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Phylogeny, Biogeography and Systematics of *Menodora* (Oleaceae)
and
The Chloroplast Genome of *Pelargonium* × *hortorum*

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Phylogeny, Biogeography and Systematics of *Menodora* (Oleaceae)
and
The Chloroplast Genome of *Pelargonium* × *hortorum*

by

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Phylogeny, Biogeography and Systematics of *Menodora* (Oleaceae)
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The Chloroplast Genome of *Pelargonium* × *hortorum*

Timothy Wayne Chumley, Ph.D.
The University of Texas at Austin, 2007

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This dissertation presents the result of two separate research programs. The first elucidates the phylogeny, biogeography and systematics of the genus *Menodora* in the olive family. A phylogeny based on the internal transcribed spacer (ITS) of nuclear ribosomal DNA and the chloroplast *rps16* and *trnL* introns and *trnL-F* intergenic spacer demonstrates that the genus is monophyletic. Within the genus, *M. robusta* of Patagonia is the first taxon to branch, followed by a monophyletic African clade and *M. spinescens* of California, though the placement of the latter does not have strong support. Most North American species are nested within the derived South Americans. A South American origin is hypothesized, with two independent dispersals to North America, and a single dispersal to Africa. The phylogeny provided new insights for the systematic treatment, where 24 species, one subspecies and six varieties are recognized, with major realignments of the *intregrifolia* and *scabra* species complexes, and a single new species described.

In the second area of research, the chloroplast genome of *Pelargonium* × *hortorum* has been completely sequenced. At 217,942 base pairs (bp), it is both the largest and most rearranged land plant chloroplast genome yet sequenced. It features two copies of a greatly expanded inverted repeat (IR) of 75,741 bp each, and diminished single copy regions of 59,710 bp and 6,750 bp. Gene content is similar to other angiosperms, with the exceptions of a large number of pseudogenes, two open reading frames (*ORF56* and *ORF42*), and the losses of *accD, trnT-ggu,* and possibly *rpoA.* The latter may be represented, however, by highly divergent set of *rpoA*-like ORFs. The IR expansion accounts for most of the size increase of the genome, but an additional 10% is related to the large number of repeats found. Most of these occur near rearrangement hotspots, and two different repeat associations (characterized by full or partial duplications of several genes) are localized in these regions. We propose simple models that account for the major rearrangements with a minimum of eight IR boundary changes and 12 inversions in addition to several sequence duplications.

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Chapter 1: Introduction

This dissertation presents the results of two divergent lines of research, one presenting the results of molecular phylogenetic and systematic studies of a small genus in the Oleaceae or olive family, and the second investigating the sequence, gene composition and organization of a large and complex chloroplast genome. These are presented in self-contained, individual chapters with their respective tables and figures, followed by a combined bibliography and relevant appendices.

Chapter 2 presents the results of a phylogenetic study using nuclear and chloroplast DNA markers to investigate evolutionary and biogeographic relationships among the species of *Menodora* Bonpl. Using the internal transcribed spacer (ITS) region of nuclear ribosomal DNA, and the *rps16* intron, *trnL* intron, and *trnL-F* spacer of chloroplast DNA in individual and combined analyses, I reconstruct and discuss hypotheses of the evolutionary and geographic history of the group.

In Chapter 3, I use the insights gained from the phylogenetic analysis in conjunction with a detailed morphological study of the group to provide a new systematic treatment for *Menodora*.

Chapter 4 presents the results of DNA sequencing and genomic annotation of the chloroplast genome of *Pelargonium* x *hortorum* Bailey. From earlier restriction site mapping studies, this genome was known to be very large and possess a complexly rearranged gene order. In this study, I largely confirm and extend the earlier studies of this genome, and provide a detailed account of its complexities. I also provide models for how this complex molecule may have evolved through a combination of inversions, duplications, and changes in the extent of a large inverted repeat.

Chapter 2: Phylogeny and biogeography of *Menodora* (Oleaceae)

INTRODUCTION

Menodora Bonpl. is a small genus of the Oleaceae consisting of 23 species and five varieties (Table 1), as treated by various authors (Steyermark 1932; Meyer 1957; Burkart 1979; Turner 1991; Turner 1995; Van Devender and Turner 1997; though not following Correa, 1999). It has an unusual distribution, with both an amphitropical disjunction between North and South America, and an amphiatlantic disjunction in southern Africa as well. On each of these three continents, it is limited to arid or semi-arid deserts and grasslands between latitudes 20° to 45°, with a few species whose individual ranges just cross into the tropics.

The study of disjunction can provide insight into evolutionary processes and the evolutionary history of many plant groups (Fryxell 1967; Wen 1999). While disjunction of plant groups between North and South America, North America and Asia, and South America and Africa has received much study, disjunctions that involve North America and Africa have received relatively little attention. Thorne (1973) concluded that genera that connect the New World and African continents are relatively rare, lists only 111 that are restricted primarily to the New World (mostly South America) and Africa; these represent less than 2.5 percent of the total number of genera found in South America and Africa alone. Only about half of those genera are found in extratropical South Africa, and most of these belong to groups that are easily dispersed (Goldblatt 1978). *Menodora* is one of only six genera (the others being *Pomaria* (*Hoffmannseggia* of Goldblatt), *Parkinsonia*, and *Haematoxylum* (all Fabaceae: Caesalpinoideae), *Thamnosma*

(Rutaceae), and *Turnera* (Turneraceae)) identified by Goldblatt (1978) that are restricted to arid lands of the New World and Africa.

Hypotheses of Species Relationships in *Menodora*

The only comprehensive hypothesis of species relationships within *Menodora* was proposed by Steyermark in 1932 (Fig. 1a), and was based upon an intuitive interpretation of morphology and an incomplete knowledge of some taxa. He proposed two primary lineages within the genus, and recognized them as distinct subgenera. Subgenus *Duogyne* contained a single species, *M. spinescens*, with a supposedly unique suite of characters: two plano-convex ovules in each cell of the ovary, a "seemingly indehiscent” (actually, irregularly dehiscent) ovoid or obovoid capsule marked by a vertical suture, the nearly separate nature of the two locules, and a spiny habit. Steyermark regarded the “pseudo-spinescent” nature of *M. robusta* as essentially unarmed; and apparently knew nothing of the fruit of the species, for it similarly contains only two ovules per cell, and is also irregularly dehiscent (Bentham 1846; Correa 1999). *Menodora spinescens* and *M. robusta* are also vegetatively very similar, at least superficially. In seeming contradiction to his “phylogenetic chart” (Fig. 1a), which in modern interpretation shows a sister relationship between his two subgenera, Steyermark believed that the advanced characters of *M. spinescens* (reduction in floral size, reduction in number of ovules), specialized habit (its thorny nature) and limited distribution clearly indicated its more recent evolution, and suggested a derivation from within the other subgenus.

Steyermark, then, viewed subg. *Menodora* as the older of the two subgenera. It contained all remaining species (including *M. longiflora* and the imperfectly known *M. robusta* as sister species, and these together as sister to the rest), and was defined as being completely unarmed, having four ovules per locule and a bilobed capsule with regularly circumscissile subglobose proximate cells. Within this subgenus, Steyermark believed that stem and pedicel habits provided important clues to relationships among the species. He suggested that species with erect habits and erect pedicels in fruit (*M. decemfida, M. intricata, M. juncea, M. longiflora, M. robusta, M. scabra,*) were primitive, and placed *M. longiflora* and *M. robusta* as sister to the rest subg. *Menodora* because of floral (extended corolla tube and included anthers; however, the anthers are exserted in *M. robusta*) and palynological similarities with *Jasminum* and *Nyctanthes*. Within this group, he also saw a trend of foliar reduction, with the leaves being reduced to awl-like or scale-like processes in *M. intricata* and *M. juncea*. An intermediate group in the subgenus features decumbent stems and erect pedicels (these are now all treated as varieties of *M. integrifolia*). The most derived group within the subgenus consists of those species with decumbent habits and recurved or arcuate pedicels in fruit (*M. africana*, *M. coulteri, M. helianthemoides, M. heterophylla, M. mexicana,* and *M. pulchella*). Steyermark considered this group to be derived from a *M. integrifolia* var. *trifida*-type ancestor, and divided it into pinnatifid and entire-leaved subgroups.

In the years since Steyermark's treatment, an additional seven species (Rehder 1935; Turner 1991; Turner 1995; Van Devender and Turner 1997) and two varieties (Meyer 1957) were described, and a number of taxonomic shifts and realignments were made (Burkart 1979; Turner 1991; Correa 1999), but no explicit hypotheses of overall phylogenetic relationships were suggested. However, descriptions of these new taxa often explicitly stated or implied individual relationships to existing species. An expanded hypothesis of species relationships based largely on that of Steyermark (1932) that takes into account these additional species as well as greater knowledge of others is shown in Fig. 1b. Early in my systematic evaluations, a data set of morphological characters was compiled from the literature and used to reconstruct a phylogeny (Fig. 1c; data not shown). The results are strikingly different from many of the particulars of Steyermark's hypothesis, but have a similar pattern of frequent biogeographic disjunction between sister taxa. Other than this rudimentary reconstruction (Fig. 1c), these various hypotheses have never been tested using modern phylogenetic methods. Given the lack of ecological diversification within the genus, morphologically-based hypotheses may be confounded by the possibility that similar morphology may be the result of convergent evolution rather than phylogenetic history. The high degree of homoplasy and lack of bootstrap support in our early analysis (Fig. 1c) seem to support this possibility. In comparison with morphology in this group, analysis of molecular characters may be less influenced by homoplasy due to the relatively character-rich nature of the datasets (potentially offsetting the influence of low frequency homoplasy), and thus may provide a better assessment of relationships. A re-examination of the group was thus warranted, and the use of molecular tools in the reconstruction of phylogeny was used to provide insight for new interpretation of morphological characters.

The Biogeography of *Menodora*

Menodora has its greatest species diversity in Mexico, where all 16 of the North American species occur; only four of these have their principal distributions north of the border in the southwestern United States. In South America, six species are found, including a variety of *M. integrifolia*. Three species occur in southern Africa, one of which is a variety of the North American *M. heterophylla*. The latter is the only species with a bi-continental distribution under current treatments, although Steyermark (1932) had recognized another by describing a North American variety of the Argentine *M. decemfida*; however, this was later placed in taxonomic synonymy in a broadly defined and highly polymorphic *M. scabra* by Turner (1991). While most species of *Menodora* are of limited geographic distribution, two species, the South American *M. integrifolia* and the North American *M. scabra* (whether broadly defined *sensu* Turner 1991 or the narrower sense of Steyermark 1932), are widely distributed and have ranges that nearly coincide with the distribution of the genus on their respective continents.

Steyermark (1932) believed that the discontinuous distribution of *Menodora* was an artifact of what in modern terms would be called vicariance. He postulated a once continuous distribution across a lost land bridge or “lost continent” connecting South America and Africa long before the end of the Cretaceous. Other authors (Cockerell 1932; Cain 1944) invoke continental drift as a possible vicariance event rather than loss of a land bridge. Although Steyermark also inferred the disjunction of *M. heterophylla* in North America to be the result of distribution across this lost continent, he regarded the primary distribution of the genus to be in the southern hemisphere, which is consistent with a Gondwanan or austral distribution pattern. Curiously, Steyermark (1932) never discussed in depth the disjunction of *M. decemfida* of Argentina and his named variety in North America.

In a modern interpretation, however, Steyermark’s ideas of a vicariant origin seem inconsistent with his concept of species relationships within the group (Fig. 1a). In a strictly vicariant scenario, we would expect some resolution of the continental polytomy shown in Fig. 2a, where each of the continental groupings of species would appear essentially monophyletic, or at least derived from an early branch near the base of the tree. A special case of the latter, supposing a Gondwanan origin, would pair the African and South American species as sister groups, with a probable derivation (dispersal) of the North American species from within the South American group (Fig. 2b). Implicit within Steyermark’s concept of species relationships, however, is the idea that several modern lineages (e.g., *M. heterophylla* and *M. decemfida* and their varieties) as well as the common ancestors of several other sister lineages arose prior to vicariance, and points toward a North American origin for the group (Fig.1a). The highly derived position of many of these transcontinental sister relationships is not really suggestive of vicariance but rather of frequent, repeated long distance dispersal.

In his epic work on phytogeography, Croizat (1952) suggested just such a mode of distribution based upon dispersal rather than vicariance. He interpreted Steyermark's (1932) two geographically redundant species as evidence for specific dispersal pathways or tracks. The disjunction of the North American *M. heterophylla* and its variety *australis* in South Africa suggested a track originating from Africa to North America, to Mexico in particular. The disjunction of *M. decemfida* of South America and its variety *longifolia* of North America was cited as "a classic disconnection Chile—Mexico" track, subsequent to the dispersal from Africa (Croizat 1952). From coastal Chile, *Menodora* then migrated into the interior of Argentina toward the Atlantic coast. Thus, in Croizat's view, the genus originated in Africa, dispersed to North America and from there to South America (Fig. 2c). While not specifically invoking a North American connection, long distance dispersal has been suggested by others as the primary cause of most New World—African disjunctions (Thorne 1973; Raven and Axelrod 1974; Goldblatt 1978) and examinations of the biotic relationship of South America and Africa have suggested that vicariance may not be sufficient to explain the similarities of their floras (Thorne 1973; Goldblatt 1978; George and Lavocat 1993; Goldblatt 1993).

Croizat's dispersal tracks for *Menodora* are suggestive of boreotropic interpretation. The boreotropic hypothesis (Tiffney 1985b; Tiffney 1985a; Wolfe 1985; Lavin 1993; Lavin and Sousa S. 1995; Lavin et al. 2000) suggests that a Tertiary land bridge connecting North America to Europe was a conduit for dispersal of a seasonally dry-adapted tropical flora from northern Africa. While *Menodora* is not a tropical lineage, the ancestor of the group could have originated in arid conditions in Western Gondwana and c migrated northward into Laurasia and across such a land bridge. Although *Menodora* is not found today in northern Africa or Europe, several species of its sister genus *Jasminum* do occur there: *J. odoratissimum* of the Canary Islands and Madeira, the widespread Mediterranean species *J. fruticans* (Green 1961), and *J. azoricum* in Madeira (Green 2001). If a common ancestor of *Menodora* and *Jasminum* migrated through the region, these species possibly could be relics of that Tertiary passage, and thus would be close relatives of *Menodora*. Short of finding *Menodora* nested within these lineages in a paraphyletic *Jasminum*, however, it might be difficult to find evidence that supports a North African-European origin.

Following a different paradigm, the biological relationship of eastern Asia and eastern North America has been well documented, and recent reviews have noted floristic affinities in western North America as well (Xiang, Soltis, and Soltis 1998; Wen 1999). Raven and Axelrod (1974) suggest such a Eurasian derivation for *Menodora*. Given that the center of diversity for *Jasminum* is in eastern Asia (ca. 50 spp.) and Malesia (ca. 70 spp.), it is possible that a now-extinct ancestor of *Menodora* may have dispersed across a Tertiary-age Bering land bridge from Asia. In this view, *Menodora* would have a North American origin, with subsequent dispersal to South America and presumably to Africa from there (Fig. 2d). Again, short of finding *Menodora* nested within an Asian lineage of a paraphyletic *Jasminum*, it would be difficult to prove this theory of Asian origin.

Comparing the simple biogeographic scenarios of Figure 2 against the hypotheses of species relationships shown in Figure 1, it would seem that none of the latter fit the former very well. The geographic scenarios presented in Figure 2 are admittedly simplistic, and are grounded with considerations of limiting vicariance or dispersal to a minimum number of events, under the assumption that long distance dispersal is rare. From the hypotheses presented in Figure 1, the situation seems to be more complex. If these intuitive hypotheses or the rudimentary phylogeny are correct, either the group contained a number of widespread and persistent species prior to vicariance, or there has been a lot of dispersal, or possibly both. The presumably basal position of *M. robusta* and *M. spinescens* and the question of whether *M. heterophylla* and its variety are closely related (vs. merely morphologically convergent) are both complicating factors in considering the biogeography of the group. These taxa are probably the most critical, as the positions they occupy in a phylogeny will do much to shape our perceptions of the geographic history of the group.

In this study, we present the results of a molecular phylogeny of *Menodora* based on the internal transcribed spacer region of nuclear ribosomal DNA (nrDNA), and the two regions of chloroplast DNA (cpDNA), the *rps16* intron and the *trnL-F* region. Our goals are to assess the monophyly of the genus against a limited sampling of its sister genus *Jasminum*, elucidate species relationships within the group (and thus test earlier hypotheses of these relationships), and to evaluate both morphological character evolution and biogeographical hypotheses within a phylogenetic context.

MATERIALS AND METHODS

Sampling

In total, 118 accessions (Table 2) were sampled for 20 outgroup taxa (22 accessions for *Jasminum*, *Syringa*, *Forsythia*, and *Nyctanthes*, all in the Oleaceae), and 26 ingroup taxa (96 accessions). The outgroup for this study consists of the sister genus to *Menodora*, *Jasminum*, as determined by an previous molecular phylogeny of the family (Wallander and Albert 2000) and other members of the family as noted above.

Ingroup sampling includes all currently recognized taxa in *Menodora* with the exceptions of *M. linoides* of Chile and *M. mexicana* of Oaxaca, Mexico, both of which were known only from their type collections until the recent rediscovery of the former (Faúndez, Larraín, and Girón 2005; Muñoz, Moreira, and León 2006). In addition to taxon sampling, an effort was made to sample geographically across the distribution of individual taxa and to sample as much as possible named variation within a particular group, whether this variation is currently recognized or not. For example, 23 accessions for *M. scabra* were sampled, representing collections from throughout the geographic distribution and range of morphological diversity of this broadly circumscribed group, which includes six formerly recognized taxa (sensu Turner 1991; three species and three varieties). Of named varieties, only *M. pinnatisecta* var. *missionum*, M. *scabra* var. *longituba*, and *M. spinescens* var. *mohavensis* were not sampled due to a lack of suitable, authentic material.

DNA Isolation, PCR, and Sequencing

Total genomic DNA was isolated from silica-dried leaf or stem tissue, herbarium specimens, or fresh, cultivated leaves (Table 2). DNA was extracted using a modified CTAB method (Doyle and Doyle 1987). Double-stranded DNA was amplified using polymerase chain reaction (PCR) for the entire ITS of nrDNA (including ITS1, the 5.8S ribosomal RNA, and ITS2), the chloroplast *rps16* intron, and the chloroplast *trnL-F* region (*trnL* intron and the *trnL-trnF* intergenic spacer).

Primers used for amplification of ITS were the ITS1A primer (Downie and Katz-Downie 1996) and ITS4 (White et al. 1990); primers ITS2 and ITS3 of White et al. (1990) were frequently used in sequencing for clarification of base determinations. Amplification of the *rps16* intron utilized the primers rpsF and rpsR2 (Oxelman, Lidén, and Berglund 1997). Four additional sequencing primers were developed to improve base determinations, and were occasionally used for PCR on some recalcitrant templates: rpsJF2 (ACGAAGTAATGTCTAAACC; ca 440 bp downstream of rpsF), rpsJF3 (CCCAGAACAAGAAAACACC, ca 487 bp downstream), rpsJF4 (CCTTTAAGCTATTTRAGAG ca 607 bp downstream), and rpsJR3 (TGGTGTTTCTTGTTCTGG; a partial reverse complement of rpsJF3). Primers used for amplifying the *trnL-F* region were *c* and *f* of Taberlet et al. (1991), although frequently the primer pairs *c-d* and *e-f* (Taberlet et al. 1991) were used when amplifying the entire region proved difficult; *d* and *e* were also used frequently as sequencing primers.

The PCR cycling protocol for ITS started with a 3 minute initial denaturation at 95° C, followed by a 30 second annealing at 50°-54° C, and a 45 second extension at 72° C. This initial reaction cycle was followed by 35 cycles consisting of a 30 second denaturation at 95° C, 30 second annealing at 50°-54° C, and a 45 second extension. The reaction was terminated with a final 7 minute extension at 72° C. For both the *rps16* intron and *trnL-F* region, the protocol was similar except that extension times were 90 seconds during cycling with a final extension time of 12 minutes.

PCRs were conducted in volumes of 25 or 50 µl, containing 2-4% by volume of template DNA, 10% by volume of 10X buffer, 2.5 mM $MgCl_2$, 0.2 mM of each dNTP, 0.2 µM of each primer, and 0.4% by volume of *Taq* polymerase (2 -- 5 units), with the remaining volume made up with ddH_2O. Occasionally 5% by volume each of dimethyl sulfoxide (DMSO) and bovine serum albumen (BSA) were required for successful amplifications.

Reaction products were purified using QIAquick columns (QIAGEN Inc., Valencia, CA) following the suggested protocol. Approximately 50-60 ng of this was used for cycle sequencing, using 3.2 pM of primer and fluorescence-labeled dye terminators (BigDye, ABI, Foster City, CA) following the manufacturer's protocol. Sequencing reactions were cleaned of excess dye using Centrisep spin columns (Princeton Separations, Adelphia, NJ). Sequencing was performed on an ABI Prism-377 or Prism-3100, or a MJ Research BaseStation.

Analysis

Sequences for the forward and reverse reaction products were combined and edited using Sequencher 4.2 (Gene Codes, Ann Arbor, MI). Resulting sequences were aligned automatically using ClustalX (Thompson et al. 1997) and manually adjusted using SeqApp 1.9 (Gilbert 1992). Phylogeny was assessed using maximum parsimony (MP), maximum likelihood (ML), and Bayesian (BA) analyses. Data sets for each marker were analyzed individually and in combination (cpDNA or nrDNA+cpDNA) under both MP and ML, and these were also analyzed with gaps excluded or as missing data, and additionally under parsimony, with gaps coded as a fifth base. Bayesian analysis was conducted only with the full, combined data set including gaps.

