0.4 to 2 cm in diameter (Ewing, 1982), with five tepals, these light pink to deep pink, magenta or almost red (Figure 5.1B). There is also a white-flowered cultivar, although it is not commonly invasive. Eight stamens are fused into a column; at the base of this column copious nectar is produced. The tepals enlarge after fertilization, become papery in texture, and surround the fruit. The fruits are achenes, 0.6 to 1.0 cm long, trigonous, acute and winged at apex, brown, dull and buoyant. The seed is large, and comprises 70% of the fruit weight (Jones and Earle, 1966), and includes ruminate endosperm. Chromosome counts for *A. leptopus* vary from *2n* = 14, 40 - 48 (Freeman and Reveal, 2005). The base number for the Polygonaceae is likely *x* = 7 (Brandbyge, 1993), suggesting that corallita (and possibly the whole genus) is of polyploid origin.

Taxonomy—

All species within the genus *Antigonon* are perennial vines, which can become semi-woody at the base. The native range of this genus extends from western Baja California south to Costa Rica (Duke, 1960). Other species of *Antigonon* are often cultivated, both within and outside their native range, for their showy flowers and prolific nectar production (Duke, 1960; Ortíz 1994; Pichardo and Vibrans, 2009), though corallita is the only species which thus far has been documented as an invasive.

Species delimitations in *Antigonon* have been taxonomically difficult with one to eight species recognized by different taxonomist (Graham and Wood,1965; Brandbyge, 1988; Brandbyge, 1993), although four species has been the common consensus (Standley and Steyermark, 1946; Duke, 1960; Ewing, 1982). Corallita (*Antigonon leptopus*) is the most morphologically variable and geographically widespread. In contrast, *A. amabile, A. cordatum*

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and *A. platypus* are relatively well-defined based on morphological characters and geographic distribution. The native ranges of the four species overlap to some extent; specifically corallita overlaps with *A. platypus* and *A. cordatum* in Mexico. Corallita can be distinguished from the latter species by the leaf petiole: corallita has a slender petiole, whereas the petiole of *A. platypus* and *A. cordatum* is winged, with the leaf lamina decurrent along the petiole. Leaf blade size and shape are phenotypically plastic (shape in particular is correlated with sun exposure) and thus are not reliable taxonomic characters.

Putative hybrid populations between corallita and *A. platypus* have been discovered in Oaxaca and Jalisco, Mexico (Burke, unpublished data). Results from comparative morphological studies suggest that invasive populations of *A. leptopus* are not of hybrid origin because they lack diagnostic characters of *A. platypus*, namely the winged petiole and small flowers. Ongoing taxonomic study by J. Burke (unpublished) has focused on species delimitation as part of a taxonomic revision of *Antigonon*. A complete taxonomic treatment, including species descriptions, distribution and key to species is forthcoming.

Distribution—

The native range of corallita has been unclear because it is cultivated as an ornamental and is also a roadside weed within Mexico (Pichardo and Vibrans, 2009), Central America, and the Caribbean. Herbarium collections have helped to clarify the history of introduction of corallita through cultivation, and thus infer its native distribution. Herbarium data suggest that corallita (and other congeners) have been introduced in the Caribbean since at least the mid-19th century. Earliest herbarium records of corallita in the Caribbean come from private gardens, often with a notation about naturalization or escape at a homestead. Based on these data, we have determined corallita is native only to Mexico where it occurs throughout most of the country

except at elevations above 1,000 m. The global geographic distribution of corallita outside its

native range is shown in Figure 5.2. A list of vouchers for spontaneous occurrence worldwide is

found in Appendix 5.1. This list documents the geographic distribution by locality, as well as the

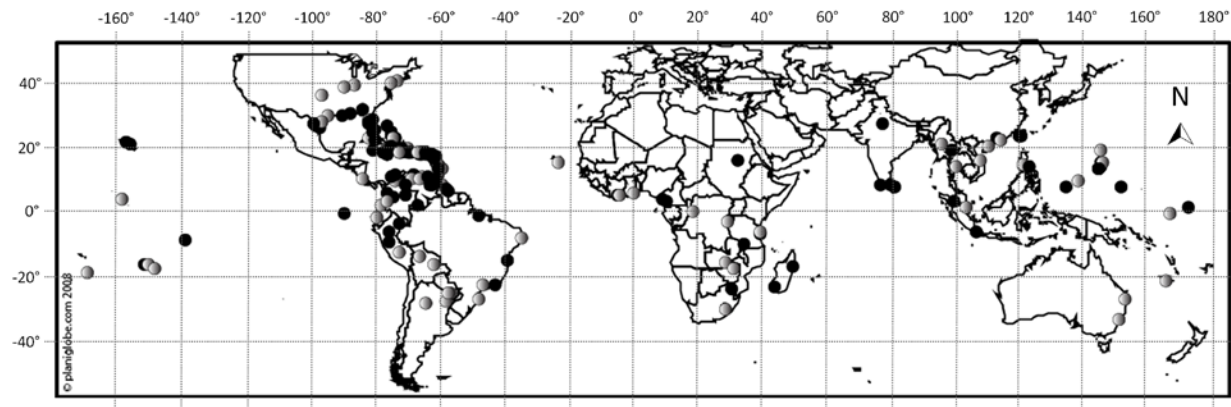oldest known herbarium specimen at each locality.

Figure 5.2. Global geographic distribution map of *Antigonon leptopus*, excluding Mexico and

Central America (its native range). Filled circles represent a collection of a plant growing

spontaneously; gray gradients circles indicate cultivated specimens. Distribution data were

drawn from herbarium specimens from BH, F, MO, NY, P, TEX and US (standardized

herbarium acronyms based on Index Herbariorum).

In the United States, corallita is cultivated in the southeastern and southwestern regions

of the country. It has become naturalized in Alabama, Florida, Georgia, Hawaii, Louisiana and

Texas (Appendix 5.1), and is cultivated as an ornamental in Arizona, California, Mississippi,

New Mexico, North Carolina and South Carolina. The authors' host herbarium, the L.H. Bailey

Hortorium (BH), is unique in its emphasis on cultivated material. From these specimens, we

have learned that corallita was frequently cultivated in botanic garden greenhouses since the

early part of the 20th century: Fairchild Tropical Botanic Garden, Miami [year 1945, *Dress 1256*

(BH)], Missouri Botanic Garden [year 1914, *Thompson 43* (MO)], and New York Botanical Garden [year 1904, *Muller s.n.* (NY)]. There is even a specimen from 1881, though only with the annotation "Botanic Garden" and no specific locality [*Smith s.n.* (US)]. Other notable collections at the US plant introduction garden in Miami [year 1916, *Popenoe 6* (BH)] and at P.J. Beckman's Company greenhouse in Augusta, Georgia [year 1917, *Bailey s.n.* (BH)] suggest that this plant was being tested for introduction into the horticultural market early on. The earliest record we have for a naturalized population in the US is in Harris Co., Texas in 1914 [*Fisher 208* (US)].

Phenology—

In areas in Mexico where there is a pronounced dry season, *Antigonon* species have a distinct flowering period following the first spring rains (February to April), although flowers can be produced year-round with adequate rainfall. After conducting a year-long study on the phenology of corallita on St. Eustatius, Ernst and Ketner (2007) failed to identify a distinct flowering season, likely due to the lack of a dry season. In tropical climates, this species usually flowers year-round (Raju et al., 2001) whereas in more temperate regions (Arizona, Texas), the foliage senesces during the winter months (Scheper, 2004).

Names and Uses—

Corallita is a common name for *A. leptopus* in the Caribbean. In Mexico, Bellísima is the most frequent common name, though it is used to refer to other species in the genus as well. In the United States, common horticultural names are Queen's Wreath and Mexican Creeper, along with Confederate Vine. In the South Pacific, Chain-of-Love is commonly used, though names such as Mountain Rose and Hearts-on-a-Chain are also used.

In Mexico, corallita is planted as an ornamental, or as nectar source for honey production. It is also used for decoration in homes or altars in churches (Ewing, 1982). The nutty flavored tuberous roots are reported to be eaten in Mexico and Guatemala (Standley and Steyermark, 1946) although recently researchers have tried to consume the roots and found them to be inedible (N. Esteban, STENAPA, personal communication). In Thailand, corallita is often grown as an ornamental, and found in bridal bouquets and salads. In other introduced regions its most popular attribute is its vigorous growth, and is used to cover fences or as an ornamental in home gardens.