Parsimony analyses were conducted using PAUP* 4.0b10 (Swofford 2001) using a heuristic search strategy and default options. Bootstrapping was used to assess support (1,000 replicates, with 10 random addition replicates and MAXTREES=100). For model-based analysis, the optimal model of sequence evolution was assessed for each data partition and the combined data set as a whole using a likelihood ratio test as implemented in ModelTest v. 3.5 (Posada and Crandall 1998). Maximum likelihood (ML) analyses and ML bootstapping (100 replicates) were conducted using GARLI v. 0.942 (Zwickl 2006) with the default GTR + Γ + I model of sequence evolution (this version GARLI does not support full model customization); five independent runs with random seeding were conducted for each data partition. ML trees were then scored using

PAUP* with the recommended model. Bayesian analysis of the combined data set was conducted using MrBayes v. 3.1 (Huelsenbeck and Ronquist 2001). Since not all models recommended by ModelTest are implemented in MrBayes, we used the next most complex model available. Two replicate runs of five million generations were conducted, with four Markov Chain Monte Carlo chains and partitioned models of evolution; we excluded the first 100,000 generations of each run.

We assessed congruence between markers using the ILD or incongruence length difference test (Farris et al. 1994; Farris et al. 1995) implemented as the partition homogeneity test in PAUP* (Swofford 2001). This test has been used extensively as a criterion for the conditional combination of partitioned data, although its utility as such has been questioned (Yoder, Irwin, and Payseur 2001; Barker and Lutzoni 2002; Darlu and Lecointre 2002; Hipp, Hall, and Systma 2004). We compared each pair of the individual markers, as well as the nrDNA vs. combined cpDNA, running 1000 permutations with MAXTREES=100 for each comparison.

We used the Shimodaira-Hasegawa or SH-test (Shimodaira and Hasegawa 1999) as implemented in PAUP* to evaluate alternative topologies against one of the best trees resulting from ML analysis of the combined data, with gaps treated as missing characters. Test parameters used the recommended GTR + Γ + I model of sequence evolution, and 1000 RELL bootstrap replicates. The alternative topologies tested are summarized in Table 6. These were created by altering the placement of branches found in the best tree being used in the comparisons. Most of these topologies were suggested by the results of phylogenetic analyses of the various partitions and permutations of the data, although we also tested a few that were not (e.g., relationships involving the *intricata* and *scoparia* clades, constraining taxa to be monophyletic in continental lineages). If the test statistic proved to be significant, then the null hypothesis that each tree is equally likely given the data was rejected, and the best tree was preferred.

Dispersal-vicarance analysis or DIVA (Ronquist 1997) was conducted using version 1.2 of the software and a simplified fully-bifurcating tree based on the results of the ML analyses (Fig. 8a). Since the topology among the basal set of taxa had weak support, and alternate topologies could not be rejected under the SH-test, we also evaluated several of the latter (Fig. 8b-8e) to see how these might affect the biogeographic interpretation. Geography was also mapped on the trees using MacClade 4.0 (Maddison and Maddison 2000). MacClade was also used for morphological character reconstructions using the simplified ML tree.

RESULTS

ITS (nrDNA)

The ITS data are aligned into a matrix of 860 bp, which when trimmed of missing data at the leading and trailing ends produces an aligned length of 712 bp. There are 76 insertions or deletions (indels) totaling 98 bp. Descriptive statistics and homoplasy indices resulting from parsimony analyses of the ITS data are shown in Table 3.

In general, all parsimony analyses of the ITS data recovered the same clades, with topological differences occurring at a few poorly supported branches (Fig. 3). The Jasmineae are strongly supported (100% bootstrap) as a monophyletic group, as is *Menodora*. The jasmines, however, appear paraphyletic with the alternate-leaved jasmines appearing as sister to *Menodora* (although this is weakly supported). Within *Menodora*, the Patagonian *M. robusta* is consistently the first branching, and is sister to all remaining taxa sampled. It is part of a basal grouping with the Mojave Desert species *M. spinescens* and the African taxa, although their relationships are poorly resolved with very low bootstrap support. The positions of *M. robusta* at the base and *M. spinescens* close to the base of the group demonstrate that neither the South American nor North American taxa are monophyletic. The African taxa are monophyletic, with moderate bootstrap support. Notably, the African variety *australis* of the North American species *M. heterophylla* appears to be imbedded within *M. africana*, while the species itself appears in a derived North American clade. The latter clade appears as sister to a strongly supported South American clade consisting of *M. pulchella* and the varieties of *M. integrifolia*, and both of these are sister to the Argentine *M. decemfida*. Within this North American clade, samples sort mostly by species as identified. The most notable exceptions are three samples that form a small clade with strong support within what we loosely define as the Galeana group (for their proximity to Galeana, Nuevo Leon, Mexico, and immediately adjacent Coahuila; this includes *M. gypsophila*, *M. hintoniorum,* and *M. muellerae*,). These samples have been morphologically identified as *M. coulteri* var. *coulteri*, *M. hintoniorum*, or *M. magniflora*, and while the morphological differences between *coulteri* and *hintoniorum* are slight and subject to interpretation, the *magniflora* specimen is quite different in its morphology. Another exception is in the broadly construed *M. scabra* sensu Turner 1991. Turner had included *M. scoparia* within his broad concept of *M. scabra*, but in our analyses, samples referable to *scoparia* appear either as sister to a *scabra s. l.* that includes *M. yecorana*, or in two of the parsimony analyses, as sister to the *helianthemoides-coulteri* group instead. Also within the *scabra s.l.* group are two specimens that appear to be misidentified, mcoco.H24734 (as *coulteri*) and mscop.M17646 (as *scoparia*). In both cases, these are intermediate specimens that lack strong diagnostic characters. Within the *scabra s.l.* group there is a very apparent and strongly supported geographic pattern, with samples separated into eastern (Chihuahuan) and western clades.

Trees (not shown) resulting from the ten maximum likelihood analyses (five runs each in which gaps were omitted or treated as missing characters) have a similar topology to that shown in Figure 3, but consistently placed the *heterophylla-longiflora* clade as sister to the remaining derived North American taxa, and the *scoparia* group as sister to *scabra s.l.*, though in both cases bootstrap support was less than 50 percent. ML trees differ from each other only in branch lengths and in the placement of samples within some terminal taxa. Scores for trees resulting from these ML analyses are shown in Table 4. Bootstrap branch support is similar to that of the parsimony analyses.

rps16 **intron and** ***trnLF*** **region (cpDNA)**

The *rps16* intron data produce an aligned matrix of 1201 bp, which when trimmed of missing data at the leading and trailing ends leaves 1055 bp. There are 56 indels, which account for 288 bp, with most of this length being found in a large insertion in the Jasmineae. The aligned matrix for the *trnL* intron and *trnL-F* spacer is 1177 bp long, which when trimmed of missing data at the ends and at the *trnL* exon junction is reduced to 954 bp (we were unable to sequence through the *trnL* exon junction area in some cases, and for this reason this region was removed from the analyses). There are 38 indels totaling 178 bp.

As might be expected, cpDNA markers provided less resolution and less support overall than the ITS data (Fig. 4), although most species groups found in the ITS analyses were also resolved in the individual chloroplast analyses. Parsimony analyses of both the *rps16* intron and *trnL-F* region again showed strong support for a monophyletic Jasmineae and a monophyletic *Menodora*, but the relative positions of the alternate-leaved and opposite-leaved jasmines varies depending on how gaps are treated. *Jasminum* appears as a monophyletic group in all but two analyses, albeit with weak support. When gaps are treated as a fifth base with the intron data, the alternate-leaved jasmines are sister to *Menodora* as with the ITS data. When gaps are omitted in analysis of the *trnL-F* data, the opposite-leaved jasmines appear as sister to *Menodora* (Fig. 4b). Again, each of these alternate topologies have weak support.

Within *Menodora*, parsimony analyses of the independent chloroplast data sets (summary statistics shown in Table 3) separate a basal group of species (*M. robusta*, *M. spinescens*, and the African taxa) from a more derived group (all remaining taxa). All analyses of the intron data recover the basal group as a single grade sister to the derived taxa, although this has less than 50% bootstrap support and the arrangements within the grade differ depending on the gap treatment; these are also poorly supported. When gaps are treated as a fifth base, this arrangement is also suggested by the *trnL-F* data, but with very strong support. Other treatments of gaps in the *trnL-F* data recover a very different topology among the basal set, with the African taxa no longer forming a monophyletic group. *Menodora africana-M. heterophylla* var. *australis* appear as sister to the rest of *Menodora*, including *M. juncea*, and relationships among the rest of the basal group are not well-defined nor strongly supported (Fig. 4b).

While species or taxa groups are almost identical to those recovered in the ITS analyses, the chloroplast data generally fails to resolve relationships between them, especially within the derived taxa (Fig. 4). The intron data show very strong support for *M. pulchella* as sister to *M. integrifolia*, while the *trnL-F* data does not have any resolution within this group, although the branch supporting the group has very strong support. The intron data do not resolve the *scabra s.l.* group, although a part of the eastern *scabra* clade is recognized with weak support. The *trnL-F* data do weakly support recognition of the *scabra s.l.* group, without any strongly supported internal branches, however. *Menodora intricata*, which was sister to the Galeana group in the ITS analyses, appears instead as sister to the *helianthemoides-coulteri* group in the intron analyses, with weak to moderate support. Conversely, the intron analyses show that the *scoparia* clade is weakly associated with the Galeana group (as in the ITS analyses), but the position of mscop.C7404 is not resolved. The *trnL-F* analyses have results that are similar to those of the intron analyses, but do not resolve the position of either the *scoparia* or *intricata* clades, although in these analyses mscop.C7404 is a member of the *scoparia* clade with good support for the clade. The same three-taxon clade (*hintoniorum et al.*) identified within the Galeana group in ITS analyses is also found in all chloroplast analyses, but in the *trnL-F* analyses *M. muellerae* is alsoincluded, rather than being sister to *M. gypsophila*.

Maximum likelihood analyses of the individual chloroplast data sets display a similar lack of resolution, with very different individual trees with the same likelihood score resulting from the GARLI analyses (Table 4). In the intron analyses, trees from both sets of analyses (with or without gaps) have identical likelihood scores regardless of which permutation of the data was used to generate them. Strict consensus trees are almost identical to the majority rule tree shown in Fig. 4a, and bootstrap support values are also similar; notably, support for a monophyletic *Jasminum* is greater, at 75%. In the *trnL-F* analyses, the African taxa form a weakly supported monophyletic group. The relative positions of the African taxa and *M. robusta* are unresolved at the base of the *Menodora* clade. Other than these differences, the strict consensus of the likelihood trees from each analysis resembles the topology shown in Fig. 4b.

Combined Datasets

Results of the ILD comparisons are shown in Table 5. The results of ILD comparisons are not significant except when gaps are treated as a fifth base, and thus we accept the null hypothesis that the data are not incongruent. Much of the incongruence between trees from the different data sets occurs at places where branches are short, poorly supported, and/or poorly resolved within individual data sets. The expectation that this lack of resolution would not preclude combining data thus appears to be supported. When gaps are treated as a fifth base, however, the number of parsimony informative characters doubles, and in general branch support is higher as well, and thus the rejection of the null hypothesis is understandable.

Results of parsimony and likelihood analyses of combined chloroplast and combined chloroplast and ITS data are shown in Tables 3 and 4, and representative trees are shown in Figures 5 and 6. All parsimony analyses of the combined chloroplast data show strong support for a monophyletic Jasmineae and a monophyletic *Menodora*; support for a monophyletic *Jasminum* is weak to moderate depending on the gap treatment. Within *Menodora*, all analyses also resolve the basal set of taxa as a weakly to moderately supported clade, although branching relationships within the group are not strongly supported. In the more derived taxa, the North American taxa are sister to or in a derived position to the South American *decemfida* and *integrifolia/pulchella* clades, but the relative positioning of these two South American clades depends on the analysis. When gaps are omitted, they appear as sister to each other with weak support and together as sister to the North Americans. In both analyses where gaps were included, the *integrifolia/pulchella* clade branches first and *decemfida* alone is sister to the North American taxa, with very strong bootstrap support. *Menodora pulchella* is also strongly supported as sister to *M. integrifolia* in all analyses. Within the moderately supported (70%-87% bootstrap) derived North American clade, most species/taxa groups recognized in the previous analyses are found, but relationships between them are not well resolved, and many of the branches supporting these groups are poorly supported (<

50% bootstrap). The *scoparia* clade is only partially resolved, and these are sister to the Galeana clade in the analyses where gaps were omitted or treated as missing characters, though with poor support. The *intricata* clade appears as sister to the *helianthemoides/coulteri* clade in all analyses, though with only poor to moderate support. *Menodora jaliscana,* which was not sampled in the ITS data, is consistently sister to *coulteri* in all analyses.

Results of the maximum likelihood analyses of the combined chloroplast data are similar to those resulting from the parsimony analyses, except that rather than a basal clade of the African taxa, *robusta* and *spinescens*, the latter two species appear as sister, and the African taxa are sister to all remaining taxa (trees not shown). These basal branches are again poorly supported, and are unresolved in the strict consensus. The relationship of the South American *decemfida* and *integrifolia/pulchella* clades is not resolved, and while the derived North American clade is strongly supported, relationships within the group are not well resolved and again often poorly supported. The *scoparia* clade is split into two parts, with different samples appearing as sister to either the *scabra s. l.* clade or the Galeana group.

In parsimony analyses of the combined nuclear and chloroplast data, the trees most closely resemble those of the ITS analyses (Fig. 5b and 6b). Each analysis provides a different resolution of the basal set of taxa. When gaps are omitted, *M. robusta* is alone at the base, and *M. spinescens* and the African taxa are together sister to the remaining taxa; support for these relationships is weak, however. When gaps are treated as missing characters, the three appear nested, with *M. robusta* again at the base, the Africans in the intermediate position, and *M. spinescens* as sister to the remaining taxa. Support for the branches is again weak. When gaps are treated as a new state, however, these three groups form a moderately supported basal grade, with *M. robusta* as sister to the other two. In all analyses, *M. decemfida* is sister to all remaining taxa, with very strong support, and the *integrifolia/pulchella* are sister to the derived North American clade, and *M. pulchella* is sister to *M. integrifolia*. Within the North American clade, relationships between groups are resolved but often with weak support, and these branches collapse in the strict consensus except when gaps are treated as a fifth base. Differences between analyses here are in the relative placements of *heterophylla-longiflora* and the *intricata*/Galeana clades as either sister to each other, or one or the other as sister to all remaining taxa. The *scoparia* clade is moderately supported as a single group, and is sister to *scabra s. l.* although with poor support.

The maximum likelihood trees (not shown) are most similar in their gross topology to those found under parsimony with gaps included as missing characters (Fig. 5b and 6b), differing only in that *Jasminum* is not monophyletic, with the alternate-leaved clade being sister to *Menodora*, and that the *heterophylla-longiflora* clade appears as sister to all remaining derived North American taxa, with the next two branches having weak support. Within and between each set of likelihood analyses, the trees differ only by arrangements within terminal taxa. Bayesian analyses provide similar results (Fig. 7), with the only topological difference with the likelihood trees being within the Galeana group where *M. muellerae* is sister to the *M. hintoniorum* clade, rather than sister to *M. gypsophila*. The two independent Bayesian analyses provided topologically identical results.

Testing Alternate Topologies

We compared 18 topological variants against one of the optimal ML trees for the combined data with gaps included using the SH-test (Table 6). Variants included differing arrangements of the basal group, the *intricata* and *scoparia* clades, and the *intricata*-Galeana and *heterophylla-longiflora* clades. Comparisons indicate that with these data, neither the North nor South American taxa are monophyletic. We cannot reject the hypotheses of alternate arrangements of the basal group of taxa except for those in which the African taxa are not monophyletic. We can reject hypotheses of a sister relationship between the *scoparia* and *intricata* clades, but can not reject the alternative positions in which they appeared in different analyses. Similarly, in the derived North American clade, we can not reject alternative positions of the *intricata*-Galeana and *heterophylla-longiflora* clades, nor the sister relationship of *M. muellerae* to the *hintoniorum* clade. Essentially, in this sampling we can reject hypotheses with topologies that were not recovered in the phylogenetic analysis of one data partition or another, but can not reject many of the alternative topologies that were.

Biogeography

For DIVA analysis, we constructed a reduced tree using only the terminal taxa as suggested by the likelihood analyses. Since we could not reject alternate arrangements of the basal taxa with the SH test, we also evaluated several of these hypotheses as well (Fig. 8). In all cases, optimal reconstructions using DIVA suggested that the modern distribution of *Menodora* is the result of vicariance with 2 dispersals. Vicariance and a single dispersal are necessary to explain the various hypotheses of relationships among the basal taxa, but interpretation of which relationship might be vicariant or the result of dispersal was in most analyses equivocal (see Fig. 8). A second dispersal to North America is inferred in all analyses (Fig. 8). It is also possible to interpret the distribution in terms of three long distance dispersals, without invoking vicariance. Mapping geography on the trees in MacClade strongly suggests a South American origin of the group, with two independent introductions into North America and a third to Africa (Fig. 8).

DISCUSSION

Phylogeny and Biogeography

Each individual set of phylogenetic analyses provides a slightly different take on the phylogeny of the group, with each data set showing some sensitivity to both optimality criterion and treatment of gaps. Most analyses identified the 11 major clades as shown in Figure 7, and differ mostly in the arrangement of these clades within three broad groups: the basal set of taxa (*M. robusta*, *M. spinescens*, and the usually monophyletic African taxa), the derived South American taxa (*M. decemfida, M. pulchella* and *M. integrifolia*), and a large, derived North American clade. Other than *M. scabra*, which was unresolved as part of a derived North American polytomy in two of the intron analyses, the only other group which was not always resolved as a clade is the *scoparia* group due to differing placements or lack of resolution of the samples mscop.C7404 and mscop.M17646. The clade is resolved in all combined analyses, with especially strong support in the likelihood and Bayesian analyses, except that the Baja California specimen mscop.M17646 is resolved as part of the western *scabra* clade.

The *scoparia* and *intricata* clades are also interesting because they change positions depending on the data set or analysis. The *scoparia* clade, though not always a monophyletic group, appears variously as sister to the *helianthemoides/coulteri* clade (MP ITS with and without gaps), sister to *scabra s.l.* (MP ITS with gaps as fifth base, ML ITS, all combined, in part in some cp analyses), or part of a polytomy with the Galeana group (all cp analyses). The *intricata* clade appears as sister to the Galeana group in all ITS and combined data analyses, but either is unresolved or sister to the *helianthemoides/coulteri* clade in the cp analyses. These differing placements according to data partition may indicate an old hybridization and possibly introgression between members of the Galeana, *helianthemoides*, and/or *scabra* clades.

Incongruence between data sets is mostly confined to branches where support is weak in all analyses. Combining data produces better resolution, but still leaves several of these branches with weak support. The trees resulting from analyses of the combined data are reasonably supported though not robust. The topologies are largely formed by the ITS data, with some refinements attributable to the chloroplast data (e.g., the resolution of *pulchella* as sister to *integrifolia*, which is strongly supported only by the *rps16* intron data). The principal weaknesses in these trees are in the structure within the basal group, and the relative positions of the *heterophylla/longiflora* and *intricata*/Galeana clades within the derived North American clade. The latter two clades are positioned differently in each of the parsimony analyses (either as sister to each other, or one or the other as sister the remaining derived North Americans). Similarly, the basal group has a different arrangement in each of the parsimony analyses. Likelihood and Bayesian analyses of the combined data reconstruct nearly identical trees (Fig. 7), which share the basal taxa arrangement with one parsimony analysis, and the structure of the derived North Americans from another.

The broad geographic distribution of the basal group of *Menodora* and the phylogenetic uncertainty about the arrangement of taxa within the group is consistent with what might be expected from a vicariant breakup of closely related ancestors. The use of molecular data in estimating phylogeny, and in particular techniques for estimating clade divergence times allows us to test whether vicariance is a viable option for explaining a discontinuous distribution (de Queiroz 2005). In *Menodora,* vicariance across the three continents seems unlikely, if only because of the great antiquity that is necessarily implied –the genus would have to be nearly as old as the estimated age of angiosperms if not older (ca 150-200 million years) to be truly vicariant in all three areas. In another study of the Jasmineae, the divergence time of *Menodora* was estimated to fall between 79 and 15.3 million years ago (mya), with the former date being a maximum estimate for divergence times of the Jasmineae and the latter being a minimum estimate for the derived North American clade (Lee et al. 2007). These estimates suggest that *Menodora* as well as the Jasmineae are far too young to be vicariant on an intercontinental scale. As with three-continent vicariance, vicariance of an ancestral population spanning two continents is similarly problematic since by ca 100 mya (Goldblatt 1993), none of the three continents were in close proximity.

The modern distribution of *Menodora* must therefore be the result of three independent long distance dispersals. A South American origin is inferred by reconstructions in MacClade, and thus two independent dispersals to North America and a third introduction across the Atlantic to southern Africa are required to explain the modern distribution. This is in complete disagreement with our preconceived notions of African or North American origins for the group, as discussed earlier (representing the Croizat or boreotropical, or Eurasian interpretations; see Fig. 2c and 2d), but does have some similarity to the multiple dispersals that were expected from the intuitive and preliminary morphological hypotheses.

One genus with a very similar distribution is *Pomaria* Cav. (Fabaceae: Caesalpinoideae), a small genus of 15 species. A recent phylogeny of the group (Simpson et al. 2006) indicates a North American origin with two separate dispersals to Africa and South America. While the direction of dispersals is very different from *Menodora* (which is more widespread in both North and South America), the pattern of multiple, independent dispersals is similar.

The three African species of *Pomaria* were until relatively recently (Simpson and Miao 1997) considered to belong in *Hoffmannseggia*. As such, *Hoffmannseggia s. l.* was cited by Goldblatt (1978) as one of six strictly arid-land genera including *Menodora* that share New World-African connections. Changing the circumscription of *Hoffmannseggia* to exclude the African taxa made *Hoffmannseggia s. s*. a purely New World genus, but one which still features an amphitropical New World disjunction (Simpson, Tate, and Weeks 2005). In this case, rather than the pattern of origin and dispersal seen in *Pomaria*, *Hoffmannseggia* has a South American origin, with four independent introductions into North America.

The other arid-land genera mentioned by Goldblatt (1978) do not strictly share the distribution pattern of *Menodora*. While *Parkinsonia* (including *Cercidium*, Caesalpinoideae, Fabaceae; ca 15 spp.) is found in the temperate New World, it is also found sporadically throughout the neotropics. Interpretation of a recent phylogeny indicates that it has a North American origin, with probable separate introductions into South America and northeast tropical Africa, although the relationship is unresolved (Haston, Lewis, and Hawkins 2005; Simpson et al. 2006). *Haematoxylum*, another Caesalpinoid legume, has a distribution in tropical Central and northern South America as well as the Caribbean, with a disjunction in Namibia. Recent molecular phylogenies indicate that it is part of the *Caesalpinia* group (Simpson, Larkin, and Weeks 2003; Haston, Lewis, and Hawkins 2005), and that the sole African member is in a derived position. *Tunera* (Turneraceae; 128 spp.) is another genus that is predominantly neotropical in distribution, but does have two African species, one in northeast tropical Africa, and the other in southern Africa. A recent molecular phylogeny did not include the African taxa within the taxon sampling, but series *Turnera*, to which they are ascribed, appears to be monophyletic, largely South American and tropical (Truyens, Arbo, and Shore 2005). Finally, *Thamnosma* (Rutaceae, 6 spp.) is distributed in western North America, northeast tropical Africa/Arabia, and southern tropical Africa. A molecular phylogeny for the group (Mike Thiv, pers. comm.) indicates a North American origin for the group, with dispersal to northern Africa followed by migration to the south. Thus, of the six genera specifically cited in Goldblatt (1978), only *Menodora* and *Hoffmannseggia s. l.* (*Hoffmannseggia s. s.* and *Pomaria)* actually have a common distribution. Only *Menodora* and *Hoffmannseggia s. s.* actually share parts of their distributions and a similar origin and pattern of dispersal, for while *Pomaria* and *Menodora* may have a coincident distribution, their respective origins and dispersal patterns are quite different. While the three genera together may share common elements of their distribution, which can be specifically qualified as disjunctions between New World deserts (Simpson, Tate, and Weeks 2005), the only thing they really share is the fact that each has had at least two or more long-distance intercontinental dispersals.

Moore et al. (2006) point out a pattern of multiple independent dispersals within other taxa having amphitropical disjunctions with multiple endemic species, and argue that this supports long-distance dispersal as the mechanism responsible for arid amphitropical disjunction. Given the growing body of evidence, this seems to be true, but Solbrig (1972) offered three possible explanations for the floristic similarities the Argentine Monte and the Sonoran Desert, and these apply to disjunction in general: 1) long-distance dispersal, 2) interruption of a once continuous distribution, or 3) parallel convergent evolution. The first is perhaps the easiest explanation to invoke (Solbrig 1972), but historically the hardest to defend (Humphries and Parenti 1999; de Queiroz 2005). The second explanation can cover vicariance, or migration (repeated short-distance dispersal) with extinction in the intervening zone (including origins and extinction within the intervening zone). The third explanation is only applicable in the case of disjunct species or species pairs. Fortunately, the use of molecular data, models of sequence evolution, and estimations of divergence times allows investigating all of these options.

The last case is the easiest to illustrate. Prior to this study, *Menodora heterophylla* and its variety *australis* appeared to be disjunct between North America and Africa, and specimens appear virtually identical. The molecular data reveals that they are in fact not closely related, and thus the morphologies are convergent. On the other hand, *Tiquilia nutallii* is disjunct between the Great Basin of North America and the Monte of Argentina, but samples from the two regions are morphologically and molecularly indistinguishable, leading to the conclusion that this was a recent dispersal (Moore, Tye, and Jansen 2006).

As a mechanism of dispersal, birds are most often cited as the vector in most New World amphitropical disjunctions (Raven 1963; Raven and Axelrod 1974), however, the fruit and seeds of *Menodora* do not seem particularly adapted for attracting birds, and there are no reports of birds feeding on *Menodora* (although it does serve as forage for herbivores in some habitats). The seeds seem rather large (3-12 mm in length) for wind distribution as well, which leaves water as the remaining potential vector. The southern Atlantic is isolated from the northern hemisphere by the dominant ocean currents, making interchange by water between North and South America unlikely. By default, then, we must agree, as in the case of *Hoffmannseggia* (Simpson, Tate, and Weeks 2005) that bird dispersal seems most likely, and similarly believe that shorebirds may be implicated, particularly in the second North American introduction. *Menodora. integrifolia* occurs in close proximity to the large river systems of the Mesopotamia region of eastern Argentina, Brazil, Paraguay and Uruguay which terminate at the Río de la Plata, so it is possible that seed could be carried from these rivers to the sea. Although the placement of the *heterophylla/longiflora* clade is weakly supported in the combined analyses at the base of the derived North American clade, it is of note that *M. heterophylla* shares a preference with *integrifolia* for grassland/savanna habitats, has lobed leaves typically as do some varieties of *integrifolia*, and occurs close to the coast along the Gulf of Mexico in Texas (although it is much more commonly collected further inland). While long-distance dispersal by birds seems most likely to explain the amphitropical disjunction of *Menodora*, there are no amphi-Atlantic migratory patterns that support such a hypothesis for the African disjunction. Recently, transoceanic dispersal has increasingly been seen to play a role in intercontinental disjunctions between South America and Africa (Givnish and Renner 2004; Renner 2004; de Queiroz 2005; Cowie and Holland 2006), and ocean currents are suggested as the most common vector (Renner 2004). Most species of *Menodora* are residents of continental interiors, with the sole exception being *M. robusta*, which predominantly occurs in coastal dune fields of northern Patagonia (although there are a few records deep inland as well). The Malvinas current runs northward along the Patagonian coast to the region of the Rio de la Plata, where it meets the southbound Brazil current and merges with the eastbound South Atlantic current. Propagules of *Menodora* could thus have been picked up along the Patagonian coast or at the Río de la Plata and rafted along the current until reaching southern Africa.

Perhaps the most puzzling problem in the genus from a both phylogenetic and biogeographic viewpoint is *Menodora spinescens*. Its placement in the phylogenetic tree suggests an early dispersal in the history of the group, yet its distribution is limited to a geologically young area, at ca 2-4 million years old, in a desert habitat that is probably only 8-10 thousand years old (Thorne 1986). This suggests that *M. spinescens* migrated into the region, probably as part of an arid Madro-Tertiary Geoflora assemblage coming from the south (Axelrod 1958; Thorne 1986). Some evidence for this may be seen from the slightly disjunct and patchy occurrence of *M. spinescens* in northern Baja California. In the Mojave, *M. spinescens* often forms extensive dominant or co-dominant stands on the landscape, thus it is curious that it seems all but completely absent from its presumed origin in northwestern Mexico.

Morphological Character Evolution

The major morphological character that defines *Menodora* and distinguishes it from *Jasminum* is its fruit, which is a deeply bilobed or testiculate capsule with each lobe or locule being obovate to globose and usually circumcissilely dehiscent, except in *M. robusta* and *M. spinescens* which have an irregular form of dehiscence. Steyermark (1932), apparently unaware of the nature of the fruit in *M. robusta*, interpreted this as an advanced character in *M. spinescens*. However, the bilobed fruit of *Jasminum* is an indehiscent berry, and thus the irregularly dehiscent capsules of *M. robusta* and *M. spinescens* could be interpreted as a plesiomorphic character representing an intermediate state. Mapping locule dehiscence in a tree based on the likelihood combined analysis demonstrates that this condition may be plesiomorphic in *M. robusta*, but is probably secondarily derived in *M. spinescens* (Fig. 9). The positioning of the African taxa with circumcissile dehiscence in between *M. robusta* and *M. spinescens* can lead to two interpretations: either circumcissile dehiscence evolved twice in the genus, once in the African taxa and again in the derived NewWorld taxa, or was lost in *M. spinescens*. The latter is more parsimonious, and may be supported by additional fruit characters. In *M. robusta,* the locule wall is rather thick and fleshy, and is quite berry-like until late in its development. It is also opaque and typically dark in color. The locule walls of all other species including *M. spinescens* are relatively thin and translucent, almost chartaceous. While *M. spinescens* lacks the definitive circumcissile suture, the individual locules often have a vertical groove. While this does not appear to be related to dehiscence, it is possible that this might be a vestigial remnant of the circumcissile dehiscence.

On the other hand, *M. robusta* and *M. spinescens* are also the only two species within *Menodora* that are armed. This, along with the shared lack of circumcissile dehiscence, provides support for alternative phylogenetic topologies that place *M. spinescens* closer to the base of the tree (as in Fig. 8b). Such an arrangement would be more parsimonious, allowing for a single origin of circumcissile dehiscence with no secondary reversion to the presumably plesiomorphic state.

Mapping woodiness on the tree indicates that it is an ancestral character in the group (Fig. 9), and that independent trends toward suffrutescence have occurred at least twice, once in the African taxa and again in the New World. The true shrubs in the genus are *M. robusta*, *M. spinescens*, *M. juncea*, *M. decemfida*, and perhaps *M. longiflora*. However, the degree of woodiness within the derived New World taxa is subject to interpretation, and it can be quite subjective whether an individual represents a shrub or a robust subshrub.

Pedicel habit (whether the fruit is held erect or pendant) was regarded by Steyermark (1932) as being a very important phylogenetic indicator, but this appears to be highly convergent (Fig. 9). The erect habit appears to be plesiomorphic, with the derived pendant habit appearing independently in *M.africana*/*M. heterophylla* var. *australis*, *M. heterophylla* var. *heterophylla*, the Galeana group, and the *helianthemoides/coulteri* group. In the latter group, *M. potosiensis* can often have both erect and pendant pedicels, often on the same individual.

Another trend noted by Steyermark (1932) is a reduction in leaf size. One of the problems with interpreting this, however, is that under less than optimal conditions, many species of *Menodora* may appear aphyllous. *Menodora robusta*, *M. spinescens*, and *M.*

juncea can be quite leafy when conditions are moist, but are commonly collected in a more dessicated and leafless state. In *M. intricata* and *M. scoparia*, the leaves can be quite reduced, but also can be significantly larger, particularly at the base. Thus, this leaf reduction does not seem to be so much of a trend but more of an interpretation based on too little data and bad timing for collections. Moreover, as with pedicel habit, mapping this character on the tree (Fig. 9) demonstrates independent derivations at three places in the tree.

Lobed leaves similarly appear to have been independently gained at least three lineages as well, although this is not quite as simple as that. In Figure 9, we have mapped whether a particular lineage has *predominantly* unlobed or lobed leaves, noting in the case of the *pulchella/integrifolia* clade that this character is equivocal. Simple unlobed leaves appear to be the plesiomorphic state. However, lobed leaves (usually trifid) have rarely or occasionally been noted in several other taxa which are predominantly simple and unlobed. *Menodora intricata* is commonly attributed as occasionally having trifid leaves (Steyermark 1932; Turner 1991). *Menodora decemfida* is reported to have lobed leaves occurring basally (Roig 1973), although due to the end-snatch type collection common for larger shrubs, this feature is absent from herbarium specimens. A single specimen of *M. spinescens*, Chumley 7344 (TEX), has been observed with a few trifid leaves. To add to this state of affairs, some individuals of taxa with predominantly lobed leaves can be found with only or predominantly simple, unlobed leaves. This occurs occasionally in *Menodora heterophylla* in North America, for example, but is quite common in the South American *integrifolia* complex where intergradations between the lobed var. *trifida* and unlobed var. *integrifolia* can make determinations problematic.

Major morphological characters in this group (e.g., dehiscence, pedicel habit in fruit, leaf reduction, leaf shape) thus appear to be convergent and subject to homoplasy, making it difficult to assess relationships based on morphology alone.

Systematic Implications

For the most part, the molecular phylogenies of *Menodora* support the traditional morphological interpretations of the species. There are, however, a number of instances in which the phylogeny can be used to reform our traditional notions.

As suggested by Cockerell (1932), the African variety *australis* of the North American species *M. heterophylla* is indeed not closely related to the species. It is instead imbedded within and appears as sister to the northern populations of *M. africana*. This is a remarkable case of morphological convergence, as var. *australis* is virtually indistinguishable from *M. heterophylla* but is quite distinct morphologically from *M. africana*. We have seen no intermediate specimens suggesting a range of intergradation between *M. africana* and var. *australis*, and thus the latter should probably be considered a variety or possibly subspecies of the former.

There appears to be no molecular support for the varieties of *M. integrifolia*, although the data do confirm that taxa placed in the species (*trifida, pinnatisecta,* and *odonelliana*) belong there, and do not support restoring var. *trifida* to specific status as suggested by Correa (1999). While it might be expected that varietal populations might interbreed, we would expect there to be some geographic structure, and where resolution exists, we do not find this. Morphologically, there are a lot of intermediate specimens that make determination difficult and problematic, as noted above, and while the varieties do exhibit some geographic tendencies, one can find them occasionally outside of what might be considered their principal range. Thus, the evidence suggests that *M. integrifolia* is a single, highly polymorphic species with no varieties.

Similarly, there is little molecular support for the use of varietal ranks within *Menodora helianthemoides* or *M. coulteri*. The data suggest that the elevation of *M. magniflora* to specific status by Turner (1991) should be reconsidered, as it seems firmly imbedded within *helianthemoides*. Surprisingly, two species named by Turner (1991) which we believed might also prove to be conspecific with *helianthemoides* appear to be evolutionarily distinct. *Menodora tehuacana* is an independent lineage, but commonly appears as sister to *M. helianthemoides* in most analyses. *Menodora jaliscana*, which morphologically falls within the *helianthemoides-tehuacana* group, is quite surprisingly sister to the *coulteri* clade in the chloroplast trees. We believe this to be a case of chloroplast capture, but since we were unable to amplify ITS we cannot test this definitively at this time.

Another species named by Turner (1991) provided a similar surprise. We considered *Menodora hintoniorum* to be very close morphologically to, if not conspecific with, *M. coulteri* var. *coulteri.* In our molecular analyses, our sample of *M. hintoniorum* did form a clade with a sample we had determined to be *M. coulteri*, however, they were not imbedded within or even closely related to *M. coulteri* as we expected, but instead, are sister to the *M. muellerae/M. gypsophila* clade. Even more surprising, though was the grouping of a third sample with the two "*hintoniorums*," one that had been determined as *M. magniflora*. This is an atypical specimen of the latter species, in that the leaves and flowers are smaller than usual, but it shares a similar vestiture. Thus it appears that the concept of *M. hintoniorum* needs to be enlarged to account for this different morphology.

Menodora scabra sensu Turner (1991) is a broadly defined and highly polymorphic group. Varieties, as defined in Steyermark (1932) are not recognized, and

Turner included *M. scoparia* and *M. decemfida* var. *longifolia* in his concept of the species. With the exception of the former, Turner's treatment of these as a single closely related group is supported by the molecular phylogeny. *Menodora scoparia*, however, appears to be a purely Chihuahuan Desert group, and is sister to a *scabra s.l.* that includes *M. yecorana*. Within the *scabra* clade, there is a strongly supported split between the eastern and western populations of the species, and these could potentially be recognized as different varieties or possibly species. Within the eastern group, there is little resolution between populations, but within the western group, there is complete resolution, including samples that can be referred to *M. scoparia* as treated in the California flora. This structure suggests a closer examination of the western group is warranted to assess variation that might be recognized at the varietal or even specific rank.

While this study was not intended to resolve taxonomic issues at higher levels within the Jasmineae, it does lead to some general conclusions. It does strongly support that *Menodora* is an independent lineage, and plainly, *Menodora* is quite morphologically distinguished from *Jasminum*. Within *Jasminum*, two lineages are evident, representing the opposite and alternate-leaved jasmines. Wallander and Albert (2000) suggested that *Jasminum* might be paraphyletic and that *Menodora* could possibly be included within *Jasminum*. Our data suggest that the problem of a paraphyletic *Jasminum* is not with the placement of *Menodora*, but with the jasmines of section *Alternifolia*. These have long been recognized as a natural grouping, and share a common suite of features (e.g., alternate leaves, yellow flowers) that distinguish them from the other jasmines, which have opposite leaves and predominantly white flowers (Green 1961; Green 2004). Thus in a traditional taxonomic treatment, it might be best to segregate section *Alternifolia* from *Jasminum* and recognize it as a distinct genus in order to resolve these questions.

CONCLUSIONS

Menodora is strongly supported as monophyletic lineage within the tribe Jasmineae, although its relative position within the group is not strongly resolved. This lack of resolution among the three major clades of the tribe (*Menodora*, *Jasminum* sect. *Alternifolia*, and all other jasmines) suggest that sect. *Alternifolia* should be segregated from *Jasminum* in order to solve questions of a paraphyletic genus. Within *Menodora*, three major groupings can be recognized: a basal set (consisting of the South American *M. robusta*, the North American *M. spinescens*, and an African clade), a derived intermediate South American set (*M. decemfida, and M. pulchella/M. integrifolia*), and a derived North American clade (all North American taxa except *M. spinescens*). Generally, specimens sampled came together in morphologically-defined species groups as expected, although relationships between groups did not conform to expectations based upon intuitive hypotheses or preliminary morphological analyses. Mapping morphological characters onto molecular trees indicates that some of them have been the result of convergent evolution, thus suggesting that gross morphology may not be a reliable indicator of relationships within the group. This is particularly true in the case of what now appear to be cryptic taxa. Most prominent among these is the North American *M. heterophylla* and its South African variety *australis*, which are so close morphologically as to be indistinguishable, but molecular data show to be only distantly related, with former in the derived North American clade and the latter as part of the basal group of monophyletic African taxa. Similarly taxa we believed might lie within *M. helianthemoides*, *M. tehuacana* and *M. jaliscana*, proved to be independent though closely related lineages. In the derived North American clade, *M. hintoniorum* forms a weakly supported clade that morphologically is difficult to distinguish from either *M.*

coulteri or *M. magniflora*, two species with very different and easily distinguishable morphologies. The latter two species are more closely related to each other than either is to the cryptic *hintoniorum*.

Support is also found for Turner's (1991) broad concept of *Menodora scabra*, with the exceptions that *M. yecorana* should be included and *M. scoparia* appears to be a more or less distinct group outside of *scabra*. However, there is strong support from the ITS and combined data that show *M. scabra* to have distinct eastern (Chihuahuan Desert) and western clades. The *scoparia* group appears to be restricted to the Chihuahuan Desert region, as western scoparioids in this study group routinely with the western *scabra*. Both *scoparia* and the not closely related the *intricata* group appear to be somewhat mobile in their placements depending on the data set, how the gaps were treated, and the optimality criterion. This could indicate that these groups may have hybrid origins.

The biogeography of *Menodora* remains an interesting study of disjunction, if only for the fact it has managed to get around so much, which is remarkable for a genus with no obvious adaptations for dispersal and with such relatively narrow ecological requirements. While early authors (Cockerell 1932; Steyermark 1932; Cain 1944) considered the distribution to be evidence of what would later be called vicariance, the estimated age of the group (Lee et al. 2007) far postdates the breakup of Pangaea or Gondwana. The morphology of *M. robusta* seems consistent with its placement along the earliest branch, and supports a South American origin for the genus. In order to explain the modern distribution of the genus, three independent dispersals out of South America are required. The first two, one to North America with the ancestor of *M. spinescens* and another to southern Africa with the ancestor of all the African taxa, may have occurred almost simultaneously, in a geologic sense, as there is weak support in this part of the tree and alternate topologies cannot be categorically dismissed. *Menodora spinescens* is plainly more closely related to either the Africans or *M. robusta* than it is to other North American species, which are derived from a single, later dispersal from South America to probably the Gulf Coast of Texas or northern Mexico. We suggest, more or less by default due to the lack of better alternatives, that bird dispersal is probably the vector for immigration in the New World, but that ocean currents may have carried propagules from South America to Africa.

As stated by Simpson et al. (2005), we must be aware that blanket terms like amphitropical or amphi-Atlantic actually incorporate a number of different patterns, and we should further qualify such statements before making comparisons between taxa that ostensibly share the same kind of distribution. The origin, direction of dispersal, actual dispositions of the disjunctions (i.e., do they occur in the same places/habitats), and the timing of dispersal or vicariance are all things that could be considered. For example, although *Menodora* and *Pomaria* (Fabaceae) largely share most of their distribution in North America, South America, and Africa, their origins and directions of dispersal are diametrically opposite. In another example, *Tiquilia* (Boraginaceae) and *Menodora* share much of their North American distribution, often occurring in the same localities, but overlap in South America only with the relatively recent dispersal of *Tiquilia nutallii* to Argentina (Moore, Tye, and Jansen 2006); *Menodora* overlaps this species only along the southern edge of its Great Basin distribution in North America, and other than *T. nutallii,* the southern distribution of *Tiquilia* is entirely in Chile, Peru and the Galapagos Islands. The only attributes these taxa share is that they got to their common points through some form of long-distance dispersal, and that it often occurred not just once but multiple times. This means that these taxa, despite appearances in some cases, are readily dispersed.

Ideally, when looking for biogeographic patterns, what we are looking for is a Clementsian ideal, a broadly-shared pattern of things going to the same places at the same time. In some cases, such as in the boreotropical or Berengian hypotheses, there is a growing body of evidence for such patterns, but at the same time, we see many examples of a more Gleasonian or individualistic pattern in the assembly of floras, and though the end results may be similar, the actual pattern is quite different. *Menodora* is a part of the larger patterns of amphitropical and amphi-Atlantic disjunction, but seems to be unique: a rugged individual, if you will, intent on finding its own path despite its dispersalist deficiencies.