INVASIVE SIGNIFICANCE

While its distribution is well documented, there are few empirical studies to date of corallita's ecological impact as an invasive. Many reports of the detrimental effects of this plant are anecdotal. The most severe infestations have been found on islands. In Guam (Pacific Ocean), it is common on sea shores, climbing and smothering native vegetation (Space and Falanruw, 1999). On Christmas Island, it has been documented to interfere with migrating crabs (Swarbrick, 1997). The species is most abundant and problematic on the island of St. Eustatius, where corallita covers at least 20% of the island (Ernst and Ketner, 2007). The increased abundance of this plant has prompted the implementation of management efforts in these affected regions. Some governments have initiated legislative action. For example, the Florida Exotic Pest Plant Council has established corallita as a Category II weed (FLEPPC, 2009): an invasive exotic which has become more prevalent, but not yet a threat to local plant communities. Australia has placed corallita on a list of documented pests (WWF-Australia, 2006). On St. Barthélemy in the Caribbean Sea, inhabitants are fined if corallita is found in their home gardens (Ernst and Ketner, 2007).

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Habitat—

Corallita will grow in almost any soil type, is quite drought tolerant, and also tolerates poor soils (Gilman, 2007). The preferred soil pH ranges from 5.0 to 5.5 (Ernst and Ketner, 2007). The plants prefer full sun (Scheper, 2004; Ernst and Ketner, 2007), but may also be found in partial shade. As a tropical plant, corallita does not tolerate temperatures below -7°C (19°F).

Dispersal—

Seeds are buoyant, allowing for dispersal after rain storms. Livestock and insects are more likely seed predators than dispersers. For example, in a livestock feeding experiment on St. Eustatius, no viable seeds were recovered in the dung of animals when fed corallita fruits (Ernst and Ketner, 2007). Locally, tubers are another possible means of introduction into new areas. Smaller tubers and roots can easily be transported to a new location with contaminated soil. This is a similar clonal mode of introduction into new areas as another aggressive weed in the Polygonaceae, *Reynoutria japonica* [= *Fallopia japonica* (Houtt.) Ronse Decr.] (Japanese knotweed).

There is no evidence for long distance dispersal by any vector besides humans. Ship ballast is a possible unintentional mode of introduction; however the tolerance of corallita seeds to salt water, especially long term exposure, needs to be evaluated. Even in remote areas of the South Pacific, plants are cultivated as ornamentals (as inferred by herbarium labels). Since we only have evidence as to the intentional introduction of corallita across the tropics, but none for animal, wind or water dispersal, we suspect that the establishment of new corallita populations in distant localities is the result of intentional introduction through cultivation, with subsequent local naturalization.

Control—

Our knowledge of corallita control is limited to two studies: Ernst and Ketner (2007) on St. Eustatius (Caribbean) and Englberger (2009) on Pohnpei (South Pacific). Mechanical control is an effective means of controlling this plant but will not eradicate it (Ernst and Ketner, 2007). The removal of aboveground tissue via cutting or mowing is not an effective method to eradicate plants because of the persistent, underground tuberous roots. To successfully control populations of this plant mechanically, the tubers need to be removed, and any re-sprouts repeatedly cut-back (Englberger, 2009). Tubers can be found as deep as one meter in soil, therefore deep tillage is necessary to remove tubers. Burning will likewise control plants above ground, and produce shorter shoots after regrowth, but is not a viable long-term option for control.

Chemical control is a more effective long-term approach of managing corallita infestations. The chemical recommendation on Pohnpei is to use triclopyr (Garlon ™ 4) (Englberger, 2009). For small plants, or new introductions, entire plants are uprooted and burned. For larger and/or more established infestations, a foliar spray application of 0.2 kg ae ha^{-1} triclopyr (0.4% Garlon ™ 4) is suggested. Approximately one week after treatment when plants have died back, the tubers are uprooted and removed to prevent re-growth. For isolated individuals, undiluted triclopyr is applied directly to cut stems: 1ml for smaller plants and 3 to 5 ml for larger plants. Revisiting treated areas is always necessary to ensure that corallita plants do not re-grow and that all the tubers have been uprooted and removed from the site.

Ernst and Ketner (2007) conducted chemical trials on St. Eustatius and reported that both 25% triclopyr (165 kg ae ha^{-1}) and 25% glyphosate (122 kg ae ha^{-1}) foliar spray applications at a total volume of 1370 L ha^{-1} and stump treatment (2 to 3 ml of undiluted herbicide) were very effective in preventing plant regrowth, with no plant regrowth six weeks after treatment. In

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addition, glyphosate was most effective at killing underground tubers. All tubers from plots treated with foliar applied glyphosate were non-viable. Although these herbicide trials were extremely effective in controlling corallita, they did involve very high rates and total spray volumes of these two herbicides which may not be environmentally or economically acceptable if large areas require treatment.

Based on these studies, for corallita control we recommend a combination of manual and chemical methods. For smaller infestations, whole plants should be removed and uprooted. Larger infestations can be controlled by first removing or burning the aboveground tissue. Three to four weeks later, the regrowth can by sprayed with a foliar application of triclopyr (0.2 kg ae ha^{-1}). Any additional re-growth can be cut back manually, or another application of herbicide may be necessary to kill remaining plants. Glyphosate is another effective herbicide, but at the moment we lack sufficient trials to make a recommendation for foliar spray application rate that is effective yet environmentally responsible. For the time being, we recommend restricting the use of glyphosate to cut-stump treatment of 2 to 3 ml of undiluted herbicide applied to large individuals.

DISCUSSION

Corallita is a common weed throughout the tropics, though not yet well-documented as such. This plant has clearly been introduced as an ornamental and is now becoming naturalized around the tropics, and needs to be controlled. When neglected, corallita can spread and persist through the development of underground tuberous roots. Local naturalization is primarily accomplished sexually through dispersal of achenes by water or asexually through the spread of tuberous roots in soil, though other undocumented means of dispersal are possible. For now, the best means of control is a combination of mechanical and chemical methods.

The extent of its distribution across the tropics is extreme. The vine occurs on islands with few inhabitants such as Agrihan (pop. 10), Ua Huka (pop. 550), and many other remote islands in the South Pacific (e.g. Guam, Tahiti, Yap). Islands are also regions where corallita poses the greatest threat to local biodiversity and ecosystem function and stability. The relative susceptibility of islands to invasion is well-documented (see Loope and Mueller-Dombois, 1989 for review). Many of the islands where corallita is a problem are sites also colonized by other invasive species, notably the brown tree snake (*Boiga irregularis* Merrem) on Guam or the Indian mongoose (*Herpestes javanicus* E. Geoffroy Saint-Hilaire) in Hawaii. The problem posed by an intentionally-introduced ornamental underscores the need for island regulatory agencies to carefully screen for new introductions on their territories.

Although many of our most problematic weeds were introduced unintentionally, a substantial proportion of invasive plants have been introduced intentionally as ornamentals. We encourage regulatory agencies from tropical island nations to include corallita on their restricted plant lists to limit its introduction onto islands. Currently corallita does not pose a major threat in the United States, though it has been documented as naturalized in Alabama, Florida, Georgia, Hawaii, Louisiana and Texas, and as a garden ornamental in six other western or southern states: Arizona, California, Mississippi, New Mexico, North Carolina and South Carolina. Climate change over the next several decades will undoubtedly affect the geographic ranges of invasive species (Clements and DiTommaso, 2011; Hellman et al., 2008). For example, *Pueraria lobata* (Willd.) Ohwi (kudzu), a leguminous vine largely restricted to the southern United States, is already spreading in Maryland, and has been documented as far north as Connecticut (Mitich, 2000) and Massachusetts. Because of likely range expansion into colder climes, and the current abundance of corallita in tropical regions, we suggest closely monitoring any introduced individuals in temperate regions to prevent spread.

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One clear conclusion from this review is the paucity of studies documenting the invasive properties of corallita and methods of control. Much of the knowledge of corallita as an invasive is anecdotal, and herbicide trials have been undertaken by land managers on relatively small areas. We call for further studies into the invasive biology of corallita, including determining the: (i) primary mode of dispersal, (ii) response of seeds to saline conditions, (iii) presence of herbivores, and (iv) response of plants to larger scale herbicide trials. In particular, a better understanding of the dispersal mode for this species may be used to identify key vectors to target and control for other global invaders as well.

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APPENDIX

APPENDIX 5.1. List of voucher specimens of corallita for documentation of non-native spontaneous occurrence worldwide; naturalized or invasive specimens included, specimens in cultivation or from the native range excluded. At least one voucher is provided per locality, and the oldest voucher was chosen to document the earliest occurrence for known presence in a county/municipality or on an island. All species determinations were made by J. Burke.