Table 1. Accepted taxa in the genus *Menodora* Bonpl. (Oleaceae) following recent treatments (Steyermark 1932, Rehder 1935, Meyer 1957, Burkart 1979, Turner 1991, 1995, Van Devender & Turner 1997) but not that of Correa (1999).

TAXON	**DISTRIBUTION**	**NOTES**
M. africana Hook.	Africa (South Africa, Botswana)	
M. coulteri A. Gray var. *coulteri*	North America (Mexico)	
M. coulteri A. Gray var. *minima* Steyerm.	North America (Mexico)	Including: *M. helianthemoides* Humb. & Bonpl. var. *engelmannii* Steyerm.
M. decemfida (Gill.) A. Gray	South America (Argentina)	
M. gypsophila B.L. Turner	North America (Mexico)	
M. helianthemoides Humb. & Bonpl.	North America (Mexico)	Including: *M. helianthemoides.* var. *parviflora* Greenman
M. heterophylla Moric. *ex* A. DC. var. *australis* Steyerm.	Africa (South Africa, Botswana)	
M. heterophylla Moric. *ex* A. DC. var. *heterophylla*	North America (USA, Mexico)	
M. hintoniorum B.L. Turner	North America (Mexico)	
M. integrifolia (Cham. & Schltdl.) Steud. var. *integrifolia*	South America (Argentina, Brazil, Paraguay, Uruguay)	
M. integrifolia (Cham. & Schltdl.) Steud. var. *odonelliana* T. Meyer	South America (Argentina)	Correa (1999), places this taxon in synonymy under *trifida*
M. integrifolia (Cham. &Schltdl.) Steud. var. *pinnatisecta* (Steyerm.) Burk.	South America (Argentina, Paraguay)	Including: **M. pinnatisecta* var. *missionum* T. Meyer
M. integrifolia (Cham. &Schltdl.) Steud. var. *trifida* (Cham. &Schltdl.) Kuntze.	South America (Argentina, Bolivia)	Including: ***M. chlorargantha* (J. Rémy) Steyerm.; *M. hassleriana* Chodat; Correa (1999) restores this taxon o species status
M. intricata T. Brandegee	North America (Mexico)	Including: *M. intricata* var. *purpusi* Steyerm.
M. jaliscana B.L. Turner	North America (Mexico)	
M. juncea Harv.	Africa (South Africa)	
****M. linoides* Phil.	South America (Chile)	
M. longiflora A. Gray	North America (USA, Mexico)	Including: *Menodora pubens* A. Gray, *M. hispida* Palmer
M. magniflora (Steyerm.) B.L. Turner	North America (Mexico)	Including: *M. helianthemoides* var. *magniflora* Steyerm. (basionym), *M. helianthemoides* var. *humilis* Steyerm.
M. mexicana (A. DC.) A. Gray	North America (Mexico)	
M. muellerae Rehder	North America (Mexico)	
M. potosiensis B.L. Turner	North America (Mexico)	
M. pulchella Markgr.	South America (Argentina, Bolivia)	
M. robusta (Benth.) A. Gray	South America (Argentina)	
M. scabra A. Gray	North America (USA, Mexico)	Including: *M. decemfida* (Gill.) A. Gray var. *longifolia* Steyerm., *M. scabra* var. *glabrescens, M. scabra* var. *laevis* (Woot. & Standl.) Steyerm., *M. scabra* var. *longituba* Steyerm., *M. scabra* var. *ramosissima* Steyerm., *M. scoparia* Engelm. *ex* A. Gray
M. spinescens A. Gray	North America (USA, Mexico)	*M. spinescens* var. *mohavensis* Steyerm.
M. tehuacana B.L. Turner	North America (Mexico)	
M. yecorana T. Van Devender & B. L. Turner	North America (Mexico)	

* Although Burkart (1979) transferred *M. pinnatisecta* to varietal status under *M. integrifolia*, he did not make any decisions on the status of variety *missionum*, but as treated here, both varieties belong to *M. integrifolia* var. *pinnatisecta.*

** Though not treated systematically in any published work, from the original description, subsequent collections from Bolivia, and examination of the type at Paris, this species is probably *M. integrifolia* var. *trifida*.

***This has similarly never been treated within the context of genus as a whole, and until December 2004 (Faundez 2005) had never been seen in Chile since the type was collected in 1863. Examination of the type and isotype at Santiago is inconclusive, and it seems probable that this may be conspecific with *M. integrifolia*, though it is quite disjunct from the range of the species. Its status at specific rank is preserved for the moment, and more data, particularly molecular, are needed to resolve its placement.

Table 2. Voucher information for samples used in this study. for species and authority names for *Menodora*, refer to Table 1. Source: h = h leaf material, f = fresh leaf material, s = silica-dried leaf or stem material, g = GenBank accessions.

					GenBank Accession Number		
Taxon	**Source**	**Voucher**	**Specimen code (in phyl. trees)**	**Locality**	**ITS**	***rps16* intron**	***trnL-F***
Nyctanthes arbortristus L.	g	Dahlstrand s.n. (GB)	Nyctanthes			AF225272	AF231863
Forsythia suspense Vahl	g	Jutila 556 (NY)	Forsythia			AF225231	AF231823
Jasminum angulare Vahl	f	commercial	J.angulare				
J. floridum Bunge	f	cultivated	J.floridum				
J. fluminense Vell.	g	L. Struwe 1098 (NY)	J.fluminense		--	AF225246	AF231837
J. humile L.	f	commercial	J.humile.2		--		
J. humile L.	h	Dahlstrand 2073 (GB)	J.humile			AF225247	AF231838
J. mesnyi Hance	f	cultivated	J.mesnyi.2		--		
J. mesnyi Hance	g	Dahlstrand 37 (GB)	J.mesnyi			AF225248	AF231839
J. molle R. Br.	f	commercial	J.molle				--
J. nitidum Skan	f	commercial	J.nitidum.2		--	TBS	TBS
J. nitidum Skan	g	Wallander 195 (GB)	J.nitidum		--	AF225249	AF231840
J. nudiflorum Lindl.	g	Wallander 193 (GB)	J.nudiflorum			AF225250	AF231841
J. odoratissimum L. var. *odoratissimum*	g	Wallander 130 (GB)	J.odoratissimum		--	AF225251	AF231842
J. officinale L.	g	Wallander 194 (GB)	J.officinale			AF225252	AF231843
J. parkeri Dunn	f	commercial	J.parkeri				
J. polyanthum Franch.	f	commercial	J.polyanthum				
J. rex Dunn	f	commercial	J.rex				
J. sambac (L.) Aiton.	f	commercial	J.sambac				--
J. sinense Hemsl.	g	Sino-American Guizhou Bot Exp. 228 (NY)	J.sinense		--	AF225253	AF213844
J. tortuosum Willd.	f	commercial	J.tortuosum		--		
Menodora africana	g/h	Dahlstrand 1081 (GB)	mafr.D1081w	Gauteng, South Africa		AF225258	AF231849

Table 2. (continued)

Taxon	**Source**	**Voucher**	**Specimen code (in phyl. trees)**	**Locality**	**GenBank Accession Number**		
					ITS	***rps16* intron**	***trnL-F***
M. africana	s	Chumley 7338 (TEX)	mafr.C7338	KwaZulu-Natal, South Africa			
M. africana	h*	Bredenkamp & Van Vuuren 45 (MO)	mafr.B45.m8	Limpopo, South Africa		--	
M. africana	s	Chumley 7339 (TEX)	mafr.C7339	KwaZulu-Natal, South Africa			
M. coulteri var. *coulteri*	h	Hinton et al. 24734 (MEXU)	mcoco.H24734	Durango, Mexico			
M. coulteri var. *coulteri*	h	Chiang et al. 8204 (TEX)	mcoco.C8204.2	San Luis Potosí, Mexico			
M. coulteri var. *coulteri*	h	Salinas et al. F3778 (TEX)	mcoco.SF3778	Puebla, Mexico			
M. coulteri var. *coulteri*	h	Rollins 7467 (TEX)	mcoco.R7467	Coahuila, Mexico			
M. coulteri var. *minima*	s	Henrickson & Vanden Heuvel 22433 (TEX)	mcomi.H22433	Nuevo Leon, Mexico			
M. coulteri var. *minima*	s	Chumley 7402 (TEX)	mcomi.C7402	Nuevo Leon, Mexico			
M. coulteri var. *minima*	s	Panero s.n. (TEX)	mcomi.Pxx	San Luis Potosí, Mexico			
M. coulteri var. *minima*	s	Chumley 7406 (TEX)	mcomi.C7406	Nuevo Leon, Mexico			
M. decemfida	s	Chumley 7371 (TEX)	mdec.C7371	Mendoza, Argentina			
M. decemfida	s	Chumley 7377 (TEX)	mdec.C7377	Mendoza, Argentina			
M. gypsophila	h[4]	G. B. Hinton 24474 (TEX)	mgyp.H24474.m11	Nuevo Leon, Mexico			
M. gypsophila	h	Hinton et al. 25863 (TEX)	mgyp.H2863	Nuevo Leon, Mexico			
M. gypsophila	s	Chumley 7394 (TEX)	mgyp.C7394	Nuevo Leon, Mexico			
M. gypsophila	s	Chumley 7396 (TEX)	mgyp.C7396	Nuevo Leon, Mexico			
M. gypsophila	s	Chumley 7397 (TEX)	mgyp.C7397	Nuevo Leon, Mexico			
M. gypsophila	s	Chumley 7399 (TEX)	mgyp.C7399	Nuevo Leon, Mexico			
M. helianthemoides (var. *helianthemoides)*	h	Martinez s.n. (MEXU)	mhehe.Msn	Hidalgo, Mexico			
M. helianthemoides (var. *helianthemoides)*	h[4]	Tenorio 6768 (TEX)	mhel.T6768.m12	Puebla, Mexico			
M. helianthemoides (var. *helianthemoides)*	h	Panero 3441 (TEX)	mhehe.P3441	Puebla, Mexico			
M. helianthemoides (var. *parviflora)*	h	Torres 15215 (TEX)	mhepa.RTC15215	San Luis Potosí, Mexico			
M. heterophylla var. *australis*	s	Chumley 7340 (TEX)	maus.C7340	Northwest, South Africa			

Table 2. (continued)

Taxon	Source	Voucher	Specimen code (in phyl. trees)	Locality	GenBank Accession Number		
					ITS	***rps16* intron**	***trnL-F***
M. heterophylla var. *australis*	h^4	C. Peeters et al. 261 (MO)	maus.P261.m13	Northwest, South Africa			
M. heterophylla var. *heterophylla*	h^4	B.L. Turner #93-168 (TEX)	mhet.T93168.m2	Texas, USA		--	
M. heterophylla var. *heterophylla*	s	Chumley 7370 (TEX)	mhet.C7370	Texas, USA			
M. heterophylla var. *heterophylla*	s	Chumley 7304 (TEX)	mhet.C7304	Texas, USA			
M. hintoniorum	h	G. B. Hinton 22066 (TEX)	mhin.H22066.m15	Coahuila, Mexico			
M. integrifolia var. *integrifolia*	s	Chumley 7420 (TEX)	mint.C7420	Misiones, Argentina			
M. integrifolia var. *odonelliana*	h	Fortunato 4745 (NY)	modon.F4745	Rio Negro, Argentina			
M. integrifolia var. *odonelliana*	s	Chumley 7424 (TEX)	modon.C7424	Rio Negro, Argentina			
M. integrifolia var. *pinnatisecta*	g/h	Tressens et al 546 (GB)	mint.T546w	Corrientes, Argentina		AF225259	AF231850
M. integrifolia var. *pinnatisecta*	s	Chumley 7409 (TEX)	mpin.C7409	Corrientes, Argentina			
M. integrifolia var. *pinnatisecta*	s	Chumley 7410 (TEX)	mpin.C7410	Corrientes, Argentina			
M. integrifolia var. *pinnatisecta*	s	Chumley 7411 (TEX)	mpin.C7411	Chaco, Argentina			
M. integrifolia var. *pinnatisecta*	s	Chumley 7414 (TEX)	mpin.C7414	Chaco, Argentina			
M. integrifolia var. *trifida*	h^4	Cristóbal et al. 1655 (MO)	mint.C1655.m1	Corrientes, Argentina		--	
M. integrifolia var. *trifida*	h	Sigle 172 (TEX)	mtrif.S172	Cochabamba, Bolivia	--	TBS	--
M. integrifolia var. *trifida*	s	Chumley 7381 (TEX)	mtrif.C7381	Cordoba, Argentina			
M. integrifolia var. *trifida*	s	Chumley 7382 (TEX)	mtrif.C7382	Salta, Argentina			
M. integrifolia var. *trifida*		Chumley 7383 (TEX)	mtrif.C7383	Salta, Argentina			
M. integrifolia var. *trifida*	s	Chumley 7413 (TEX)	mtrif.C7413	Chaco, Argentina			
M. integrifolia var. *trifida*	s	Bastión 821 (TEX)	mtrif.B821	Tarija, Bolivia			
M. intricata	h^4	Webster & Armbruster 20545 (TEX)	mintr.W20545.m15	Tamaulipas, Mexico			

Table 2. (continued)

Taxon	**Source**	**Voucher**	**Specimen code (in phyl. trees)**	**Locality**	**GenBank Accession Number**		
					ITS	***rps16* intron**	***trnL-F***
M. intricata	s	Chumley 7400 (TEX)	mintr.C7400	Tamaulipas, Mexico			
M. intricata	s	Chumley 7401 (TEX)	mintr.C7401	San Luis Potosí, Mexico			
M. intricata	h	Chiang F-2256 (TEX)	mintr.CF2256	Puebla, Mexico			
M. jaliscana	h	Rios 291 (MEXU)	mjal.R291	Jalisco, Mexico	--		
M. juncea	s	Chumley 7342 (TEX)	mjunc.C7342	Beaufort West, South Africa			
M. juncea	h[4]	Oliver et al. 138 (MO)	mjunc.O138.m16	Northern Cape, South Africa			
M. longiflora	s	Chumley 7301 (TEX)	mlong.C7301	Texas, USA			
M. longiflora	s	Chumley 7393 (TEX)	mlong.C7393	Nuevo Leon, Mexico			
M. longiflora	s	Chumley 7356 (TEX)	mlong.C7356	Nuevo Leon, Mexico			
M. longiflora	h[4]	B. L. Turner 97-447 (TEX)	mlong.T97447.m18	Texas, USA	--		
M. longiflora	h[4]	A. Prather 1464 (TEX)	mlong.P1464.m17	Nuevo Leon, Mexico			
M. longiflora	s	Moore 122 (TEX)	mlong.M122	Texas, USA			
M. longiflora	s	Chumley 7358 (TEX)	mlong.C7358	New Mexico, USA			
M. longiflora	s	Chumley 7403 (TEX)	mlong.C7403	Nuevo Leon, Mexico			
M. magniflora	h	Hinton et al. 21048 (TEX)	mmag.H21048	Coahuila, Mexico			
M. magniflora	h	Hernandez et al. 9741 (MEXU)	mmag.H9741	Guanajuato, Mexico			
M. muellerae	h	Hinton et al. 25349 (TEX)	mmuel.25349t	Nuevo Leon, Mexico			
M. potosiensis	h	Chiang et al. 8137 (TEX)	mpot.C8137	San Luis Potosí, Mexico			
M. pulchella	s	Simpson 1-II-00-7 (TEX)	mpul.S12007	Jujuy, Argentina			
M. pulchella	s	Panero 8503 (TEX)	mpul.P8503	Jujuy, Argentina			
M. robusta	s	Chumley 7422 (TEX)	mrob.C7422	Chubut, Argentina			
M. robusta	s	Chumley 7422a (TEX)	mrob.C7422a	Chubut, Argentina			
M. scabra *(decemfida* var. *longifolia)*	h	Palmer 429 (NY)	mscab.P429	Durango, Mexico			
M. scabra (M. scoparia)	s	Chumley 7361 (TEX)	mscab.C7361	Arizona, USA			
M. scabra (M. scoparia)	s	Henrickson 23750 (TEX)	mscop.H23750A	Coahuila, Mexico			

Table 2. (continued)

Taxon	Source	Voucher	Specimen code (in phyl. trees)	Locality	GenBank Accession Number		
					ITS	***rps16* intron**	***trnL-F***
M. scabra (M. scoparia)	s	Henrickson 23108 (TEX)	mscop.H23108	Coahuila, Mexico			
M. scabra (M. scoparia)	h	Moran 17646 (LL)	mscop.M17646	Baja California Norte, Mexico			
M. scabra (M. scoparia)	h[4]	Miller et al. 5109 (MO)	mscop.M5106.m24	Texas, USA		--	
M. scabra (M. scoparia)	s	Chumley 7404 (TEX)	mscop.C7404	Nuevo Leon, Mexico			
M. scabra (var. laevis)	s	Moore 126 (TEX)	mscab.M126	Texas, USA			
M. scabra (var. laevis)	s	Moore 147 (TEX)	mscab.M147	Texas, USA			
M. scabra (var. laevis)	s	Moore et al. 268 (TEX)	mscab.M268	Coahuila, Mexico			
M. scabra (var. laevis)	s	Chumley 7306 (TEX)	mscab.C7306	Texas, USA			
M. scabra (var. laevis)	s	Chumley 7391 (TEX)	mscab.C7391	Coahuila, Mexico			
M. scabra (var. laevis)	h[4]	Turner 99-442 (TEX)	mscab.T99442.m22	Texas, USA		--	
M. scabra (var. ramosissima)	s	Chumley 7318 (TEX)	mscab.C7318	Arizona, USA			
M. scabra (var. ramosissima)	s	Chumley 7313 (TEX)	mscab.C7313	Texas, USA			
M. scabra (var. ramosissima)	s	Chumley 7314 (TEX)	mscab.C7314	New Mexico, USA			
M. scabra (var. ramosissima)	s	Moore et al. 231 (TEX)	mscab.M231	Arizona, USA			
M. scabra (var. scabra)	s	Moore et al. 244 (TEX)	mscab.M244	Chihuahua, Mexico			
M. scabra (var. scabra)	s	Moore et al. 256 (TEX)	mscab.M256	Chihuahua, Mexico			
M. scabra (var. scabra)	h	Chumley 7367 (TEX)	mscab.C7367	Colorado, USA			TBS[3]
M. scabra (var. scabra)	s	Chumley 7363 (TEX)	mscab.C7363	Colorado, USA			
M. scabra (var. scabra)	s	Chumley 7392 (TEX)	mscab.C7392	Coahuila, Mexico			
M. spinescens	h	Prigge 798 (TEX)	mspin.P2	California, USA			
M. spinescens	h[4]	Morefield 4399 (MO)	mspin.M4399.m25	Nevada, USA		--	
M. spinescens	h[4]*	Morefield 4399 (TEX)	mspin.M4399.m26	Nevada, USA		--	
M. spinescens	s	Chumley 7347 (TEX)	mspin.C7347	Nevada, USA			
M. tehuacana	h[4]	Chiang et al. 2332 (TEX)	mteh.C2332.m27	Puebla, Mexico			
M. tehuacana	h	Salinas et al. 5487 (MEXU)	mteh.S5487	Puebla, Mexico			

Table 2. (continued)

Taxon	**Source**	**Voucher**	**Specimen code (in phyl. trees)**	**Locality**	**GenBank Accession Number**		
					ITS	***rps16* intron**	***trnL-F***
M. yecorana	h	Reina 97-1188 (TEX)	myec.R971188	Sonora, Mexico			
Syringa vulgaris L.	g		Syringa				

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[1] ITS sequences provided by Eva Wallander, whom we would also like to thank for pre-publication access to *rps16* intron and *trnL-F* sequences. [2] ITS sequenced at the University of Texas-Austin from DNA provided by Eva Wallander. [3] Only *trnL* intron was successfully amplified and sequenced. [4] Sequenced at Yeungnam University, Korea.

Table 3. Summary statistics of parsimony analyses. Gap treatments: O – gaps omitted from analysis; ? – gaps included as missing characters; 5 – gaps included as a fifth base. PI = parsimony informative; MP = most parsimonious; CI = consistency index; RI = restriction index; RC = rescaled consistency index. Homoplasy indices calculated with parsimony uninformative characters excluded.

marker	gap treatment	# taxa	total # characters	# characters used	# PI characters	# MP trees	length	CI	RI	RC
ITS	O	108	860	614	266	2054100*	1161	0.431	0.823	0.355
		108		712	299	2084071*	1293	0.443	0.824	0.365
	5	108		712	358	1768491	1583	0.466	0.831	0.388
rps16	O	108	1201	767	151	10242	292	0.781	0.96	0.75
intron	?	108		1055	168	2138000*	342	0.778	0.958	0.745
		108		1055	432	6378	927	0.723	0.942	0.681
trnL-F	O	115	2390[†]	776	146	36515	277	0.781	0.963	0.752
?		115		954	147	1979300*	293	0.783	0.961	0.753
		114		954	309	249699	685	0.684	0.915	0.626
combined	O	118		1543	297	1979300*	578	0.766	0.958	0.734
cp	?	103		2009	317	1962900*	615	0.781	0.956	0.747
5		103		2009	730	6898	1551	0.63	0.876	0.552
combined	O	119	4451	2157	569	1887100*	1777	0.523	0.877	0.459
?		95		2721	563	1962900*	1793	0.54	0.856	0.462
5	5	95		2721	1016	3840	2956	0.551	0.856	0.472

***** Analysis terminated at out of memory error. All other analyses swapped to completion. [†]Aligned length includes 1213 bp of the *trnT-L* spacer for some taxa.

5

?

Table 4. Likelihood and parsimony scores of trees resulting from maximum likelihood analysis using GARLI. Each data set was analyzed with gaps omitted or included as missing characters, and five independent runs were made using each permutation. Resulting trees were scored in PAUP* using the optimal model of evolution as suggested by ModelTest, and all 10 resulting trees from a particular dataset were scored using both permutations. Scores in bold highlight the best score(s) within a particular dataset permutation.

		gaps omitted (-O)					gaps as missing characters (-?)				
marker - gaps	**model**	**1**	**2**	**3**	**4**	**5**	**1**	**2**	**3**	**4**	**5**
ITS-O	GTR +G+I	7457.39	7452.09991	7453.79297	7457.45414	7454.12857	**7450.40101**	7450.46758	7450.40114	7450.40113	**7450.40101**
	pscore	1317	1316	1316	1318	1317	**1314**	1315	**1314**	**1314**	**1314**
	pscore	**1179**	1180	1180	1180	1180	**1179**	1180	**1179**	**1179**	**1179**
rps-O	TVM +G	3687.73235	3687.73235	3680.71269	3686.60038	3687.73235	**3673.99119**	**3673.99119**	**3673.99119**	**3673.99119**	**3673.99119**
	pscore	344	344	343	344	344	**342**	**342**	**342**	**342**	**342**
-	pscore	**292**	**292**	**292**	**292**	**292**	**292**	**292**	**292**	**292**	**292**
trn-O	K81uf +G	**2861.71717**	**2861.71717**	2861.71722	2861.71722	**2861.71717**	2864.32399	2864.324	2864.32393	2864.324	2864.32393
	pscore	**278**	**278**	**278**	**278**	**278**	279	279	279	279	279
	pscore	329	329	329	329	329	**328**	**328**	**328**	**328**	**328**
cp-O	TVM +G	**6065.18346**	6065.18438	**6065.18347**	6065.18364	**6065.18347**	6068.01131	6068.00782	6068.00764	6068.00756	6068.01121
	pscore	**578**	579	579	579	579	579	**578**	579	579	579
	pscore	683	684	684	684	684	680	**679**	680	680	680
com-O	GTR +G+I	**13336.8498**	**13336.8498**	**13336.8498**	13337.5387	13337.5402	13343.9748	13343.9768	13343.9749	13343.9748	13343.9748
	pscore	1780	1780	1780	1780	1780	**1777**	**1777**	**1777**	**1777**	**1777**
	pscore	2022	2022	2022	2022	2023	**2013**	**2013**	**2013**	**2013**	**2013**

Table 5. Results of internal length difference (ILD) tests from PAUP*. Tests compared individual data partitions against each other, and the ITS data against the combined chloroplast data. The different gap treatments were also compared.

partition 1:partition 2	**gaps omitted**	**gaps as missing**	**gaps as 5th base**
ITS:rps16 intron	0.269	0.023	0.001
ITS:trnL-F	0.986	0.973	0.001
ITS: combined cp	0.111	0.053	0.001
rps16 intron: trnL-F	0.245	0.026	0.001

Table 6. Results of Shimodaira-Hasegawa test comparing an optimal ML tree with gaps included against 18 alternative topologies.

tree	modification	p value
1	*muellerae* sister to *hintoniorum*	0.412
2	basal clade *robusta* (*spinescens*-Africans)	0.220
3	basal monophyletic South American	0.000*
4	derived monophyletic North American	0.000*
5	derived monophyletic South American	0.000*
6	*intricata-scoparia* sister, together sister to *scabra*	0.036*
7	*intricata-scoparia* sister, together sister to Galeana clade	0.042*
8	*intricata-scoparia* sister, together sister to *helianthemoides*	0.036*
9	*intricate* and *scoparia* swap places	0.037*
10	*scoparia* sister to *helianthemoides*	0.309
11	*scoparia* sister to Galeana group, *intricata* sister to *helianthemoides*	0.130
12	*intricata*/Galeana sister to remaining derived North American	0.229
13	*intricata*/Galeana & *heterophylla-longiflora* sister, both sister to remaining derived North American	0.304
14	monophyletic *Jasminum*	0.440
15	basal clade Africans (*robusta* - *spinescens*)	0.222
16	basal nested Africans-(*robusta* - *spinescens*)	0.104
17	basal nested Africans - *robusta* - *spinescens*	0.121
18	basal clade, Africans not monophyletic	0.014*

* $p < 0.05$

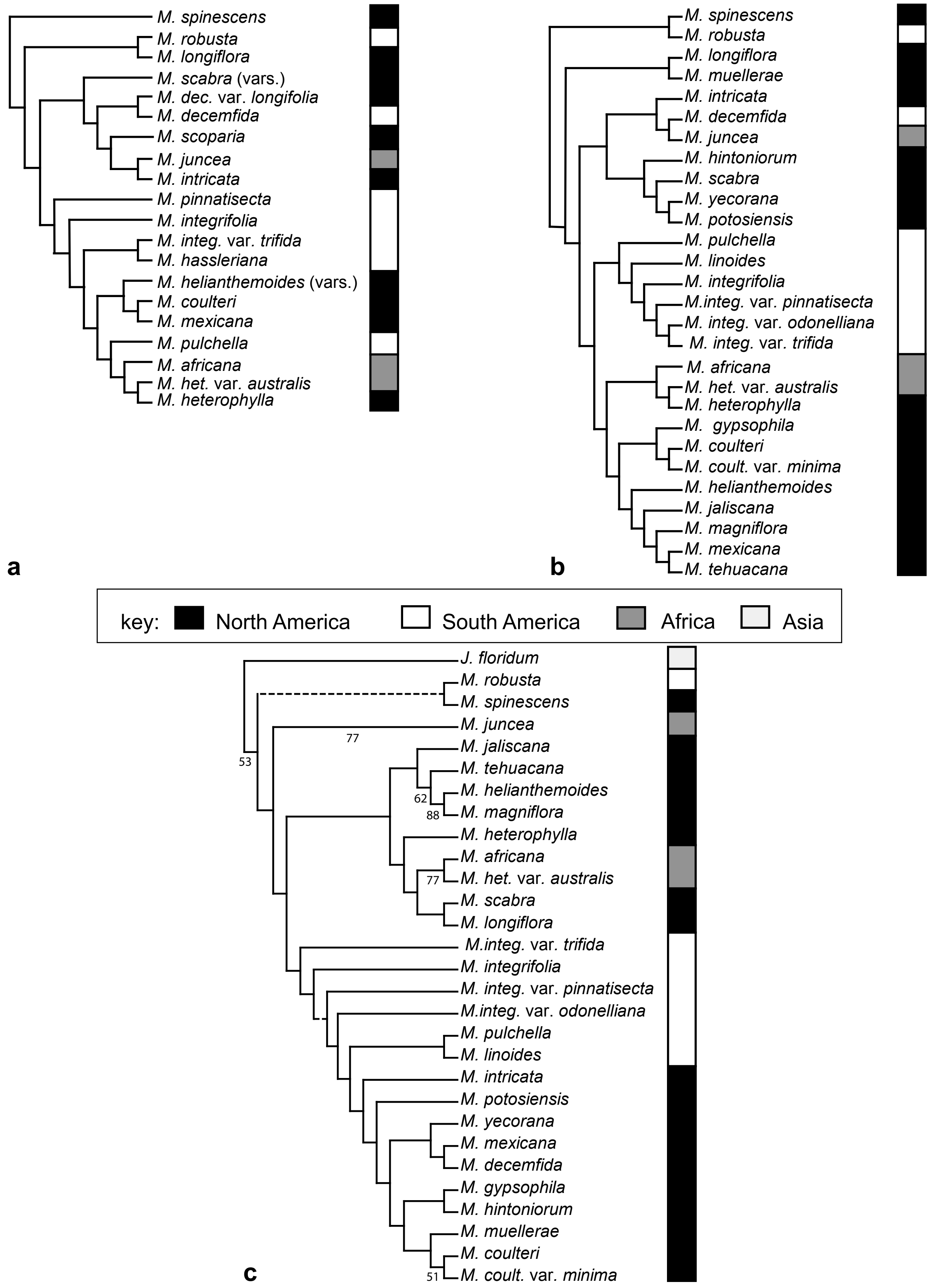
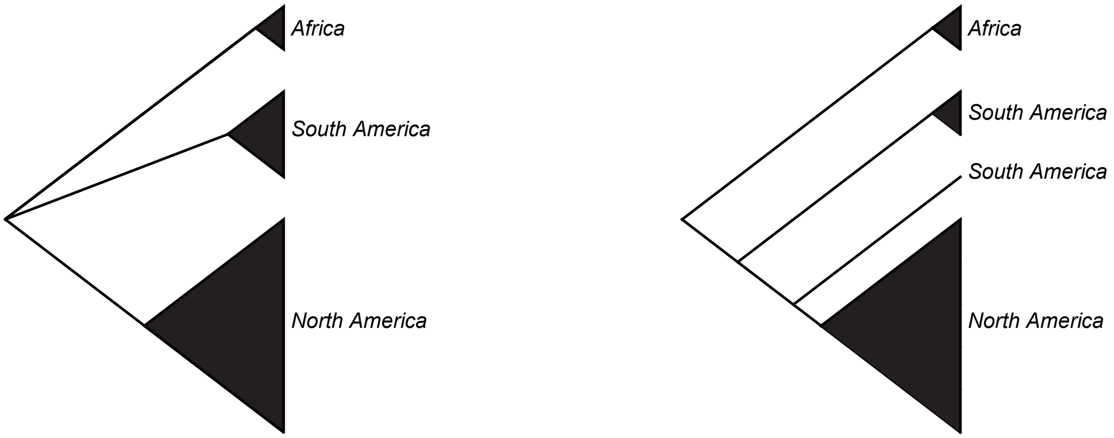
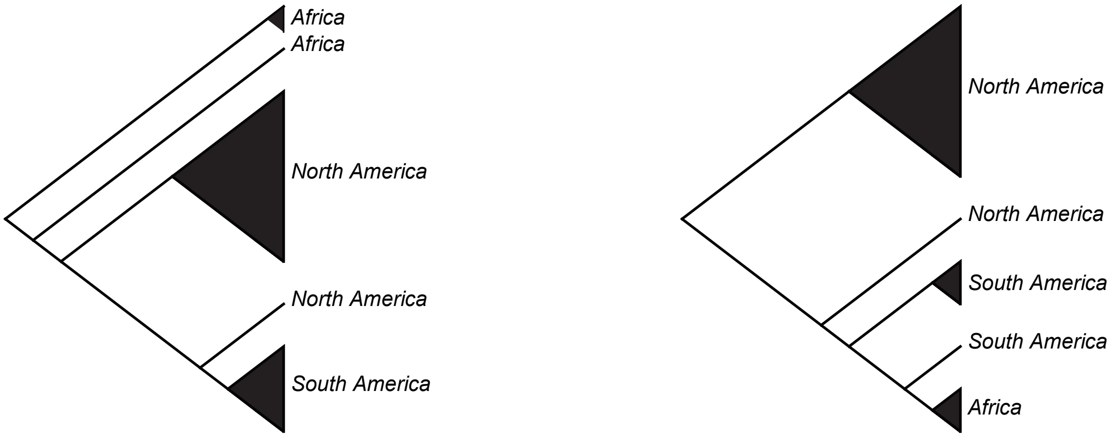

M. spinescens
M. robusta
M. longiflora
M. scabra (vars.)
M. dec. var. longifolia
M. decemfida
M. scoparia
M. juncea
M. intricata
M. pinnatisecta
M. integrifolia
M. integ. var. trifida
M. hassleriana
M. helianthemoides (vars.)
M. coulteri
M. mexicana
M. pulchella
M. africana
M. het. var. australis
M. heterophylla
a
M. spinescens
M. robusta
M. longiflora
M. muellerae
M. intricata
M. decemfida
M. juncea
M. hintoniorum
M. scabra
M. yecorana
M. potosiensis
M. pulchella
M. linoides
M. integrifolia
M.integ. var. pinnatisecta
M. integ. var. odonelliana
M. integ. var. trifida
M. africana
M. het. var. australis
M. heterophylla
M. gypsophila
M. coulteri
M. cult. var. minima
M. helianthemoides
M. jaliscana
M. magniflora
M. mexicana
M. tehuacana
b
key: ■ North America ☐ South America ▨ Africa ☐ Asia
J. floridum
M. robusta
M. spinescens
M. juncea
77
53
M. jaliscana
M. tehuacana
62
M. helianthemoides
88
M. magniflora
M. heterophylla
M. africana
77
M. het. var. australis
M. scabra
M. longiflora
M.integ. var. trifida
M. integrifolia
M. integ. var. pinnatisecta
M.integ. var. odonelliana
M. pulchella
M. linoides
M. intricata
M. potosiensis
M. yecorana
M. mexicana
M. decemfida
M. gypsophila
M. hintoniorum
M. muellerae
M. coulteri
51
M. coult. var. minima
c

Fig. 1. Hypotheses of species relationships within *Menodora*. Geographic affinities for each taxon are indicated in the bar to the right of each figure. a) A hypothesis based on Steyermark's "phylogenetic chart" (1932). In contrast with his chart, Steyermark believed *M. spinescens* to be recently derived within the group. b) An interpretation of relationships based largely on Steyermark's but including all currently accepted taxa and assessments of relationships from various authors (Rehder, 1935; Meyer, 1957; Burkart, 1979; Turner, 1991 and 1995; Van Devender and Turner 1997). c) Tree 3 of 4 resulting from a preliminary phylogenetic parsimony analysis of 39 morphological characters drawn from the literature (data not shown). Dashed lines indicate branches that collapse in strict consensus – trees differed only in the placement of *M. robusta* and *M. spinescens* as either sister or nested branches (*M. robusta* branching first in that case), and whether the branch supporting *pinnatisecta* and the remaining taxa was resolved or not. Numbers below the branch are bootstrap values (1000 replicates). TL=165, CI=0.358, RI=0.581, RC=0.208. Little bootstrap support was found, and indices indicate a high degree of homoplasy within the data.



a) strict vicariance

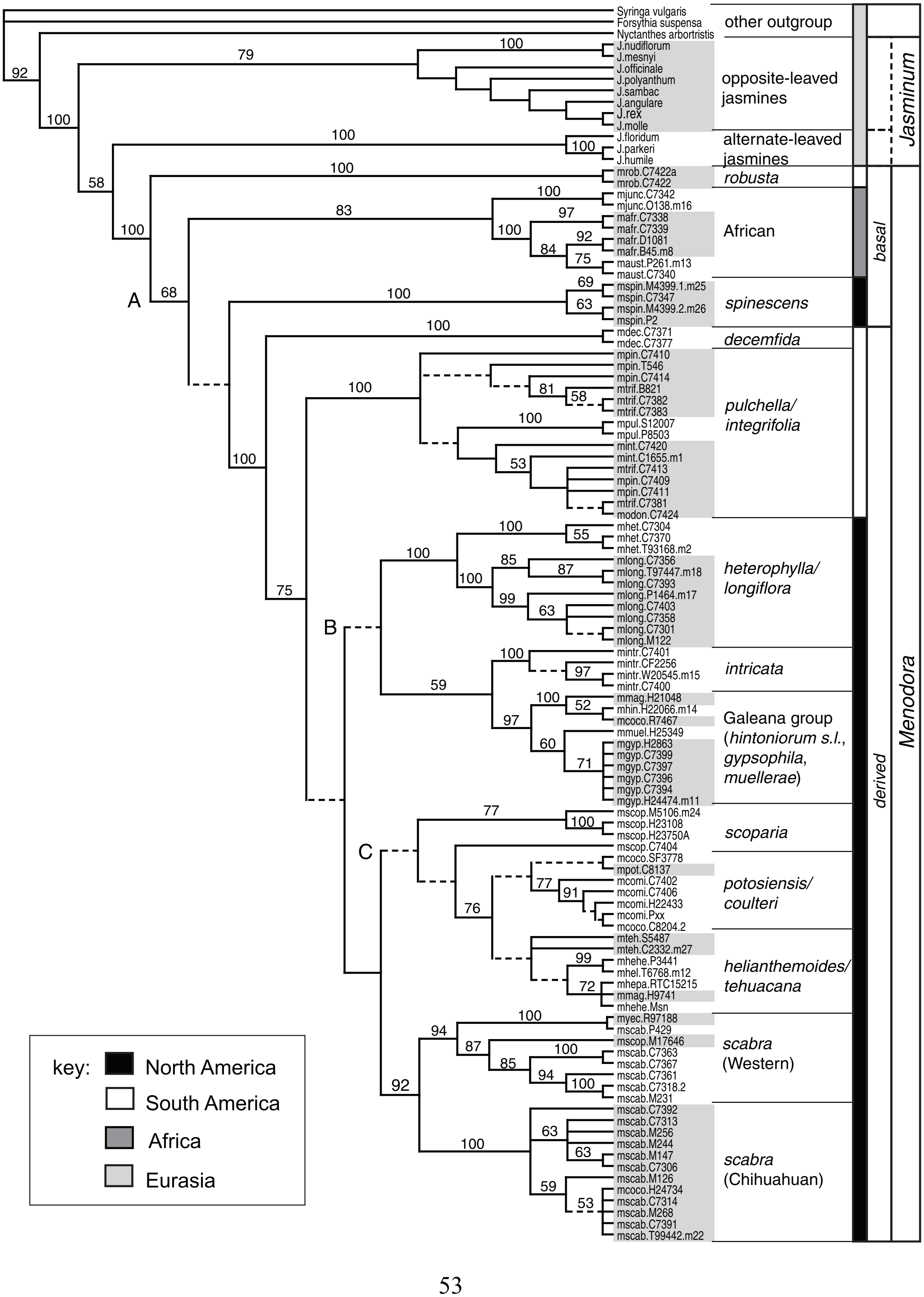
b) Gondwanan vicariance and dispersal



c) Boreotropic dispersal

d) North American origin and dispersal

Fig. 2. A few biogeographic hypotheses for *Menodora*. a) Under strict vicariance, we would expect each continental lineage to be monophyletic, assuming a single or closely related group of common ancestors. b) In a Gondwanan scenario, the African and South American species would form sister groups, and the North American species, resulting from a single dispersal, would be imbedded within the South American clade. c) Consistent with the boreotropic hypothesis, dispersal would have occurred in two stages, first from Africa to North America, and then to South America. The North American species would thus be imbedded within the African, and the South American within the North. d) If the origin for the genus is placed in North America, dispersals to South America and then to Africa would result in a nesting of those groups.


Syringa vulgaris
Forsythia suspensa
Nyctanthes arbortristis
J.nudiflorum
J.mesnyi
J.officinale
J.polyanthum
J.sambac
J.angulare
J.rex
J.molle
J.floridum
J.parkeri
J.humile
mrob.C7422a
mrob.C7422
mjunc.C7342
mjunc.O138.m16
mafr.C7338
mafr.C7339
mafr.D1081
mafr.B45.m8
maust.P261.m13
maust.C7340
mspin.M4399.1.m25
mspin.C7347
mspin.M4399.2.m26
mspin.P2
mdec.C7371
mdec.C7377
mpin.C7410
mpin.T546
mpin.C7414
mtrif.B821
mtrif.C7382
mtrif.C7383
mpul.S12007
mpul.P8503
mint.C7420
mint.C1655.m1
mtrif.C7413
mpin.C7409
mpin.C7411
mtrif.C7381
modon.C7424
mhet.C7304
mhet.C7370
mhet.T93168.m2
mlong.C7356
mlong.T97447.m18
mlong.C7393
mlong.P1464.m17
mlong.C7403
mlong.C7358
mlong.C7301
mlong.M122
mintr.C7401
mintr.CF2256
mintr.W20545.m15
mintr.C7400
mmag.H21048
mhin.H22066.m14
mcoco.R7467
mmuel.H25349
mgyp.H2863
mgyp.C7399
mgyp.C7397
mgyp.C7396
mgyp.C7394
mgyp.H24474.m11
mscop.M5106.m24
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mscop.H23750A
mscop.C7404
mcoco.SF3778
mpot.C8137
mcomi.C7402
mcomi.C7406
mcomi.H22433
mcomi.Pxx
mcoco.C8204.2
mteh.S5487
mteh.C2332.m27
mhehe.P3441
mhel.T6768.m12
mhepa.RTC15215
mmag.H9741
mhehe.Msn
myec.R97188
mscab.P429
mscop.M17646
mscab.C7363
mscab.C7367
mscab.C7361
mscab.C7318.2
mscab.M231
mscab.C7392
mscab.C7313
mscab.M256
mscab.M244
mscab.M147
mscab.C7306
mscab.M126
mcoco.H24734
mscab.C7314
mscab.M268
mscab.C7391
mscab.T99442.m22
other outgroup
opposite-leaved jasmines
alternate-leaved jasmines
robusta
African
spinescens
decemfida
pulchella/ integrifolia
heterophylla/ longiflora
intricata
Galeana group (hintoniorum s.l., gypsophila, muellerae)
scoparia
potosiensis/ coulteri
helianthemoides/ tehuacana
scabra (Western)
scabra (Chihuahuan)
Jasminum
basal
derived
Menodora
A
B
C
92
100
58
100
68
79
100
100
100
100
100
83
97
100
92
84
75
69
100
63
100
100
81
58
100
100
53
100
55
100
85
87
100
75
99
63
100
97
59
100
52
97
60
71
77
100
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91
76
99
72
100
94
87
100
85
94
100
92
63
100
63
59
53
key:
■ North America
□ South America
▩ Africa
▨ Eurasia

Fig. 3. Majority rule tree based on MP analysis of ITS data with gaps treated as missing characters. Numbers above branches are bootstrap values. Branches that collapse in the strict consensus are shown as dashed lines. Letters at nodes indicate where different topologies were recovered when treating gaps in different ways (by removing them, as missing characters, or as a fifth base). A) When gaps were eliminated from the analysis, *M. spinescens* and the African taxa appear as sisters, with < 50% bootstrap support. B) When gaps are eliminated, the relative positions of the *heterophylla-longiflora* and *intricata*-Galeana group taxa are unresolved, appearing in individual trees either with one or the other as sister to the remaining North American taxa, or as shown here. When gaps are treated as a fifth base, the *intricata*/Galeana group is sister to the remaining taxa, though without strong support. C) When gaps are treated as a fifth base, the *scoparia* samples (less mscop.M17646) form a single clade sister to *scabra* s.l. but with <50% bootstrap support. Maximum likelihood trees based on GARLI analyses are similar, but do not resolve relationships within some end taxa (*integrifolia-pulchella, gypsophila, helianthemoides, scoparia*, and the eastern clade of *scabra*). ML trees place the *scoparia* group (less mscop.M17646) as sister to *scabra* s.l., but vary in the placement of mscop.C7404, and resolve the *heterophylla-longiflora* grade as sister to the remaining North American taxa; both of these have less < 50% bootstrap.