NORTH AMERICA

United States. ALABAMA. Mobile Co.: south side of Mobile along highway, 22 Sep 1969, *Kral 37385* (US). **FLORIDA. Dade Co.:** Black Point bridge, 27 Feb 1920, *Young 352* (BH). **Lee Co.:** Middle Captiva Island, 21 Dec 1972, *Brumbach 8143* (NY, US). **Monroe Co.:** Big Pine Key, 8 Sep 1980, *Brumbach 9731* (NY). **Orange Co.:** 24 Oct 1981, *D.S. & H.B. Correll 52930* (NY). **Pasco Co.:** Along C-41 0.5 mi E of junction with I-75, 10 Jun 1984, *Hansen 9949* (TEX). **GEORGIA. Dougherty Co.:** vacant lot near railroad station, Albany, 5 Aug 1947, *Thorne 5865* (BH). **HAWAII. Lanai**: 15 Aug 1963, *Degener et al. 28542* (NY). **Oahu:** Halekulani, 20 Feb 1920, *Marquand s.n.* (NY). **LOUISIANA. Terrebonne Parish:** Houma, 20 Sep 1936, *Arceneaux 190* (BH). **TEXAS. Cameron Co.:** near Brownsville, 1 Dec 1945, *Cory 51416* (NY). **Duval Co.:** 1 mi NE of Realitos, 30 May 1969, *Correll & Correll 37367* (TEX). **Harris Co.:** Houston, 3 Oct 1914, *Fisher 208* (US). **Kleberg Co.:** NE part of Naval Air Station Kingsville, 19 Jul 2006, *Carr 24936* (TEX). **Starr Co.:** 2.1 miles SW of southern jct. US Rt 83 and F.M. 2098, 19 Apr 1994, *Carr 13597 and Elliott* (TEX). **Travis Co.:** near Austin, 27 Jul 1943, *Harpin & Waldorf 45* (NY). **Webb Co.:** 1100 block of San Dario St., Laredo, 25 Apr 1965, *Martinez & Cantu 5* (TEX).

CARIBBEAN

Antigua and Barbuda. ANTIGUA. Parham, 26 Aug 1937, *Box 995* (US).

Bahamas. CAT ISLAND. near Dumfries, 22 Oct 1967, *Byrne 372* (NY). **CROOKED ISLAND.** Hills NE of Cabbage Hill, 22 Feb 1975, *Correll 44478* (F-2, NY). **CENTRAL ABACO.** Great Abaco, E side of Marsh Harbour, 16 Mar 1975, *Correll & Meyer 44716* (NY). **EXUMA.** Hummingbird Cay, near cistern, Mar 1978, *Blair 4799* (MO, US).

Cayman Islands (UK). GRAND CAYMAN ISLAND. Midland district, Bodden town, 2 Jun 1963, *Crosby 46* (TEX).

Cuba. CIENFUEGOS. Castillo de Jagua, 16 Sep 1895, *Combs 563* (F, MO, NY, US); Soledad, 3 Mar 1926, *Jack 4163* (US). **MAYABEQUE.** Canasi to Boca de Canasi, 18 Feb 1956, *Morton 10228* (US). **SANTIAGO DE CUBA.** Crucero de Firmeza, 9 Sep 1951, *Lopez 113* (US).

Dominica. ST. PETER. Between Coulibistri and Colihaut, 30 Jul 1964, *Wilbur et al. 8119* (F,

MO, NY, TEX, US).

Dominican Republic. LA ROMANA. W side of Río Chavon, NW of Presa Chavon, 1.5 km N of La Romana-Presa Chavon road, 17 Nov 1980, *Mejia & Zanoni 9122* (MO, NY). **MONTE CRISTI.** Monción, *Valeur 255* (F, MO, NY, US). **PERAVIA.** Paso del Joba, 12 km NW of Bani, entry to La Monteria, 6 May 1981, *Mejia et al. 13237* (NY). **SANTO DOMINGO.** Ciudad Trujillo, 1 mi W of city, 4 Nov 1945, *Allard 13038* (US).

Guadeloupe (FRANCE). BASSE-TERRE ISLAND. Gourbeyre, 1892, *Duss 2182* (F, NY, US).

Haiti. NIPPES. Miragoane , 20 Sep 1927, *Eyerdam 543* (US). **NORD.** Chaine Bonnet Leveque, next to the Palacio Sans Souci en Milot, 19 Nov 1982, *Zanoni et al. 24475* (MO, NY). **NORD-OUEST.** vicinity of Jean Rabel , 7 Feb 1929, *Leonard & Leonard 12753* (NY, US). **OUEST.** Plaine Cul-de-Sac, north bank of lake Etang /Trou Caiman, 27 Jan 1984, *Zanoni et al. 28758* (NY).

Jamaica. Cornwall Co.: St. James Parish, Montego Bay, 28 Mar 1920, *Maxon & Killip 1660* (F, US); St. Elizabeth Parish, Balaclava, 11 Mar 1927, *Orcutt 696* (MO). **Middlesex Co.:** St. Catherine Parish, near Spanish Town, 30 Aug 1908, *Britton 3071* (NY). **Surrey Co.:** Kingston Parish, Causeway bay near Kingston, Jan 1974, *Katsuro 54* (TEX), St. Andrew Parish, Halfway Tree, 27 Jul 1939, *Philipson 505* (NY), St. Thomas Parish, between Easington and Llandewy, 24 Nov 1963, *Proctor 24240* (TEX).

Montserrat (UK). Coconut Hill, 27 Jan 1907, *Shafer 716* (F, NY, US).

Puerto Rico (US). Mpio. Bayamon: Santurce, 1899, *Goll 75* (US). **Mpio. Camuy:** Bo. Santiago, Rte. 488 next to Río Camuy, 2 Jul 1991, *Axelrod et al. 2594* (NY). **Mpio. Cataño:** Isla de Cabra, 29 Jul 1979, *Woodbury s.n.* (NY). **Mpio. Coamo:** near Coamo, 8 Feb 1929, *Britton & Britton 9213* (NY). **Mpio. Fajardo:** Seven Seas, carr. 987, 4 Apr 1987, *Ortiz & Davila 26* (NY). **Mpio. Guayanilla:** along rte 335, 5 km S of Yauco, 20 Jun 1991, *Miller et al. 6499* (MO). **Mpio. Vieques:** Isla de Vieques, Las Marias, 5 Feb 1914, *Shafer 2706* (NY, US).

Saint Barthélemy (France). Gustavia, 27 Nov 1937, *Questel 80* (NY).

Saint Eustatius (Netherlands). Oranjestad, 24 Jun 2009, *Burke 1-17* (BH).

Saint Kitts and Nevis. St. Kitts: Basseterre, 23 Aug 1932, *Johnson 1090* (NY).

Saint Vincent and the Grenadines. St. Vincent: near Kingstown, 10 May 1947, *Morton 5735* (US).

Trinidad and Tobago. TRINIDAD. Moruga, 19 Mar 1921, *Britton & Broadway 2452* (NY, US).

U.S. Virgin Islands. ST. CROIX. Diamond Ruby, 3 Dec 1925, *Thompson 1051* (NY). **St. John:** Caneel Bay, Dec 1940, *Woodworth 241* (F). **ST. THOMAS.** Villa Olga, 22 Sep 1962, *Croat 80* (MO).

SOUTH AMERICA

Brazil. BAHIA. 190 km S of São Paulo de Paraiso, 8 Feb 1985, *Gentry 49950* (MO). **PARA.** Belem, Mar 1929, *Dahlgren & Sella 402* (F, US). **RIO DE JANIERO.** Rio de Janiero, 20 Dec 1923, *Bailey & Bailey 267* (BH).

Colombia. ATLÁNTICO. Barranquilla, Puerto Colombia, 20 Apr 1974, *Plowman 3542* (US). **BOLÍVAR.** Santa Catalina, Loma Las Puas, via Arroyo Grande a Las Canoas, 4 Feb 1987, *Cuadros 3290* (MO). **CHOCÓ.** Quibdó, barrio Pan de Yuca, 24 Aug 1984, *Cordoba & Garcia 331* (MO). **CASANARE.** Orocue, Río Meta, 3 Nov 1933, *Cuatrecasas 4418* (F). **CUNDINAMARCA.** Poblado de Nariño, 15 Feb 1986, *Fernandez 5197 & Jaramillo* (MO). **MAGDALENA.** Río Manzanare. 29 Dec 1948, *Giacometto 1058* (US).

Ecuador. GALÁPAGOS. Santa Cruz Island, Graffer farm, 6 Mar 1960, *Leveque 33* (US).

Guayana. DEMERARA-MAHAIACA. Georgetown, S. Rumveldt Park, Houston Estate, 21 Sep 1986, *Pipoly et al. 8699* (NY, TEX, US). **MAHAICA-BERBICE.** Arbary River mouth and along canals, 28 Mar 1987, *Pipoly et al. 11254* (NY, TEX, US).

Peru. HUÁNUCO. Tingo Maria, frente a Tingo Maria, izquierda Río Huallaga, 10 Oct 1959, *Ferreyra 13861* (US). **LORETO.** Near Iquitos, 17 Jul 1929, *Williams 1529* (F). **SAN MARTÍN.** Tarapoto, 10 Dec 1929, *Wiliams 5949* (F).