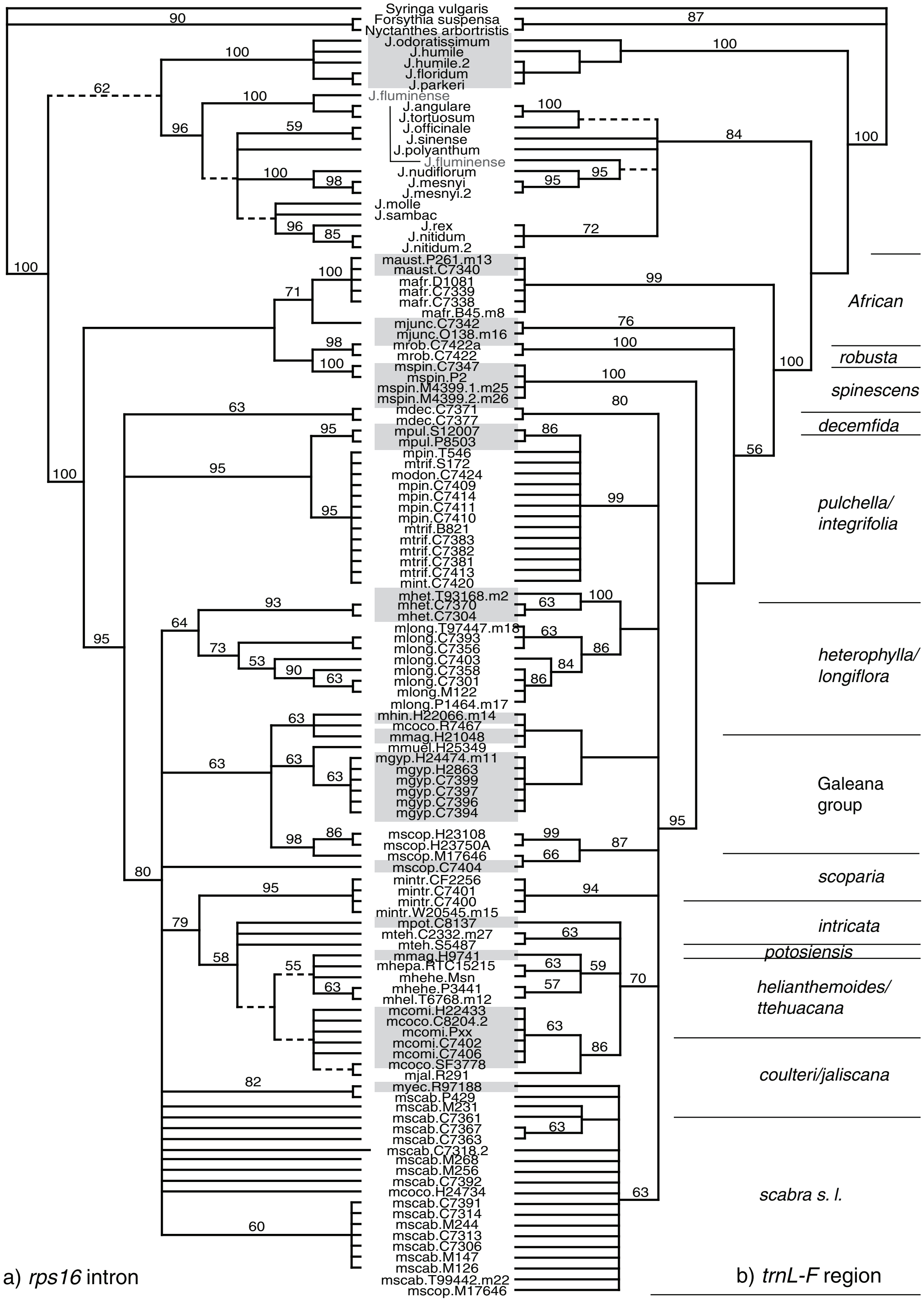

Syringa vulgaris
Forsythia suspensa
Nyctanthes arbortristis
J.odoratissimum
J.humile
J.humile.2
J.floridum
J.parkeri
J.fluminense
J.angulare
J.tortuosum
J.officinale
J.sinense
J.polyanthum
J.fluminense
J.nudiflorum
J.mesnyi
J.mesnyi.2
J.molle
J.sambac
J.rex
J.nitidum
J.nitidum.2
maust.P261.m13
maust.C7340
mafr.D1081
mafr.C7339
mafr.C7338
mafr.B45.m8
mjunc.C7342
mjunc.O138.m16
mrob.C7422a
mrob.C7422
mspin.C7347
mspin.P2
mspin.M4399.1.m25
mspin.M4399.2.m26
mdec.C7371
mdec.C7377
mpul.S12007
mpul.P8503
mpin.T546
mtrif.S172
modon.C7424
mpin.C7409
mpin.C7414
mpin.C7411
mpin.C7410
mtrif.B821
mtrif.C7383
mtrif.C7382
mtrif.C7381
mtrif.C7413
mint.C7420
mhet.T93168.m2
mhet.C7370
mhet.C7304
mlong.T97447.m18
mlong.C7393
mlong.C7356
mlong.C7403
mlong.C7358
mlong.C7301
mlong.M122
mlong.P1464.m17
mhin.H22066.m14
mcoco.R7467
mmag.H21048
mmuel.H25349
mgyp.H24474.m11
mgyp.H2863
mgyp.C7399
mgyp.C7397
mgyp.C7396
mgyp.C7394
mscop.H23108
mscop.H23750A
mscop.M17646
mscop.C7404
mintr.CF2256
mintr.C7401
mintr.C7400
mintr.W20545.m15
mpot.C8137
mteh.C2332.m27
mteh.S5487
mmag.H9741
mhepa.RTC15215
mhehe.Msn
mhehe.P3441
mhel.T6768.m12
mcomi.H22433
mcoco.C8204.2
mcomi.Pxx
mcomi.C7402
mcomi.C7406
mcoco.SF3778
mjal.R291
myec.R97188
mscab.P429
mscab.M231
mscab.C7361
mscab.C7367
mscab.C7363
mscab.C7318.2
mscab.M268
mscab.M256
mscab.C7392
mcoco.H24734
mscab.C7391
mscab.C7314
mscab.M244
mscab.C7313
mscab.C7306
mscab.M147
mscab.M126
mscab.T99442.m22
mscop.M17646
African
robusta
spinescens
decemfida
pulchella/ integrifolia
heterophylla/ longiflora
Galeana group
scoparia
intricata
potosiensis
helianthemoides/ ttehuacana
coulteri/jaliscana
scabra s. l.
a) rps16 intron
b) trnL-F region

Figure 4. Majority rule trees resulting from chloroplast parsimony analyses of (a) rps16 intron and (b) trnL-F region data with gaps omitted from the analysis. Numbers above branches are bootstrap values. Branches that collapse in the strict consensus are shown as dashed lines.

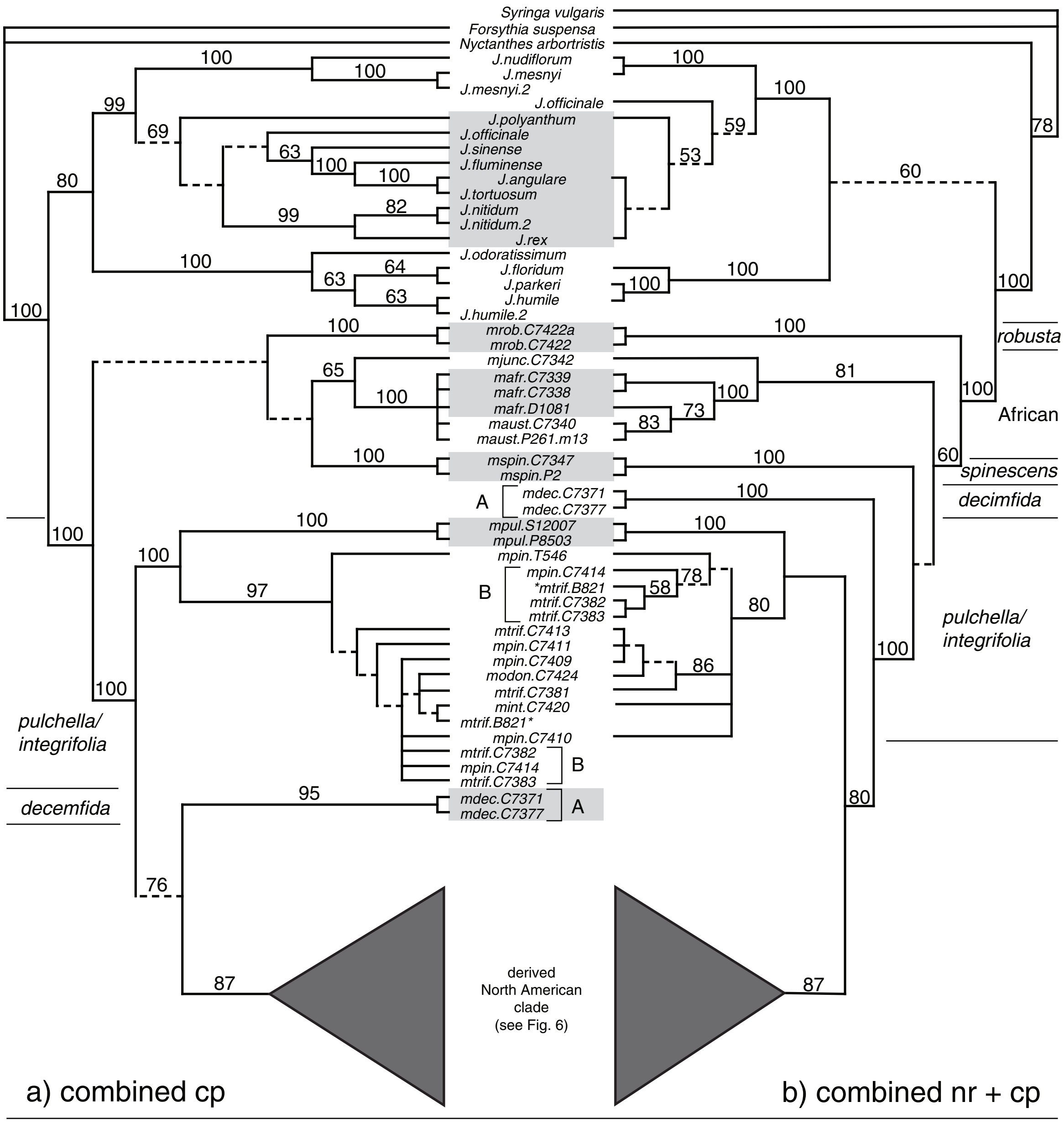

Syringa vulgaris
Forsythia suspensa
Nyctanthes arbortristis
J.nudiflorum
J.mesnyi
J.mesnyi.2
J.officinale
J.polyanthum
J.officinale
J.sinense
J.fluminense
J.angulare
J.tortuosum
J.nitidum
J.nitidum.2
J.rex
J.odoratissimum
J.floridum
J.parkeri
J.humile
J.humile.2
mrob.C7422a
mrob.C7422
mjunc.C7342
mafr.C7339
mafr.C7338
mafr.D1081
maust.C7340
maust.P261.m13
mspin.C7347
mspin.P2
A
mdec.C7371
mdec.C7377
mpul.S12007
mpul.P8503
mpin.T546
B
mpin.C7414
*mtrif.B821
mtrif.C7382
mtrif.C7383
mtrif.C7413
mpin.C7411
mpin.C7409
modon.C7424
mtrif.C7381
mint.C7420
mtrif.B821*
mpin.C7410
mtrif.C7382
mpin.C7414
mtrif.C7383
B
mdec.C7371
mdec.C7377
A
derived
North American
clade
(see Fig. 6)
100
100
99
69
63
100
100
82
99
80
100
64
63
63
100
100
100
65
100
100
100
100
100
97
100
76
95
87
100
100
59
53
78
60
100
100
100
100
100
81
100
73
83
100
60
100
100
100
78
58
80
86
100
80
87
robusta
African
spinescens
decimfida
pulchella/
integrifolia
pulchella/
integrifolia
decemfida
a) combined cp
b) combined nr + cp

Fig. 5. Majority rule trees resulting from parsimony analyses of a) combined cp and b) combined nuclear and cp data, both with gaps treated as missing data. Details for the derived North American clade can be seen in Figure 6. Numbers above branches are bootstrap values. Branches that collapse in the strict consensus are shown as dashed lines. Brackets A and B, and * indicate taxa that are positioned differently in the results of the two analyses. The analyses differ primarily in the relative placement of the decemfida and integrifolia/pulchella clades, by positioning of individual samples within integrifolia, and differences in the structure within the derived North American clade (not shown, see Fig. 6).

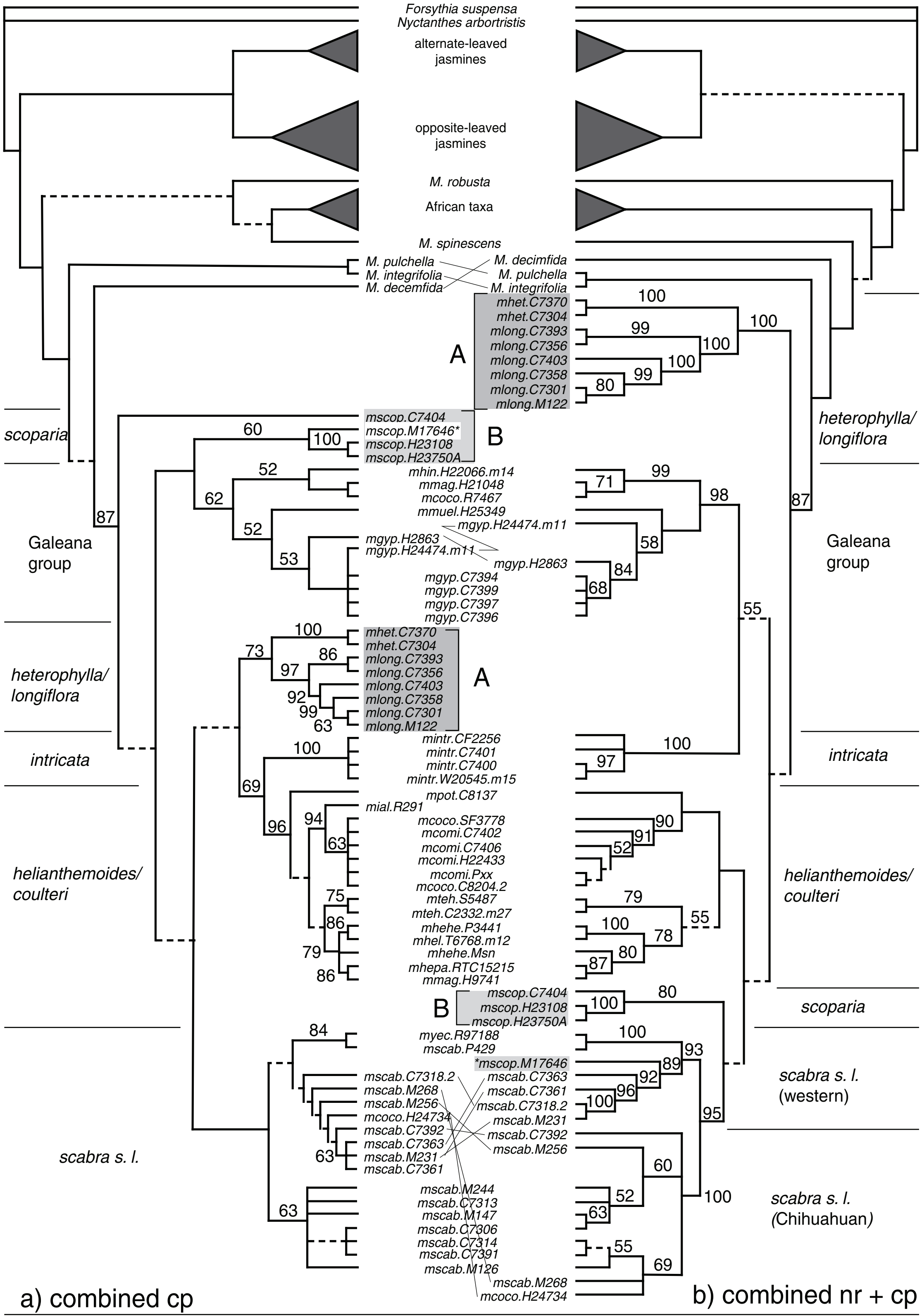

Forsythia suspensa
Nyctanthes arbortristis
alternate-leaved jasmines
opposite-leaved jasmines
M. robusta
African taxa
M. spinescens
M. pulchella
M. integrifolia
M. decemfida
M. decimfida
M. pulchella
M. integrifolia
mhet.C7370
mhet.C7304
mlong.C7393
mlong.C7356
mlong.C7403
mlong.C7358
mlong.C7301
mlong.M122
A
100
99
100
100
99
80
100
scoparia
heterophylla/ longiflora
mscop.C7404
mscop.M17646*
mscop.H23108
mscop.H23750A
B
60
100
52
mhin.H22066.m14
mmag.H21048
mcoco.R7467
mmuel.H25349
mgyp.H24474.m11
mgyp.H2863
mgyp.H24474.m11
mgyp.H2863
mgyp.C7394
mgyp.C7399
mgyp.C7397
mgyp.C7396
62
52
53
87
71
99
98
58
84
68
87
Galeana group
Galeana group
heterophylla/ longiflora
mhet.C7370
mhet.C7304
mlong.C7393
mlong.C7356
mlong.C7403
mlong.C7358
mlong.C7301
mlong.M122
A
100
73
97
86
92
99
63
55
intricata
intricata
mintr.CF2256
mintr.C7401
mintr.C7400
mintr.W20545.m15
100
97
100
69
mpot.C8137
mial.R291
mcoco.SF3778
mcomi.C7402
mcomi.C7406
mcomi.H22433
mcomi.Pxx
mcoco.C8204.2
mteh.S5487
mteh.C2332.m27
mhehe.P3441
mhel.T6768.m12
mhehe.Msn
mhepa.RTC15215
mmag.H9741
96
94
63
75
86
79
86
90
91
52
79
100
78
55
80
87
helianthemoides/ coulteri
helianthemoides/ coulteri
mscop.C7404
mscop.H23108
mscop.H23750A
B
100
80
scoparia
84
myec.R97188
mscab.P429
100
93
*mscop.M17646
mscab.C7318.2
mscab.M268
mscab.M256
mcoco.H24734
mscab.C7392
mscab.C7363
mscab.M231
mscab.C7361
63
mscab.C7363
mscab.C7361
mscab.C7318.2
mscab.M231
mscab.C7392
mscab.M256
89
92
96
100
95
scabra s. l. (western)
scabra s. l.
mscab.M244
mscab.C7313
mscab.M147
mscab.C7306
mscab.C7314
mscab.C7391
mscab.M126
mscab.M268
mcoco.H24734
63
60
52
63
100
55
69
scabra s. l. (Chihuahuan)
a) combined cp
b) combined nr + cp

Fig. 6. Details of the derived North American clade from majority rule trees resulting from parsimony analyses of a) combined cp and b) combined nuclear and cp data, both with gaps treated as missing data. Details for branches above the derived North American clade can be seen in Figure 5. Numbers above branches are bootstrap values. Branches that collapse in the strict consensus are shown as dashed lines. Brackets A and B, and * indicate taxa that are positioned differently in the results of the two analyses. Topological differences between the analyses concern the relative positions of the *heterophylla/longiflora* and *intricata/Galeana clades*, the place and composition of the *scoparia* group, especially samples mscop.M17646 and mscop.C7404, and the placement of individual samples within the *gypsophila* and *scabra s.l.* clades.