Venezuela. AMAZONAS. 20 km S of confluence of Rio Negro and Brazo Casiquiare , 21 Apr 1979, *Liesner 6848* (MO). **ANZOÁTEGUI.** Independencia, Río Orinoco, alrededores de Corrientoso, Sep 2003, *Diaz 6535* (MO). **BOLÍVAR.** Ciudad Bolívar, 4 Nov 1929, *Holt & Gehriger 22* (US). **DELTA AMACURO.** Lower Orinoco, Sacupana, May 1896, *Rusby & Squires 35* (F, MO, NY-2, US-2). **FALCÓN.** Downtown Guamachito, 24 Jan 2007, *Luckow et al. 4630* (BH, VEN). **NUEVA ESPARTA.** Isla Margarita, El Valle, Aug 1901, *Miller & Johnson 53* (F, MO-2, NY, US). **Mérida:** Mpio. La Punta: Dto. Liberator, a la La Parroquia, 14 Mar 1972, *López-Palacios 2763* (US). **MIRANDA.** San Jose de los Altos, 26 Nov 1984, *Fernandez 17* (MO). **MONAGAS.** Between La Toscana and Chaguaramal, 11 Mar 1967, *Pursell et al. 8847* (NY, US).

AFRICA

Cameroon. SOUTH PROVINCE. Near Bipindi, 15 Jan 1987, *Manning 1358* (MO).

Côte d'Ivore. Grand Lahou, sur le cordon lagunaire, 18 Oct 1986, *Gautier 505* (MO).

Equatorial Guinea. BIOCO. Malabo- Luba, 27 Jul 1986, *Carvalho 2110* (NY). **Madagascar. ANALANJIROFO.** Along rte. 5 from Fenerive [Fenoarivo] to Maroantseta , 28 Feb 1975, *Croat 32538* (MO). **ATSIMO-ANDREFANA.** 8-16 km E of Tulear [Toliara] on road to Tananarive [Antananarivo], 7 Feb 1975, *Croat 30983* (MO).

South Africa. LIMPOPO. Transvaal, Legalameetse Nat. Res., Paris, near house Scott Branch, 2 Apr 1985, *Stalmans 524* (MO).

Sudan. Khartoum, 26 Apr 1975, *D'Arcy 9155* (MO).

Tanzania. DAR ES SALAAM. Dar es Salaam, low sea cliffs along Kenyatta Dr., 21 Dec 1984, *Gereau 1546* (MO). **IRINGA.** Ludewa, Lake Nyasa shore up to Lupingu, 31 Jan 1991, *Gereau & Kayombo 3795* (MO).

ASIA

China. GUANGDONG. Guangzhou, vicinity of Canton, 4 Sep 1934, *Guo 80469* (MO).

Indonesia. JAVA. Ngadirejo [?], 1875, *Kuntze s.n.* (NY-2). **SUMATRA.** Air Joman, Asahan, E of Serbangan, Jul 1935, *Boeea 8253* (NY, US).

Philippines. LUZON ISLAND. Orion Province: Bataan, Nov 1914, *Merrill 3314* (NY, US).

Sri Lanka. EASTERN. East side of Valachchenai bridge, on hwy A15, 20 Apr 1968, *Mueller-Dombois 680420-17* (US). **NORTH WESTERN.** 0.5 mi beyond Kalpitiya, 14 Nov 1970, *Fosberg & Jayasuria 52756* (MO, US).

Taiwan. Chiayi Hsien: Chuchi Hsiang, near Hsiangkuang Temple, 5 May 1994, *Lin 460* (MO). **Tainan Co.:** Matou, 23 Oct 1988, *Tateishi & Kajita 25015* (MO).

Thailand. CHIANG MAI. Chiang Mai, 4 Aug 2008, *Skema 436* (BH).

Vietnam. KON TUM. Dak Gley, 28 Nov 1995, *Averyanov VH2118* (MO).

OCEANIA

Federated States of Micronesia.TRUK-MOEN. Nantaku, 20 Aug 1980, *Fosberg 60387* (US).

French Polynesia. LEEWARD ISLANDS. Maupiti, E coast, Maupiti village, 23 Aug 1985, *Fosberg 64926* (US). **MARQUESAS ISLANDS. Ua Huka:** village of Vaipaee, 30 Jun 1997, *Perlman 15867* (NY).

Guam. Sumay, 7 Apr 1936, *Bryan 1086* (NY, US), Pipeline Rd. in Chaot River Ravine, 26 Jun 1980, *Fosberg 59663* (US), Orote Peninsula, 18 Mar 1946, *Moore 331* (US), near Finaguayac, 29 Aug 1954, *Moran 4488* (US).

Kiribati. Betio Island: 9 Mar 1968, *Adair 132* (US).

Northern Mariana Islands (USA). Rota Mun.: behind W dock, 16 May 1966, *Evans 1966* (NY, US). **Tinian Mun.:** Lake Hagoya, N end of island, 8 Jun 1946, *Fosberg 24794* (NY, US).

Palau. KOROR. Koror island, 16 Dec 1966, *Blackburn E29* (US).

CHAPTER 6

INTEGRATING SYSTEMATICS AND INVASION BIOLOGY: A CASE STUDY OF THE
PANTROPICAL PERENNIAL VINE *ANTIGONON LEPTOPUS* (CORALLITA)

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Abstract. The field of systematics produces data about taxonomy and evolutionary

relationships, providing crucial information on fundamental species biology, as well as

producing phylogenies, evolutionary hypotheses and classification schemes. In addition to

providing a touchstone for species identification, systematic studies have potential for broader

application. In this study, we ask how such studies can be applied to the field of invasion science

and management. We present a case study of *Antigonon leptopus*, a pantropical vine particularly

invasive on islands. Data from hebarium labels are used to track the spread of *A. leptopus* over

space and time, showing the history of *A. leptopus* introduced as a garden ornamental, with

subsequent naturalization and escape. Molecular data from plastid DNA sequences are analyzed

in a phylogenetic context. Results suggest introductions outside the native range were not from

one seed source, as exemplified by the genetic variation found within one island locality.

Information on introduction vectors and pathways is crucial to target future introductions and

spread, especially in areas with limited points of entry (i.e. islands). The relatively high variation

among populations indicates there is not one genetically-similar, invasive lineage; information

which is valuable to managers interested, for example, in implementing a biological control program. The results demonstrate how systematics studies, with an emphasis on sampling of invasive populations, can advance our understanding of the biology, ecology and management of invasive plants. This work also underscores the need for greater communication and collaboration between plant systematists, invasion ecologists, and land managers.

Keywords *Antigonon*, herbarium specimens, island invasion, phylogenetics, Polygonaceae

INTRODUCTION

The field of invasion biology has progressed greatly during the last decade, often through interdisciplinary collaborative efforts. Recently, calls for better communication between taxonomists and ecologists (Pyšek et al., 2004), and between scientists and land managers (Shaw et al., 2010), have underscored the need for greater integration of these research disciplines.

Systematists collect large amounts of data for investigations either into the taxonomic identity or evolutionary relationships of a particular study taxon. Beyond addressing systematic questions, these same data can also be used to garner information of the biology and ecology of a particular taxon. If the group of interest includes an invasive species, these data have critical role in understanding invasive species biology, and subsequently, can be used to inform management of the target species.

Systematists generate DNA sequence data to reconstruct molecular phylogenies or networks to test hypotheses of evolutionary relationships. There is now an increased appreciation for the value of molecular data to inform invasive species biology. If the selected molecular regions are variable enough, these data can provide information about genetic variation even

within a species. Data from molecular phylogenetics can be applicable to invasive studies by: (1) clarifying the taxonomy of an invasive species or species complex, (2) quantifying genetic variation, or (3) inferring the origin of an invasive plant species.

Recent studies of invasive species biology have applied knowledge of a molecular phylogeny or network to help identify an invasive entity, whether a species (e.g. *Lepidium draba*, Gaskin et al., 2005), a species complex (e.g. *Tamarix*, Gaskin and Schaal, 2003), or hybrids between introduced species (e.g. *Anigozanthos*, Le Roux et al., 2010). This is especially informative among plant species that are morphologically difficult to distinguish, such as aquatic vegetation (Les et al., 2006; Moody et al., 2008; Thum et al., 2011). Such studies are critical to accurately identify plants to be targeted for control.

Thorough quantification of genetic variation is often made through comparative population genetic studies utilizing broad sampling and highly variable molecular markers (e.g. AFLPs, RAPDs). Molecular phylogenies or networks can also be used to ascertain a preliminary assessment of the amount of genetic variation between invasive species or populations. In a phylogenetic context, DNA sequences can also be used to assess genetic distance (e.g. Gammon and Kesseli, 2010) or infer origin of an invasive plant or animal (e.g. Marisco et al., 2011). Knowledge about the genetic variation of lineages and native sources of introduction is essential for selecting effective and host-specific biological control agents or narrower spectrum herbicides for management.

In addition to morphological or, more frequently, molecular data collection, a systematic study often requires an examination of herbarium specimens. Usually loans from major herbaria are compiled to complete this task. The specimens are then used to assess the geographic distribution and morphological variation both within and between species of a given taxon. Moreover, the label data can also provide information about the introduction of a plant, not only

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by providing its location and date, but also its provenance, or naturalized status. Herbarium specimens have become used progressively more for data mining to describe the spread of invasive species, though usually at a regional scale (Pyšek and Prach, 1993, 1995; Lavoie et al., 2003; Barney, 2006; Fuentes et al., 2008; Miller et al., 2009;). Herbarium specimen data records can be used to infer the earliest occurrence of a non-native plant at a given location, to track its rate of spread to new localities, or track the total area colonized over time (Delisle et al., 2003; Lavoie et al., 2007; Veldtman et al., 2010). Analysis of herbarium specimen data are useful to identify the primary and secondary vectors or pathways for introduction; directing management to effectively target the appropriate modes of introduction.

The overall objective of this study is to demonstrate how the integration of plant systematics and invasion ecology research can benefit both disciplines. The specific objective is to investigate the introduction history, spread, and genetic similarity of populations of the perennial vine *Antigonon leptopus* at a global scale. This will be achieved by using herbarium specimen data in combination with DNA sequence data from a molecular phylogenetic study, highlighting how these data can be of relevance to management efforts.

METHODS

Study Species—

The target species for this study is *Antigonon leptopus* Hook. & Arn. (Polygonaceae), a tropical perennial vine native to Mexico, that has successfully become established across much of the tropics. *Antigonon leptopus*, or corallita, has been introduced intentionally as an ornamental vine, prized for its vigorous growth and showy pink flowers. Plants can bloom year-round when water is not limiting (Raju et al., 2001). Flowers of *A. leptopus* produce copious nectar, attracting bees, wasps, butterflies, flies and birds (J. M. Burke, pers. observation), hence

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native pollinator availability does not limit sexual reproduction outside of its native range. Early herbarium specimens of *A. leptopus* (from the 19th century) have documented the frequent occurrence of *A. leptopus* as a garden escape (Fig. 6.1 for habit). Neglected plants can easily persist via the production of numerous underground tuberous roots. Unintentional dispersal to new localities may occur through the movement of soil, or through the dispersal of the achene fruits, which can float in water.

Figure 6.1. Antigonon leptopus growing over an abandoned homestead in Bolivar, Venezuela, a typical habit.

   Antigonon leptopus has become particularly problematic on islands, especially those in the Caribbean and South Pacific. For example, on St. Eustatius, a small island in the Caribbean, this vine covers ca. 20% of the island (Ernst and Ketner, 2007). Other islands such as Guam and Pohnpei (South Pacific) also have large infestations (Space and Falanruw, 1999; Englberger,

2009). Burke and DiTommaso (in press) have recently completed a review of *A. leptopus* as an invasive species.

Taxonomy—

The species circumscription within *Antigonon* has been contentious; previous taxonomists working in the flora region (Mexico and Central America) or in the family have not agreed on the number of species nor their taxonomic standing. As such, estimates of species number have ranged from one (Brandbyge, 1988) to eight (Howard, 2001; Aymard and Howard, 2004), though three to five species is the most common treatment (Standley and Steyermark, 1946; Duke, 1960; Ewing, 1982). Burke (unpublished) has undertaken a systematic study to address the taxonomic issues within *Antigonon* and to produce a phylogenetic hypothesis of how the species may be related from an evolutionary perspective. The phylogenetic and morphological analyses led to the conclusion that there are four species in the genus, of which only *A. leptopus* is invasive. *Antigonon platypus*, a low-growing species with white flowers and winged petioles, is most closely-related to *A. leptopus.* Hybrid populations between these two species have been collected in Mexico (Table 6.1). A complete taxonomic revision, including key to the species of *Antigonon*, is forthcoming, and the methods used to determine the circumscription and identification of species will not be discussed further here.

Herbarium data—

Herbarium data were gathered from specimens of *Antigonon leptopus* representing relatively recent worldwide collections that were on loan from five major herbaria: Field Museum of Natural History (F), Missouri Botanical Garden (MO), New York Botanical Garden (NY), Smithsonian Institution (US), University of Texas at Austin (TEX/LL),

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TABLE 6.1. Voucher information for specimens used for molecular sampling of *Antigonon*.

Species	Accessions no.	Locality	Specimen location
Antigonon amabile	Veliz 14514	Chiquimula, Guatemala	MO
Antigonon amabile	Luckow 4634	Caracas, Venezuela	BH, VEN
Antigonon cordatum	Burke 2	Veracruz, Mexico	BH
Antigonon cordatum	Burke 6	Veracruz, Mexico	BH
Antigonon cordatum	Burke 8	Veracruz, Mexico	BH
Antigonon cordatum	Burke 11	Veracruz, Mexico	BH
Antigonon cordatum	Burke 36	Oaxaca, Mexico	BH
Antigonon leptopus	Broome s.n.	Miami, FL	BH
Antigonon leptopus	Burke 12	Veracruz, Mexico	BH
Antigonon leptopus	Burke 22	Oaxaca, Mexico	BH
Antigonon leptopus	Burke 23	Oaxaca, Mexico	BH
Antigonon leptopus	Burke 40	Oaxaca, Mexico	BH
Antigonon leptopus	Burke 42	Oaxaca, Mexico	BH
Antigonon leptopus	Burke 44	Oaxaca, Mexico	BH
Antigonon leptopus	Burke 47	Yucatán, Mexico	BH, CICY
Antigonon leptopus	Burke 69	Quintana Roo, Mexico	BH, CICY
Antigonon leptopus	Burke 78	Yucatán, Mexico	BH, CICY
Antigonon leptopus	Burke 1-13	St. Eustatius	BH
Antigonon leptopus	Burke 1-18	St. Eustatius	BH
Antigonon leptopus	Burke 2-36	St. Eustatius	BH
Antigonon leptopus	Burke 2-39	St. Eustatius	BH
Antigonon leptopus	Burke 3-7	St. Eustatius	BH
Antigonon leptopus	Burke 3-10	St. Eustatius	BH
Antigonon leptopus	Luckow 4533	Bolívar, Venezuela	BH, VEN
Antigonon leptopus	Luckow 4630	Falcón, Venezuela	BH, VEN
Antigonon leptopus	Pinzl 8469	Baja California Sur, Mexico	NY
Antigonon platypus	Burke 19	Oaxaca, Mexico	BH
Antigonon platypus	Burke 20	Oaxaca, Mexico	BH
Antigonon platypus	Burke 25	Oaxaca, Mexico	BH
Antigonon platypus	Burke 37	Oaxaca, Mexico	BH
Antigonon platypus	Burke 124	Michoacán, Mexico	BH, MEX
Antigonon platypus	Burke 125	Michoacán, Mexico	BH, MEX
Antigonon leptopus x platypus	Burke 24	Oaxaca, Mexico	BH
Antigonon leptopus x platypus	Burke 130	Guerrero, Mexico	BH, MEX

The specimens were sorted and identified to species, based on species concepts developed for the genus (J. M. Burke, unpublished data). Locality data were entered as country, primary administrative unit and secondary administrative unit and subsequently sorted by primary administrative unit (e.g., a state in the US). Each island was considered an independent locality

regardless of any other administrative units. Even though size of administrative units varies by country, this was the most tractable proxy to designate a new introduction site/occurrence on a global scale. Information from field notes or distribution was used to designate a 'wild status' for each specimen: native, escaped, naturalized, or cultivated. Specimens from Mexico and the Pacific Coast of Guatemala and El Salvador were considered native. Escaped specimens were designated when it was clear the plant had been previously cultivated, such as an abandoned homestead. Naturalized specimens were designated if they occurred spontaneously, such as along roadsides. If no inference of wild status could be made based on label data, no designation was given.

Each new locality outside of the native range was sorted by date, from 1875 to 2003. Linear regression and exponential regression lines were drawn in Microsoft Excel® to summarize these data. Specimen data for wild status were sorted by period, from 1900-1949 and 1950-2000. These data were analyzed with a chi square test of homogeneity performed in JMP® to determine if the wild status proportions were significantly different ($P < 0.01$) between these periods.

Molecular phylogeny—

Sampling and DNA Extraction— Thirty-four samples were included from *Antigonon*, including all four species and putative hybrids. For *Antigonon leptopus*, sampling was intensive for populations within the native range of Mexico (eight samples) and for invasive populations in the Yucatán peninsula, the Caribbean, South America and the United States (11 samples). Six of the invasive samples were from St. Eustatius: two each from three sites on the island. The only species in the genus *Brunnichia*, *Brunnichia ovata* (Walter) Shinners, was used as an outgroup. Previous work has shown this to be the sister taxon to *Antigonon* (Burke et al., 2010).

Molecular Data Collection— DNA was extracted from silica-dried leaf material using

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the Qiagen DNeasy Mini Plant Kit (Qiagen, Valencia, California, US). Two samples were extracted from herbarium specimens (*Pinzl 8469*, *Veliz 15414*, Table 6.1). This was accomplished by first manually grinding tissue with a mortar and pestle, then incubating for 18 h at 42°C with 600 µL of an SDS-based buffer and 30 µL of proteinase K, before continuing with the protocol for the DNeasy kit, with a final elution of 100 µL.