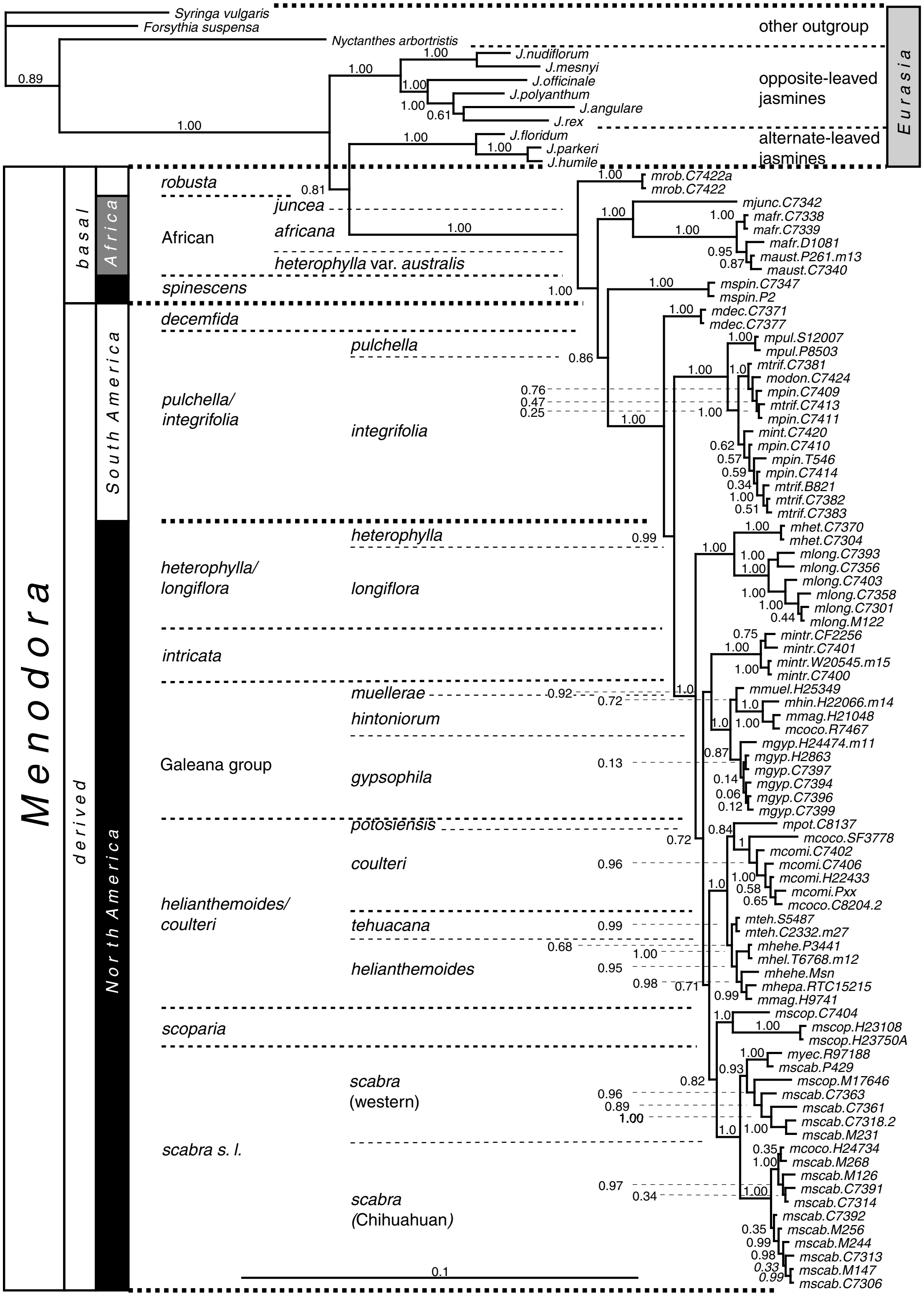

Syringa vulgaris
Forsythia suspensa
Nyctanthes arbortristis
J.nudiflorum
J.mesnyi
J.officinale
J.polyanthum
J.angulare
J.rex
J.floridum
J.parkeri
J.humile
0.89
1.00
0.81
0.61
other outgroup
opposite-leaved jasmines
alternate-leaved jasmines
Eurasia
Menodora
basal
derived
Africa
South America
North America
robusta
juncea
africana
African
heterophylla var. australis
spinescens
decemfida
pulchella
pulchella/ integrifolia
integrifolia
heterophylla
heterophylla/ longiflora
longiflora
intricata
muellerae
hintoniorum
Galeana group
gypsophila
potosiensis
coulteri
helianthemoides/ coulteri
tehuacana
helianthemoides
scoparia
scabra (western)
scabra s. l.
scabra (Chihuahuan)
0.1
mrob.C7422a
mrob.C7422
mjunc.C7342
mafr.C7338
mafr.C7339
mafr.D1081
maust.P261.m13
maust.C7340
mspin.C7347
mspin.P2
mdec.C7371
mdec.C7377
mpul.S12007
mpul.P8503
mtrif.C7381
modon.C7424
mpin.C7409
mtrif.C7413
mpin.C7411
mint.C7420
mpin.C7410
mpin.T546
mpin.C7414
mtrif.B821
mtrif.C7382
mtrif.C7383
mhet.C7370
mhet.C7304
mlong.C7393
mlong.C7356
mlong.C7403
mlong.C7358
mlong.C7301
mlong.M122
mintr.CF2256
mintr.C7401
mintr.W20545.m15
mintr.C7400
mmuel.H25349
mhin.H22066.m14
mmag.H21048
mcoco.R7467
mgyp.H24474.m11
mgyp.H2863
mgyp.C7397
mgyp.C7394
mgyp.C7396
mgyp.C7399
mpot.C8137
mcoco.SF3778
mcomi.C7402
mcomi.C7406
mcomi.H22433
mcomi.Pxx
mcoco.C8204.2
mteh.S5487
mteh.C2332.m27
mhehe.P3441
mhel.T6768.m12
mhehe.Msn
mhepa.RTC15215
mmag.H9741
mscop.C7404
mscop.H23108
mscop.H23750A
myec.R97188
mscab.P429
mscop.M17646
mscab.C7363
mscab.C7361
mscab.C7318.2
mscab.M231
mcoco.H24734
mscab.M268
mscab.M126
mscab.C7391
mscab.C7314
mscab.C7392
mscab.M256
mscab.M244
mscab.C7313
mscab.M147
mscab.C7306
0.95
0.87
0.86
0.76
0.47
0.25
0.62
0.57
0.59
0.34
0.51
0.99
0.44
0.75
0.92
0.72
0.87
0.13
0.14
0.06
0.12
0.84
0.96
0.58
0.65
0.99
0.68
0.95
0.98
0.71
0.93
0.82
0.89
0.97
0.35
0.33

Fig. 7. Tree resulting from Bayesian analysis with the combined nuclear and chloroplast data, with gaps included. Numbers shown are posterior probablities. Tree is almost topologically identical to trees resulting from likelihood analyses, with the exception of the placement of *M. muellerae* in the Galeana group, which appears as sister to gypsophila with weak support in the likelihood analyses.

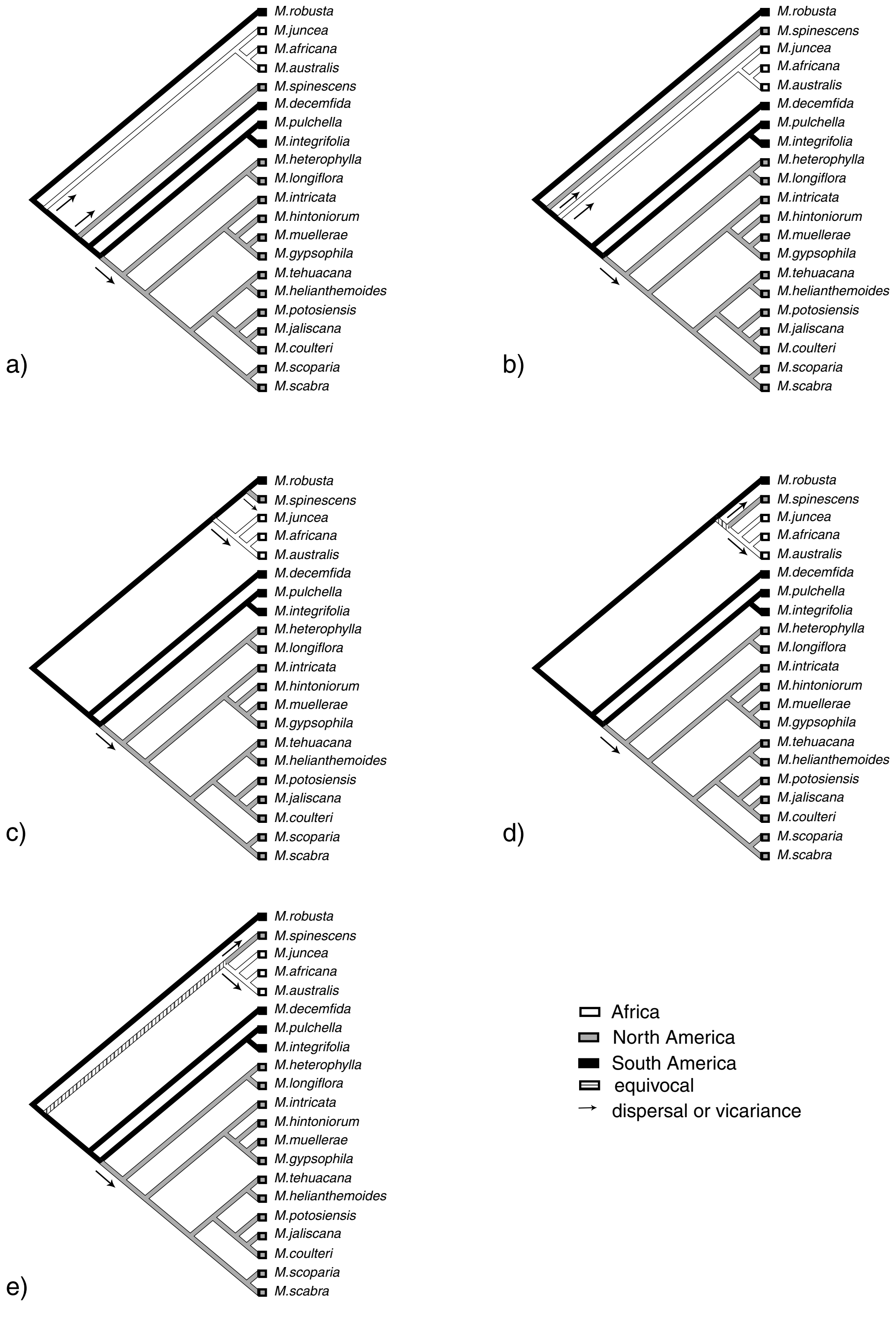

M.robusta
M.juncea
M.africana
M.australis
M.spinescens
M.decemfida
M.pulchella
M.integrifolia
M.heterophylla
M.longiflora
M.intricata
M.hintoniorum
M.muellerae
M.gypsophila
M.tehuacana
M.helianthemoides
M.potosiensis
M.jaliscana
M.coulteri
M.scoparia
M.scabra
a)
M.robusta
M.spinescens
M.juncea
M.africana
M.australis
M.decemfida
M.pulchella
M.integrifolia
M.heterophylla
M.longiflora
M.intricata
M.hintoniorum
M.muellerae
M.gypsophila
M.tehuacana
M.helianthemoides
M.potosiensis
M.jaliscana
M.coulteri
M.scoparia
M.scabra
b)
M.robusta
M.spinescens
M.juncea
M.africana
M.australis
M.decemfida
M.pulchella
M.integrifolia
M.heterophylla
M.longiflora
M.intricata
M.hintoniorum
M.muellerae
M.gypsophila
M.tehuacana
M.helianthemoides
M.potosiensis
M.jaliscana
M.coulteri
M.scoparia
M.scabra
c)
M.robusta
M.spinescens
M.juncea
M.africana
M.australis
M.decemfida
M.pulchella
M.integrifolia
M.heterophylla
M.longiflora
M.intricata
M.hintoniorum
M.muellerae
M.gypsophila
M.tehuacana
M.helianthemoides
M.potosiensis
M.jaliscana
M.coulteri
M.scoparia
M.scabra
d)
M.robusta
M.spinescens
M.juncea
M.africana
M.australis
M.decemfida
M.pulchella
M.integrifolia
M.heterophylla
M.longiflora
M.intricata
M.hintoniorum
M.muellerae
M.gypsophila
M.tehuacana
M.helianthemoides
M.potosiensis
M.jaliscana
M.coulteri
M.scoparia
M.scabra
e)
Africa
North America
South America
equivocal
dispersal or vicariance

Fig. 8. Simplified trees used in the DIVA analysis, with geographic traces from MacClade. a) Tree as suggested by the likelihood analyses of the combined data, b-e) topological variants of the basal group of taxa (*M. robusta*, *M. spinscens*, and the African taxa) as suggested by various independent analyses of independent or combined data sets. In all cases, DIVA suggests vicariance with two dispersals, with it being equivocal in most cases which of the two initial events might represent vicariance or dispersal. MacClade reconstructions are consistent with this, but also suggest a South American origin with three dispersals.

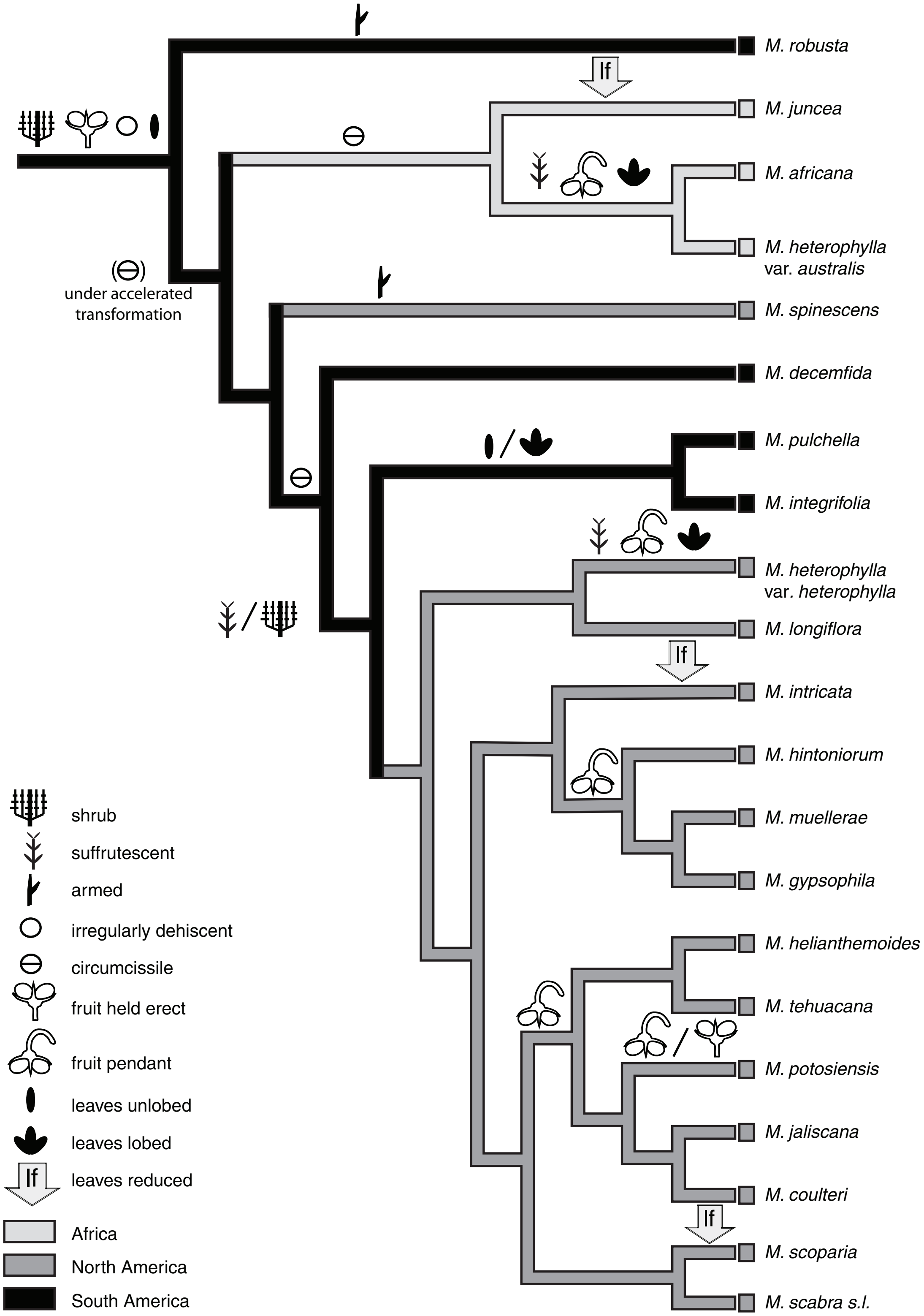

M. robusta
lf
M. juncea
M. africana
M. heterophylla var. australis
(⊖) under accelerated transformation
M. spinescens
M. decemfida
M. pulchella
M. integrifolia
M. heterophylla var. heterophylla
M. longiflora
lf
M. intricata
M. hintoniorum
M. muellerae
M. gypsophila
M. helianthemoides
M. tehuacana
M. potosiensis
M. jaliscana
M. coulteri
lf
M. scoparia
M. scabra s.l.
shrub
suffrutescent
armed
irregularly dehiscent
circumcissile
fruit held erect
fruit pendant
leaves unlobed
leaves lobed
lf leaves reduced
Africa
North America
South America

Fig. 9. Morphological characters mapped on a summary tree based on the results of the likelihood analyses of the combined data. Several of the characters (fruiting pedicel habit, dehiscence, leaf reduction) believed to be phylogenetically important by Steyermark (1932) appear convergent on this tree.

Chapter 3: A systematic revision of *Menodora* Bonpl. (Oleaceae)

INTRODUCTION

Menodora Bonpl. as treated here is a small genus of suffrutescent or fruticose perennials consisting of 24 species, a single subspecies and six varieties. It has an unusual disjunct distribution, and is found in dry, temperate grasslands and deserts in North and South America and southern Africa (Fig. 1). In contrast with earlier studies, here I have determined that there are no species with an intercontinental distribution. In North America, which is the center of species diversity, the distribution extends westward from central Texas to California, and south to Oaxaca. In South America, the genus is centered in Argentina but ranges eastward to the bordering regions of Uruguay, Brazil, and Paraguay, and north to central Bolivia; a single endemic species of very limited distribution is found in Chile. In Africa, the distribution is almost entirely South African, with a slight overlap into southern Botswana.

This study presents a synthesis of earlier works and is informed by recent studies of species relationships based upon molecular phylogenetic analyses, examination of circa 3400 herbarium specimens, field observation and collection.

Taxonomic history

Menodora was first collected in central Mexico by Alexander von Humboldt and Aimé Bonpland during their historic journey of discovery through the New World of 1799-1804. The type collection of *M. helianthemoides*, though without date, was most likely made in the early summer (May to June; Sprague 1924) of 1803 in the Mexican state of Hidalgo, "*inter Actopan et vicum Magdalenae*" ("between Actopan and the village of Magdalena") about 90 kilometers north of Mexico City. The name was published in *Plantae Aequinoctiales* (Humboldt and Bonpland 1809) and was later elaborated by Kunth (Humboldt, Bonpland, and Kunth 1825); rarely authorship for the name of the type species or genus is given incorrectly as the latter.

Historically, attribution for the names of the genus and the type species was given to both Humboldt and Bonpland (*e.g.*, *Menodora* Humb. & Bonpl., *Menodora helianthemoides* Humb. & Bonpl.) and the date of publication has been cited as the beginning date for the *Plantae Aequinoctiales* (1809). However, the *Plantae* was initially published by subscription in serial form, with the fascicle containing *Menodora* not being validly published until 1812 (Sherwood and Woodward 1901). Although traditionally both Humboldt and Bonpland have been cited, Bonpland has long been acknowledged as the author of the *Plantae* (e.g., Sarton 1943). The vernacular French and scholarly Latin title pages of the *Plantae* cite both Humboldt and Bonpland as the authors of the work, but the scholarly Latin title page notes in particular "*in ordinem digessit Amato Bonpland*" ("properly arranged by Aimé Bonpland"). Further, Humboldt writes in the introduction to the first volume, "*Quoique les Plantes équinoxiales, comme tous les travaux de mon expédition, portent le nom de M. Bonpland et le mien à la fois, il s'en faut de beaucoup que nous ayons eu une égale part à cet ouvrage. M. Bonpland ne l'a pas seulement rédigé lui seul d'après nos manuscrits, mais c'est à lui aussi qu'est due la plus grande partie de ce travail botanique.*" Thus, while Humboldt did contribute to the botany and wrote and annotated some descriptions in the botanical manuscripts of the journey (Lack 2004), he gives full credit to Bonpland for authorship of the published work. In the strict interpretation of the code of botanical nomenclature, Bonpland is therefore the sole author for names of genera and species recognized in the *Plantae*, especially since no mention is made of the contribution of other authors in the published species descriptions. The full citation for these names thus should read "Bonpland in Humboldt et Bonpland." Nonetheless, until fairly recently many species named in the *Plantae* continued to carry the appellations of both Humboldt and Bonpland, and it is unclear when or by whom formal corrections began to be made. Both editions of *Taxonomic Literature* (Stafleu 1967; Stafleu and Cowen 1976) point out "*in ordinem digessit Amato Bonpland*" but list the *Plantae* under Humboldt's entries. Brummitt (1992) attributes authorship of *Menodora* to Bonpland alone, but as I write this, the on-line version of *Index Kewensis* (http://www.ipni.org/index.html; January, 2007) maintains both authors for the genus and type species. Thus it appears that botanical revisionists began to make the correction at some point in the last quarter of the twentieth century, but this convention has been by no means uniformly adopted.

The specimen collected by Bonpland in Mexico lacked mature fruit, and the original description of the fruit is thus somewhat ambiguous, being described as either a berry or capsule with two locules. This ambiguity was a hindrance to familial placement of the genus, and it was tentatively assigned to the Jasmineae of Jussieu (1789), though possibly with affinities to the Gentianeae. Kunth later would describe the fruit (*fide* Bonpland's field notes) more certainly, though incorrectly, as a bilocular, bivalved capsule with two ovules per locule, and would place it instead in the Acanthaceae (Humboldt, Bonpland, and Kunth 1825).

This lack of precise knowledge concerning the fruit of *Menodora* would lead in 1826 to the description of a second genus, and subsequently a quarter century of botanical confusion ensued. The new genus, named *Bolivaria* by Rudolf von Chamisso and Dietrich von Schlechtendal in honor of the great liberator of South America, Simon Bolivar, consisted of two species, *B. integrifolia* Cham. & Schltdl. and *B. trifida* Cham.

& Schltdl. (1826). *Bolivaria* was considered distinct on the basis of its five calyx lobes and bilobed fruit with circumscissile locules, as opposed to the ten to fourteen calyx lobes and supposedly bivalved capsule of *Menodora*. Its affinities were thought to be with the Jasmineae.

Adding to the confusion was another nomenclatural proposition in the 1831 edition of Linnaeus' *Species Plantarum*. The editor, Albert Dietrich, apparently did not favor naming taxa after historical figures, or at least those without botanical credentials (translated here from the Latin): "Bolivar's name in history … is clear, [but] in things botanical is not so accomplished, in order to thence be named …" (Dietrich 1831). He therefore proposed to substitute *Calyptrospermum* in place of the (in his view) illegitimate name *Bolivaria*. This suggestion seems to have been immediately relegated into synonymy, as subsequent authors would continue to recognize the priority of *Bolivaria*.