DNA sequence data were generated using primers for *psaI-accD* (Shaw et al., 2007), an intergenic spacer region on the chloroplast genome. This region was amplified with PCR conditions of 25 µL volume reaction with 5 µL flexi buffer, 2 µL MgCl$_2$, 1 µL each primer (10µM], 0.13 µL *Taq* polymerase. Products were amplified following "slow and cold" PCR cycling program recommended by Shaw et al. (2005). PCR products were run on a 1% agarose gel stained with ethidium bromide. Plastid intergenic spacers were cleaned with enzymes Exonuclease I and Antarctic Phosphotase (New England BioLabs, Ipswich, Massachusetts) to remove residual PCR primers before adding one sequencing primer. Cleaned products were sequenced at the Cornell Biotechnology Resource Center on an Applied Biosystems (Foster City, California) 3730 DNA analyzer.

Data analysis— Sequences were aligned using MUSCLE (Edgar, 2004). Tails on either end of the aligned sequences were trimmed to exclude amplified primer sequence. The aligned matrix was then analyzed under a maximum parsimony criterion using WINCLADA (Nixon, 2002), analyzed with TBR and xmult with 10 starting trees and 10 search replicates per search with 1000 replicates. Support values were calculated with a statistical bootstrap. Parametric bootstraps were conducted in WINCLADA with 10 starting trees and 10 search replicates, saving the best tree, for 1000 replicates.

RESULTS

Herbarium data—

Data from 608 unique (excluding duplicates) herbarium specimens of *Antigonon leptopus* were included. Of these, the majority, 407, occurred outside of the putative native range. Specimens were recorded from 69 countries or territories, with a distribution of specimens represented in all tropical continents, including many areas which are often under-represented in botanical collections: remote islands in the South Pacific and several countries in Africa (Fig. 6.2). Temporal distribution of the specimens was not uniform. The oldest specimen was collected from Mexico in 1842, as were the subsequent specimens until 1875. The first specimen collected outside of the native range was from Java, Indonesia in 1875. The greatest collection of *A. leptopus* specimens occurred in the 1920s and 1980s (Fig. 6.3).
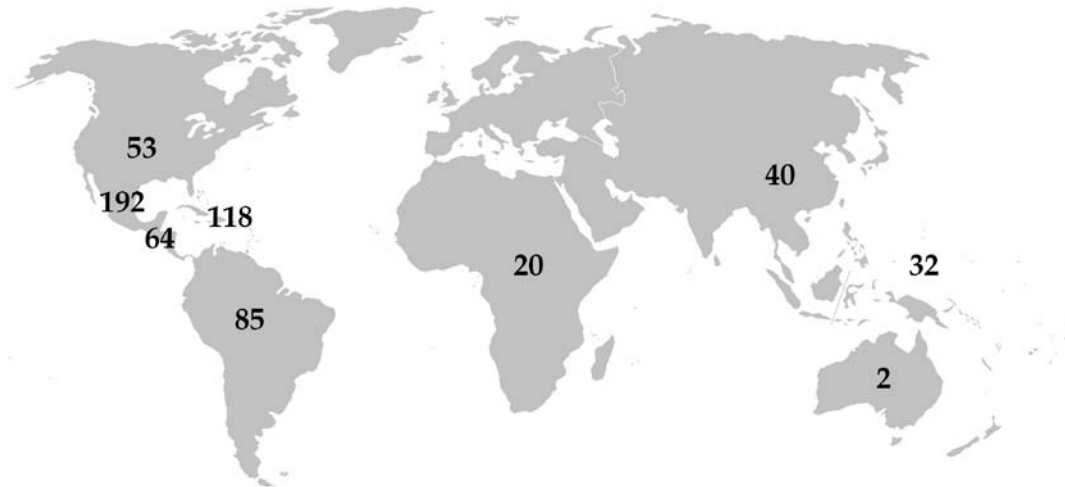

Figure 6.2. Geographic distribution of *Antigonon leptopus* herbarium specimens
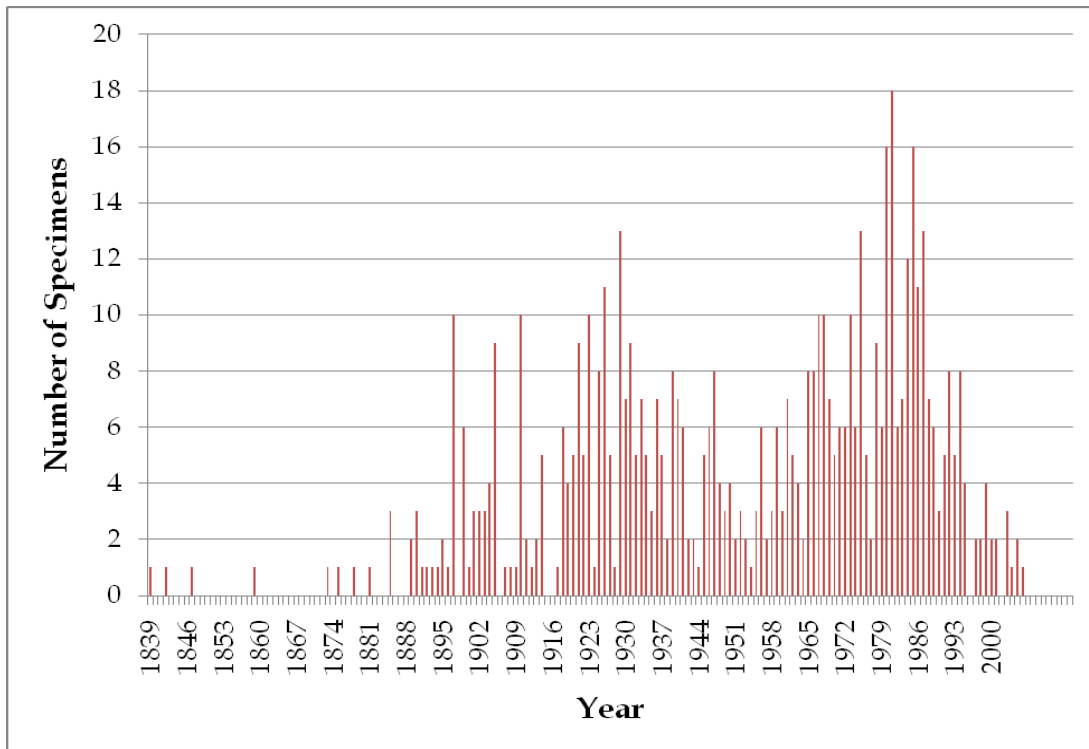
Figure 6.3. Number of *Antigonon leptopus* herbarium specimens collected by year

New localities for new *A. leptopus* plants were documented at a near-linear rate of increase, only appearing to decrease in rate in the past 15 years (Fig. 6.4). The slope of the exponential regression curve, or 'invasion curve' over the total time (Pyšek and Prach, 1993) for this species was $b = 0.053$ ($R^2 = 0.44$), where $y = e \wedge b*x$, the linear regression slope was $b = 1.41$ ($R^2 = 0.94$), where $y = b*x + 1$. In this instance, a linear model explained the data better than a standard exponential model.

All specimens were used to calculate the relative proportions of 'wild status' for the specimens (Table 6.2). Between the two ranges the percentage of native specimens collected was almost identical: 27.5% earlier, 26.5% later. Later in the century, the percentage of specimens without a site description decreased, from 22.2% to 14.9%. Conversely, the percentage of escaped or naturalized collections increased: 10.2% and 13.7% versus 13.7% and 24.1% for escaped and naturalized collections, respectively (Table 6.2). Overall, the percentage of
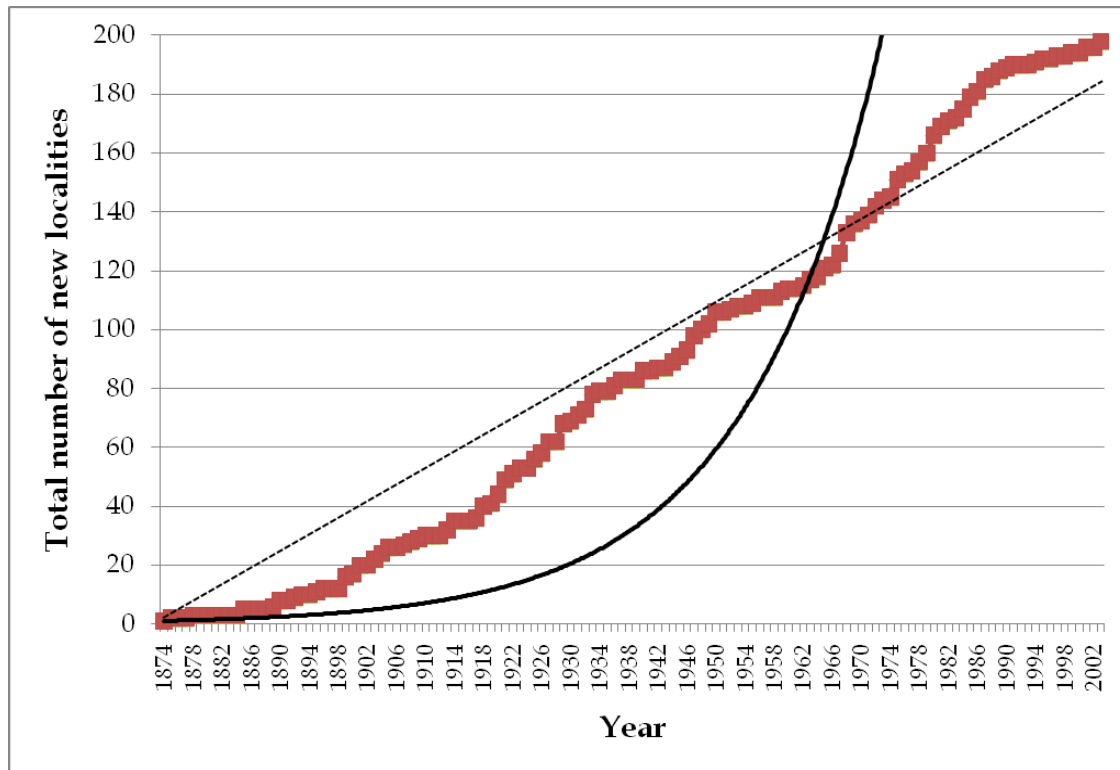
Figure 6.4. Cumulative Number of Localities for *Antigonon leptopus*. Expontential regression line is solid, linear regression line is dashed.

spontaneous collections outside of the native range increased between the first and second half of the second century, from 24.0% to 37.8% of total collections. The chi-square test of homogeneity showed that the proportions of the two different year ranges (first and second half of the 20th century) were significantly different ($P < 0.01$). Therefore, there was a significant difference in the relative proportions of cultivated, native, and naturalized specimens collected in the first half versus the second half of the 20th century.

TABLE 6.2. Number of *A. leptopus* herbarium specimens for different naturalization status

| | Years | |
	1900-1949	1950-1999
native	62	87
cultivated	59	68
escaped	23	45
naturalized	31	79
unknown	50	49
n	225	328

Molecular phylogeny—

The amplified region was ca. 900 base pairs long; the final aligned matrix was 890 base pairs long. Of these, only 2.7% characters were parsimony informative. The phylogenetic analysis of the parsimony informative characters produced 8 trees, L = 36, CI = 72, RI = 90.

The four species of *Antigonon* form two clades: *A. amabile* W. Bull and *A. cordatum* M. Martens & Galeotti are most closely related to each other, and *A. platypus* Hook. & Arn. and *A. leptopus* are most closely related (Fig. 6.5). Based on this phylogeny produced from one chloroplast intergenic spacer, the species *A. leptopus* and *A. platypus* are not reciprocally monophyletic. Of the 19 *A. leptopus* samples included, there were 10 different haplotypes. Most invasive samples of *A. leptopus* were not identical, nor were they more closely related to each other than the samples included from across Mexico (11 samples, 5 haplotypes). The six samples from three different sites on the tiny island of St. Eustatius (total area = 21 km^2) were not genetically identical. There was no sequence variation within sites #1 and #3 (the sequences were identical within each site), but the two samples from site #2 differed by one base pair change (Fig. 6.5). Sequences from site #3 were the most divergent, differing from the samples at the other two sites by four base pair changes, a relatively large difference compared with the total genetic divergence within the species as a whole.

Figure 6.5. A strict consensus of 8 most parsimonious trees based on *psaI-accD* sequence data. Bootstrap values are below branch based on 1,000 replicates. Filled circles indicate a nucleotide base change/ point mutation, and white circles indicate a reversal or new nucleotide at the same base. Accessions of four different *Antigonon* species are indicated in different color typeface. Accessions of *A. leptopus* collected outside its native range are surrounded with a shaded relief: VE= Venezuela; YU= Yucatán, Mexico; ST= St. Eustatius, Netherlands Antilles; FL= Miami, Florida.
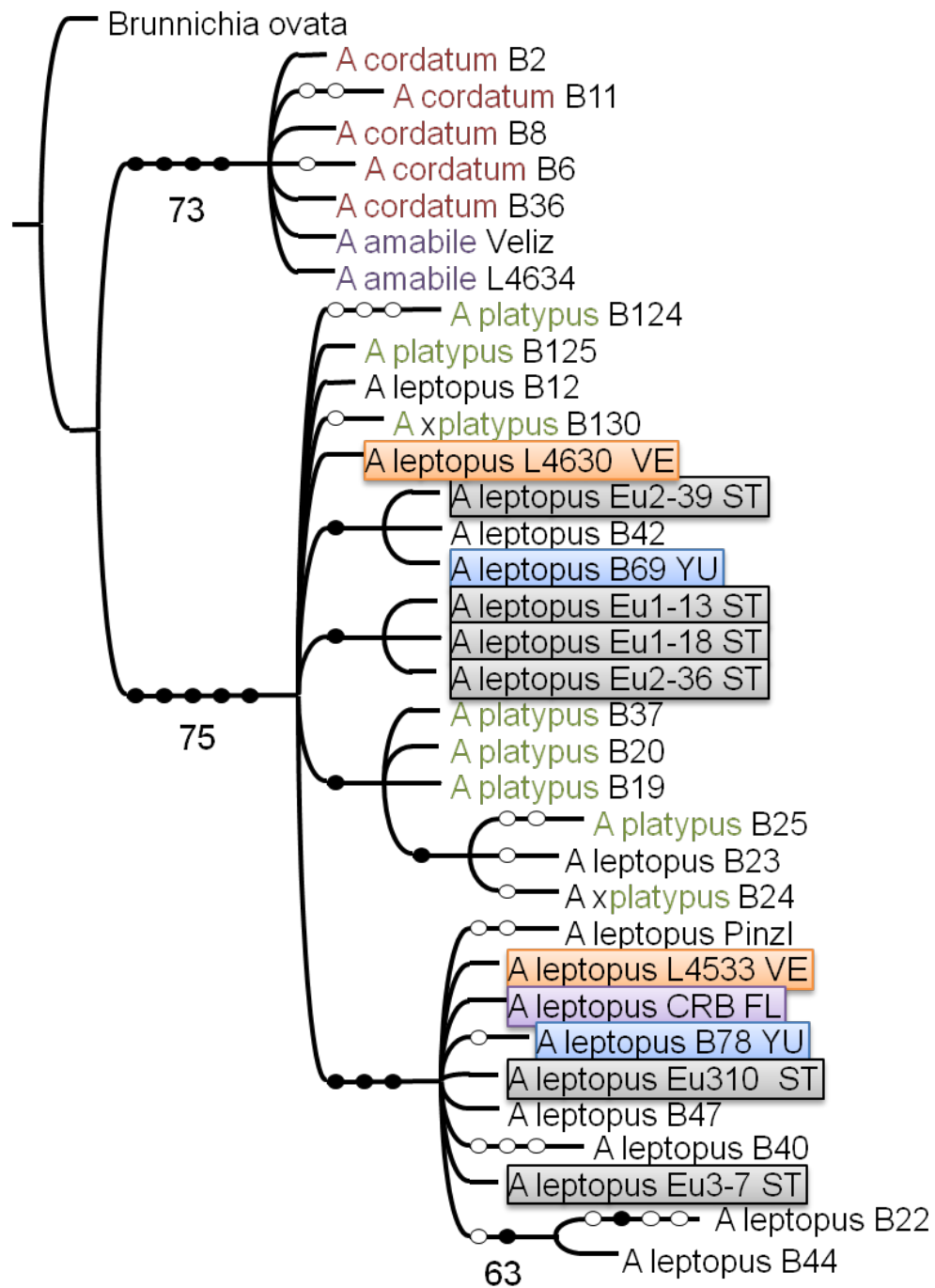
DISCUSSION

The data collected in this study illuminate several aspects of *Antigonon* biology and introduction history. Herbarium records showed a shift from *A. leptopus* collected as a native or cultivated plant, to an escaped or naturalized plant (Table 6.2). Another notable difference is the decrease in the number of specimens that have an unknown origin. This is encouraging because it suggests that more collectors are recording vital information which can be used to infer the wild status of a given plant. Both land managers and plant collectors are urged to include these key data when making new collections.

The general shape of the trend lines summarizing cumulative number of new localities of *A. leptopus* over time (Fig. 6.4) differ from those that have been generated from data collected at the regional level (Pyšek and Prach, 1993; Delisle et al., 2003; Barney, 2006; Lavoie et al., 2007). For some estimates of 'invasion curves', an exponential regression line is usually fitted to the data. This is largely due to the occurrence of a 'lag phase' or time early in the plant's colonization when a plant has been introduced, but its range is not greatly expanding. Other data have shown a later plateau, or a decrease in new localities reporting a given species following rapid colonization (Delisle et al., 2003). In our study, a linear regression best explained the cumulative herbarium collection data. It is not surprising that a lag phase or colonization plateau does not exist for our data. The concept of a lag phase is based on ecological principles such as founder effect and propagule pressure; these ecological phenomena only apply to interactions at the population level. Likewise, though a colonization plateau may be reached for any particular population of *A. leptopus*, it is highly unlikely the species has already spread to all suitable habitats on a global scale.

The use of data collected from herbarium records introduces an inherent bias based on location and timing of collection efforts. This bias has been addressed recently by using

'proportion curves' to compare invasive vs. native species distributions (Delisle et al., 2003; Fuentes et al., 2008). Crawford and Hoagland (2010) compared non-expansive native to non-native invasive species to control for collection bias. Mihulka and Pyšek (2001) corrected for collection bias by using the total number of herbarium specimens per institution. These proposed methods to correct for sampling bias are only functional at the regional scale, and presume extensive holdings at a given herbarium for the study region. Using herbarium specimens at a global scale introduces new bias: it is impossible to sample from all localities of the world, over the complete time period of interest. One straightforward way to help correct for this is to increase sampling; a saturation of specimens, i.e. independent collections from the same locality, will indicate that as many specimens as possible have been included. A desirable study would be to generate multiple datasets of globally-invasive species living in similar habitats with collections from the same herbaria, and compare trends in spread over time. As of now, these data are not available, but it elicits broader ecological questions for a global invader: what is the shape of a global invasion curve? These types of data will be useful for managers across broad geographic areas to compare introduction pathways to target for weed identification and removal.

For *A. leptopus,* herbarium data have clearly documented a trend of intentional anthropogenic introduction and subsequent naturalization and the origin of colonization is frequently an abandoned homestead. This information is useful not only to target pathways for new introductions, but also identify sources of future potential problems. *Antigonon leptopus* is most problematic on islands, which have limited entry points. Therefore, island administrators should control the importation of this plant. Secondly, cultivated vines which have been neglected and are thriving should be controlled and targeted for removal to prevent further spread.

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The molecular phylogeny elucidated a number of genetic characteristics of invasive *A. leptopus* populations. The populations from Florida, the Yucatan peninsula, Venezuela and the Caribbean were not identical; instead they differed by as many as four base pairs. Compared to the total variation in the genus, the genetic distance between invasive populations is rather large. Our findings show that the invasive populations of *A. leptopus* are not genetically identical, suggesting the plants have been introduced independently from different seed sources. On the small island of St. Eustatius there was also remarkable variation between populations on either side of this small island.

Our data refute the idea of colonization with one 'all purpose genotype' (sensu Baker, 1965). Instead, new areas of introduction appear have been colonized by distinct genotypes. Genetics can be used as tools to refine the selection of appropriate biological control agents (Roderick and Navajas 2003), but with *A. leptopus* biological control agents will have to target the whole species, and not just one lineage. Comparison of invasive haplotypes with those from the native range may also be useful to target geographic areas from which to select biological control agents. Here, invasive populations do not trace back to one geographic region; instead surveys across the native range will be needed to identify potential natural predators.

Further population genetic work, with increased sampling, should be undertaken to more thoroughly quantify genetic variation within and between populations. Individuals of *A. leptopus* attract generalist pollinators, and are therefore capable of reproducing sexually outside of their native range. More thorough sampling would allow for the comparison of haplotypes from Mexico with those from introduced areas; to test if the observed haplotypes are novel, and are the result of diversification after introduction, or if they are identical to native populations.

From a taxonomic perspective, invasive populations fell into one morphological species, *A. leptopus*, but based on our molecular data, this species is not monophyletic. The molecular

marker that was used, an intergenic region of the chloroplast, is often used in molecular phylogeny reconstruction, since it is variable at the species level or below. However, plastid markers often trace phylogeographic patterns instead of phylogenetic ones, and are used frequently in phylogeographic studies (e.g. Gaskin et al., 2005; any issue of *Molecular Ecology*). When comparing genetic variation of nuclear regions, the two species had genetically-distinct profiles (J. M. Burke, unpublished). This incongruence in findings does not necessarily have implications for identification of invasive populations: *A. platypus* is clearly differentiated from *A. leptopus* based on leaf morphology and flower color, and *A. platypus* does not occur outside of Mexico. However, these data highlight the inconsistencies which can occur between different data sources, and hence require careful interpretation. Conclusions of taxonomic identity should be drawn from multiple datasets to better inform taxonomic identity, and in turn, management efforts of a species or taxon.

CONCLUSIONS

This study investigated the spread and introduction of an invasive species on a global scale. The molecular data did not clearly identify the species, but informed us of relative genetic differences between and within invasive populations. We also identified the primary vectors of introduction, and documented the spread of this invasive species across the world over the past 150 years.

With the continued globalization of world economies and transport systems, the number of invasive species having a cosmopolitan distribution will no doubt continue to increase. Herbarium records have previously been used to trace the spread of invasive plant species, but mostly on a regional scale. Studies with a larger scope, such as the one described here, allow us to draw generalized conclusions about the rate of spread and mode of introduction of potentially

invasive species at a global scale and more such studies are needed.

Scientists investigating invasive species natural history or biology do so with the goal of more effective control. Traditional taxonomic studies provide keys to identify species or subspecies and more recent techniques allow for identification based on a molecular profile. Molecular data are increasingly used to aid in identification of plants that have few diagnostic morphological characters. These data are essential for proper identification and early detection of an invasive species in a new area. When reconstructing molecular phylogenies, or preparing a taxonomic key, more systematists should be aware of the applied aspect of their research, and when applicable, include multiple accessions of an invasive species from their taxon of study. A combined sampling of morphological or molecular character variation assists the effort by characterizing the relatedness of invasive populations, and may trace them back to a seed source or native population, information useful for land managers and/or weed scientists.

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CHAPTER 7

CONCLUSIONS

From this dissertation work, the systematics of tropical Polygonaceae has greatly progressed. Chapter 2 presented the first phylogenetic study to integrate data from both molecular and morphological characters. From this we have learned that the Eriogonoideae, in the strict sense, is still a monophyletic group, but is nested within a paraphyletic assemblage of woody, tropical genera. In addition, Coccolobeae and Triplarideae, as traditionally circumscribed, are not monophyletic. The revised phylogenetic hypothesis has implications for the interpretation of character evolution: it now appears the 6-tepal floral bauplan in the Polygonaceae was derived from 5-teapls, which is the inverse of traditional evolutionary interpretation. Polygamodioecy has evolved multiple times in Polygonaceae, and endosperm rumination is a variable character.

A comprehensive subfamily and tribal treatment of the family was presented in Chapter 3. Based on findings of previous phylogenetic studies, three subfamilies in Polygonaceae are recognized, with an amended circumscription of traditional Eriogonoideae and Polygonoideae, and the resurrection of Symmerioideae. We proposed a new tribal classification for Eriogonoideae, with six recognized tribes and the creation of two new tribes: Leptogoneae and Gymnopodieae. Our evolutionary classification can now be used as reference not only for information of relationships between genera, but also as a reference for identification of tribes and genera in the field.

In Chapter 4, the species circumscription and relationships between *Antigonon* species were clarified. The phylogenetic study elucidated species relationships that are largely concordant with gross morphological differences between species and geographic distribution.

Four species are recognized, and careful morphological work has discerned the presence of two subspecies within *Antigonon leptopus*. Based on these findings, I proposed a new subspecies, *Antigonon leptopus* subsp. *coccineum.* This study can now be used as a reference to identify plants in the native range.

Our review of *Antigonon leptopus* in Chapter 5 has documented the extent of its distribution across the tropics. The vine occurs on islands with few inhabitants and many other remote islands in the South Pacific. Corallita has been primarily dispersed anthropogenically, and its spread through the horticultural market should be restricted, especially on islands. Even though we give herbicide recommendations and suggestions for control, the review has highlighted the paucity of studies about the invasive properties of corallita and methods of control. Therefore, we hope this action alert will call attention to the invasive species, and may provide an impetus for further study.

In Chapter 6, we investigated how data gathered for a systematic study can help inform invasion biology. Systematists may not always realize the potential for broader application of their work; therefore we encourage systematists who are studying a taxon with an invasive species to increase sampling efforts and publish information about species biology and identification in journals read by weed scientists and/or land managers. For our exemplar study taxon, *Antigonon leptopus*, its standing as a global invader introduced more than 150 years ago provides a unique model species to study the introduction history and spread of an invasive species over large scales in time and space, a scope which has become especially relevant as global trade has increased. Our results showed that the proportion of *Antigonon leptopus* naturalized populations is increasing, and often originates from secondary spread from garden escapes. However, the invasive populations are not genetically similar; instead *A. leptopus* has likely been introduced many times independently, likely from different native seed sources.