The familial placement and generic circumscription of the two genera would remain uncertain throughout the second quarter of the nineteenth century, during which four additional species of *Bolivaria* [*B. decemfida* Gill. ex Hook. & Arn. (1834), *B. chlorargantha* J. Rémy (1847), *B. mexicana* A. DC. in DC. (1844), and *B. robusta* Benth. (1846)] and two of *Menodora* [*M. heterophylla* Moric. ex DC. (1844), *M . africana* Hook. (1842)] would be described including the first from southern Africa. Sprengel (1830) would recognize both genera, but recognized *Bolivaria* as part of the Jasmineae and followed Kunth in placing *Menodora* in the Acanthaceae. Bartling (1830) also recognized both genera but was unsure of their familial placement. Lindley (1836) united the genera, but did not recognize the priority of *Menodora* and placed his expanded *Bolivaria* in the Jasminaceae. Don (1838) would later recognize both genera but assigned them to the Columellieae, citing the presence of a perigynal disk that made the ovary half-inferior, as opposed to hypogenous ovary of his Jasmineaceae; his descriptions of the two genera plainly demonstrate the high level of confusion concerning the supposed characters of the group. Grisebach (1839) also recognized the two genera but placed them in their own family, the Bolivariaceae, with affinities to the Gentianeae. Endlicher (1841) similarly maintained the two genera. Steudel (1841) would transfer *B. integrifolia* and *B. trifida* to *Menodora*, referring *Bolivaria* to synonymy under *Menodora*. Hooker (1842) would also suggest that the two were congeneric in his description of *M. africana*, although he did not formally make any nomenclatural transfers; he referred *Menodora* to the Jasmineae. De Candolle (1844), however, maintained the two as distinct genera but also placed both within the Jasmineae. His treatment also perpetuated the misconceptions about the number of seeds per locule, number of calyx lobes, and manner of dehiscence. One new species for each genus was also described, and subsequently, questions of the familial placement of the two genera appear to have been resolved. Bentham (1846) agreed with de Candolle's (1844) concept of the two segregate genera, and suggested that *Menodora africana* should be transferred to *Bolivaria*, apparently due to the nature of the fruit.

As *Menodora* began to reach its first half-century of recognition, *Bolivaria grisebachii* was described by Scheele (1852). In the same year, Asa Gray made the case for combining the species of the two genera under a single nomenclatural banner. Examining fruiting material of what otherwise appeared to be *M. helianthemoides*, he concluded that the observations of a bivalved capsule and two ovules per locule were both most likely in error, and that the number of calyx lobes was variable across a number species and thus probably of "no generic consequence" (Gray 1852). He therefore followed the lead of Steudel (1841) and formally transferred all recognized species of *Bolivaria* into *Menodora* (with the exception of *B. grisebachii*, of which he was apparently unaware at the time), and named in addition four new species for North America, *M. coulteri*, *M. scabra*, *M. longiflora* and *M. pubens.* He also recognized three sections, based on the number of calyx lobes or the length of the corolla tube: 1) section *Bolivaria* Cham. & Schltdl., plants with five calyx lobes, including *M. integrifolia*, *M. trifida* and *M. robusta*, 2) section *Menodora* Bonpl., plants with ten or more (rarely fewer) calyx lobes, tubes of the corollas much shorter than the lobes, including *M. africana*, *M. coulteri*, *M. decemfida*, *M. helianthemoides*, *M. heterophylla*, *M. mexicana*, *M. scabra* and and 3) section *Menodoropsis* A. Gray, plants with ten calyx lobes and very long (30-50 mm) corolla tubes, including *M. longiflora* and *M. pubens*.

Despite Gray's (1852) convincing arguments for unification of the two genera under *Menodora*, some confusion briefly persisted. The year 1853 would see the publication of two different species using the same epithet, one for each genus, each of different continents but cultivated from seed in Europe. *Bolivaria pinnatifida* Schltdl. was named from seed received from Bolivia (Schlechtendal 1853); neither its exact provenance nor the collector are noted in the detailed description. *Menodora pinnatifida* Mart. was grown in Munich from seed provided by Ferdinand Lindheimer, and was probably collected in central or south Texas (Martius 1853). As Gray's treatment began to reach a wider circulation, the relegation of *Bolivaria* to synonymy was accepted, and no further species were recognized in that genus.

The 1860's saw the recognition of three additional species, one for each continent in the distribution of the genus: *Menodora. linoides* Phil. (1863; 1864) in Chile, *M. spinescens* A. Gray (1867) in California, and *M. juncea* Harv. (1868) in southern Africa. Gray would name the last new species of the nineteenth century, *M. scoparia* A. Gray (1876) from a manuscript by George Engelmann and would later provide a treatment of all North American species (Gray 1878). Although family placement of *Menodora* appears to have been settled by de Candolle (1844), Eichler (1868) segregated the Jasmineae (consisting only of *Menodora*, *Jasminum*, and *Nyctanthes*) from the closely related Oleaceae, but these would later be integrated as a tribe into the more or less modern conception of the Oleaceae as recognized by Bentham and Hooker (1876).

The first subspecific segregate in the genus was recognized by Otto Kuntze in 1898 with the relegation of *M. trifida* to a variety of *M. integrifolia*. Kuntze also recognized a South African species of *Jasminum* (*J. angulare* Vahl) as another variety of *M. integrifolia*. Neither of these transfers was recognized in subsequent botanical literature until Burkart (1979) noted Kuntze's transfer of *trifida*. The nineteenth century would close with the description of another variety, *M. helianthemoides* var. *parviflora* (Greenman 1899), which was segregated from the species chiefly on the basis of flower size.

Five more species would be described in the first three decades of the twentieth century. Two of these were from South America, *M. hassleriana* Chod. (1903) and *M. pulchella* Markgr. (1922), while the rest were North American [*M. intricata* T. S. Brandegee (1913), *M. laevis* Wooton & Standl. (1913), and *M. hispida* Palmer (1929)]. John Small (1903) would raise the sectional recognition of Gray's *Menodoropsis* to a segregate genus. As with Dietrich's *Calyptrospermum*, this transfer was relegated to synonymy in subsequent treatments.

Julian Steyermark (1932) produced the first comprehensive treatment of the genus since Gray (1852). In this work, he recognized 17 species including a single new one for Argentina (*M. pinnatisecta*), relegated *M. laevis* and *M. trifida* to varietal status under *M. scabra* and *M. integrifolia* respectively (apparently being unaware of Kuntze's earlier transfer (1898) of *trifida*), and recognized ten new varieties within seven species. Unfortunately, Steyermark was not able to examine type material (the only known collections) of *M. linoides* or *M. chlorargantha*, and so included these as "Species Imperfectly Known."

Steyermark's treatment provided the basis for treatments in local floras until superseded by the regional treatments of Verdoorn (1956) for South Africa, Meyer (1957) for Argentina, and Turner (1991) for North America. Between 1932 and 1991, only one additional species was described, *Menodora. muellerae* Rehd. (1935) from Mexico. Verdoorn's treatment (1956) of the South African taxa followed that of Steyermark, with some elaboration. Meyer's treatment (1957) of Argentine species generally did so as well, recognizing five species but placing *M. hassleriana* into synonymy and introducing two new varietal names, *M. integrifolia* var. *odonelliana* from Rio Negro, and *M. pinnatisecta* var. *missionum* from Misiones; again the Chilean *M. linoides* and the Bolivian *M. chlorargantha* were not examined, although the presence of *M. integrifolia* var. *trifida* in Bolivia was noted, and that of var. *integrifolia* in Bolivia was noted as in error. Arturo Burkart (1979) later treated *M. pinnatisecta* as a variety of *M. integrifolia*, but did not make a disposition for variety *missionum*. Both Meyer (1957) and Burkart (1979) commented on the possibility of raising *M. integrifolia* var. *trifida* to specific distinction, but declined to do so due to its polymorphic nature.

Billie Turner's 1991 overview of the North American taxa realigned species boundaries between *Menodora. helianthemoides* and *M. coulteri*, and redefined and broadened the concept of *M. scabra*. Steyermark's varieties of *M. helianthemoides* were done away with by placing var. *parviflora* in synonymy with the species, raising var. *magniflora* to a distinct species, and placing var. *engelmannii* in synonymy under *M. coulteri*. In Turner's view, *M. scabra* is a highly polymorphic species, including both *M. scoparia* and Steyermark's *M. decemfida* var. *longifolia* within his broadened concept of the species and dispensing with all varieties. In addition, Turner also named four new species, all from Mexico: *M. hintoniorum, M. jaliscana, M. potosiensis,* and *M. tehuacana*. Turner later circumscribed two additional species, again from Mexico: *M. gypsophila* B. L. Turner (1995) of Nuevo Leon, and with Tom Van Devender, *M. yecorana* Van Devender & B. L. Turner (1997) of Sonora.

Finally, Correa (1999) resurrected the species status of *M. trifida* and place *M. integrifolia* var. *odonelliana* in synonymy under it, citing a near complete morphological intergradation between the two.

To summarize then, in the view of these various authors prior to our study, the genus *Menodora* consisted of 23 species and two varieties. In addition to these, two named species, *M. chlorargantha* of Bolivia and *M. linoides* of Chile, have never been examined within the larger context of genus, and thus their status prior to this study was undetermined.

This treatment presents a substantial realignment of species based in part upon knowledge gained from a molecular phylogeny of the group, an extensive review of herbarium specimens, and experience in the field. While a similar number of taxa are recognized (24 species, one subspecies, and six varieties; Table 1), there are major differences in this treatment from earlier works. Both of the previously untreated South American species have been examined. Examination of the type of *Menodora chlorargantha* confidently allows it to be placed in synonymy under *M. integrifolia*. Examination of the type of *M. linoides* and photographs from its recent rediscovery in Chile (Faúndez, Larraín, and Girón 2005; Muñoz, Moreira, and León 2006) have allowed me to integrate it formally within the ranks of species. Only a single new species, *M. henricksonii*, is proposed to recognize a cryptic polymorphic group from central Mexico. Subspecific categories have been extensively overhauled. After much deliberation, varieties of *M. integrifolia* in South America have been done away with in recognition of the highly polymorphic nature of the species and a high degree of intergradation between the described varieties. In contrast with Turner's similar concept (1991) of a highly polymorphic *M. scabra* in North America, I have broken this group into five species and recognized an additional three varieties, two of which are newly described. While Turner (1991) included *M. spinescens* var. *mohavensis* within the species, it appears to be florally distinct as well as slightly geographically isolated, and similarly another variety is suggested (pending examinations of specimens) from Baja California. Further, the following names are placed in synonymy (see Table 1): *M. potosiensis*, *M. hintoniorum*, and *M. magniflora*.

Generic relationships

Menodora has long been considered close to *Jasminum* (Chamisso and Schlechtendal 1826; de Candolle 1844; Eichler 1868; Knobloch 1895; Taylor 1945; Johnson 1957). Steyermark (1932) remarked only briefly about the relationship of *Menodora* to other Oleaceae, noting only the similarity of floral structures between *Menodora* and the exclusively Old World genera *Jasminum* and *Nyctanthes*. The floral and fruit morphology of *Menodora* and *Jasminum* show clear affinities: gamosepalous calyces with 5 to many linear lobes, infundibuliform or subrotate white or yellow corollas with 5 or more lobes, and fruits divided deeply in half by a deep constriction, forming either a bilobed berry (*Jasminum*; in some species, it is a single berry through abortion of one locule) or bilobed capsule (*Menodora*). A phytochemical analysis of iridoid compounds within the Oleaceae also supported the close relationship of the two genera (Jensen, Franzyk, and Wallander 2002). Anatomical studies of fruit and seed structure by Rohwer (1993; 1995a; 1995b; 1997) showed that *Jasminum* and *Menodora* share a unique fruit and seed structure in the Oleaceae. Rohwer (1997) concluded that *Jasminum* might be paraphyletic with respect to *Menodora* and suggested close relationships between *Menodora* (especially *M. spinescens*) and the yellow-flowered jasmines (*Jasminum* sect. *Alternifolia,* and the two species of sect. *Primulinum*, *J. mesnyi* and *J. nudiflorum*). Molecular phylogenetic studies of the Oleaceae also support the close relationship of the two genera (Wallander and Albert 2000). The limited sampling in the family-wide analysis of Wallander and Albert (2000) showed a monophyletic *Menodora* nested within a paraphyletic *Jasminum*. More extensive molecular studies of the tribe (see the previous chapter), however, have not yet satisfactorily resolved relationship of the three major lineages defined: *Menodora*, *Jasminum* sect. *Alternifolia* (the alternate-leaved, yellow-flowered jasmines), and the rest of *Jasminum* (with opposite leaves and predominantly white corollas, but including the two species of the opposite-leaved and yellow-flowered sect. *Primulinum*). A recent examination of chloroplast gene rearrangements within the group confirmed a common history for the tribe, suggested that sect. *Alternifolia* may be basal in the group, and that both *Menodora* and sect. *Primulinum* have independent series of rearrangements. A sample-limited phylogeny using about 30 kilobases of chloroplast sequence in these rearrangement regions again did not provide an unequivocal estimation of relationships among the three major clades, however (Lee et al. 2007). It has been suggested (see previous chapter) that rather than including the morphologically distinct *Menodora* within a broadened concept of *Jasminum*, *Jasminum* should be more narrowly construed through the exclusion of the species of sect. *Alternifolia*.

In the classification of the Oleaceae by Wallander and Albert (2000), *Jasminum* and *Menodora* were the two genera of tribe Jasmineae, and this is sister to the large tribe Oleae which contains the majority of genera in the family. At the base of the family tree are three clades whose relative positions are unresolved. These were recognized as tribes Fontanesieae (*Fontanesia*), Forsythieae (*Abeliophyllum, Forsythia*), and Myxopyreae (*Myxopyrum, Nyctanthes,* and *Dimetra*). The family is positioned in the Angiosperm Phylogeny Group II euasterid I clade in order Lamiales, and is close to the base of order (APG II, 2003).

Species Relationships, Distribution and Speciation

Menodora is primarily found in the temperate latitudes of North and South America and southern Africa, with only a few species whose individual distributions cross into the tropics (Fig. 1). The distribution is both amphitropical in the New World and amphi-Atlantic. A recent molecular phylogeny of *Menodora* (see the preceding chapter) found two basic groups: 1) a basal group consisting of *M. robusta* of Patagonia, *M. spinescens* of the Mojave Desert, and the African species, and 2) a derived group with the Argentine *M. decemfida* as sister to two clades separating the South American sister species *M. pulchella* and *M. integrifolia* from the remaining majority of North American species (Fig. 2). Although there was a lack of strong support for the placement of *M. spinescens*, the data suggest a South American origin for the group. This interpretation requires three distinct long distance dispersals to explain the modern distribution – two separate introductions to North America, and a third to Africa. As discussed in the previous chapter, the vector for the northern dispersals was most likely migratory shore birds, while dispersal across the Atlantic was probably by southern Atlantic ocean currents. The first dispersal to North America and the dispersal to Africa both occurred very early in the history of the group. The second, more recent dispersal to North America resulted in a rapid radiation of the majority of species in the genus, and, as a result, while North American species groups in the phylogeny are usually well defined, the relationships between or within them are often not strongly supported.

While intercontinental disjunction is one of the important features of the distribution, there are also species or population disjunctions on each of the three continents as well. In South America, the most prominent of these is the disjunction of *Menodora linoides* on the west side of the Andes, where it only known from two recently discovered localities (Faúndez, Larraín, and Girón 2005; see Fig. 3); all other South American species occur east of the Andes. The most widespread species of South America, *M. integrifolia*, has a discontinuous distribution with gaps separating the northern (Bolivian) populations and the southern (Patagonian) populations from the major, central body of the distribution (Fig. 3), and there appears to be small gap in the historical collections between northern and southern Paraguay as well. Even the largely coastal species *M. robusta* has a few disjunct collections far from the coast in the interior of Argentine Patagonia. In South Africa, both *M. juncea* and *M. africana* subsp. *africana* have discontinuous distributions (Fig. 4). *Menodora juncea* inhabits parts of the central and eastern Great and Little Karoos, and is disjunct in Namaqualand. In the latter region there also appears to be a small gap in collections separating the northern and southern populations. The distribution of *M. africana* subsp. *africana* appears in general to be quite fragmented (Fig. 4). The southern populations of KwaZulu-Natal are isolated from the northern populations by the Great Escarpment, which in this region represents the northward extension of the Drakensberg. *Menodora africana* subsp. *australis* also has a few collections that appear remote from its main distribution.

In North America, there are a number of examples of such species or population disjuncts as well (see Figs. 5-7). *Menodora longifolia*, *M. yecorana* of Sonora and *M. jaliscana* of the Jalisco-Michoacan border are all restricted in their ranges and appear disjunct from the major body of the distribution of the genus in Mexico. The distributions of *M. helianthemoides* and *M. intricata* have a shared gap between central Mexico and the Tehuacán region of Puebla to the south (and *M. tehuacana*, a sister species to *M. helianthemoides*, is endemic to this southern region). *Menodora mexicana* shares the northern part of their distribution, but otherwise is known from a few even more southerly collections from near Oaxaca. The distribution of *M. scoparia* appears to be somewhat patchily interspersed within that of the more widely spread *M. laevis*. A small disjunct population of *M. scabra* var. *scabra* occurs in the middle Arkansas River valley of Colorado in the region between Cañon City and Pueblo, with the nearest known populations occurring in north central New Mexico. The distribution of *M. spinescens* appears to be broken into three distinct components, with the major, more northerly populations of Nevada and adjacent California being slightly disconnected from populations to the south representing var. *mohavensis*, and these in turn are quite remote from sporadic collections made in the northern Baja peninsula representing var. *bajense*.

These species or population-level disconnections may be the result of several different factors or the interaction of several different processes. First, gaps could be an artifact of sampling – simply no botanist may have ever collected in the gap region in question at a time when plants were flowering or in fruit. An extension of this is the possibility that collections may exist in the gap but were not reviewed. Secondly, given that long-distance dispersal by *Menodora* has apparently been a relatively common event, perhaps short-distance dispersal or migration is also common. Thirdly, gaps may represent the contraction of a larger ancestral range due to the introduction of physical or ecological barriers (i.e., vicariance).

The first case – that gaps may be an artifact of sampling – may be the easiest to prove, but requires access to the accumulated botanical collections of an entire region.

However, databases of collections remain largely institutional, if they exist at all, and without integration of these resources to provide a complete regional view, it may be difficult to draw conclusions about the presence of spatial or temporal gaps in collecting. Sampling errors may also result not from lack of collections but simply from not reviewing all available accessions from all available sources.

The second and third cases concerning dispersal or fragmentation of an ancestral distribution are considerably harder to prove. For example, populations of *Menodora. integrifolia* of Rio Negro and Chubut in Argentina frequently have the obtuse leaf apices that led to the description of var. *odonelliana*. This character is also present at some low frequency throughout the central range of the species. Arguably, its increased frequency in the southern populations could have become fixed either through drift of a once contiguous population that became isolated or through a founder effect following dispersal.

Whatever its causes, fragmented population distributions within a species thus seems to be a common pattern in *Menodora* on all three continents, and in some cases this isolation has probably resulted in allopatric speciation (e.g., *M. yecorana, M. longifolia,* and *M. jaliscana*, and probably all of the South American and African species). In North America, however, the majority of species are sympatric over some portion of their ranges with at least one or more other species (Figs. 5-7). This is most true in central Mexico, along the cordillera of the Sierra Madre Oriental between southern Coahuila and Nuevo Leon south to Hidalgo, where 10 of the 16 North American species have overlapping distributions. Some of this overlap is probably due to range expansion, particularly of the more widespread northern species *M. heterophylla, M. longiflora* and *M. laevis*, and possibly *M. coulteri*. Even discounting overlaps with these four species, it seems likely that some form of sympatric speciation may have been at work within this relatively limited geographic area, especially given the limited distribution of species with specialized edaphic preferences, e.g., adaptations to gypseous substrates (*M. henricksonii*, *M. gypsophila*). On the other hand, migration can almost never be ruled out, or proven, for that matter, in these historically arid, non-fossil forming environments. For sympatric speciation to have occurred, some isolating mechanism must be in place. *Menodora muellerae*, for example, with its elongated corolla tube, may have evolved in response to the preferences of a particular pollinator who specializes on *M. muellerae*, effectively limiting gene flow between the species. Adaptation to particular pollinators is certainly one of the major driving forces behind the evolution of the spectacularly long corolla tube of *M. longiflora* and the floral differences between the varieties of *M. spinescens*. In the case of the sympatric species of central Mexico, however, another as yet unexplored isolating mechanism could be stasipatry, in which changes in chromosomal organization or number may have isolated particular breeding populations in the past and allowed them to diverge.

Despite the proximity of a number of different species in central Mexico, there is little direct evidence for hybridization within group there or anywhere. However, in phylogenetic analyses (see the previous chapter), two North American species (*M. intricata* and *M. scoparia*) appeared to change places in independent analyses of data from different genomic partitions. Because of differing modes of inheritance of nuclear and chloroplast genes, incongruence between nuclear and chloroplast analyses can be interpreted as potential evidence of hybridization. Rather than appearing as sister to different species in the nuclear versus chloroplast analyses, however, the two species appear as sister to different entire clades. In the combined chloroplast analyses, *M. intricata* appears as sister to the helianthemoid clade, but in the ITS and combined data analyses it is sister to the Galeana clade. The situation in *M. scoparia* is a bit more complicated, since it is well resolved and well supported in only the combined analyses where it is sister to the rest of the scabroid clade. In the individual marker analyses, the group often does not appear to be monophyletic. In the ITS analyses it appears in part as sister to the scabroids and/or the helianthemoids, and similarly in the chloroplast analyses it appears in part as sister to the scabroids and/or the Galeana clade, when it is resolved at all. Thus, to some extent, *M. intricata* and *M. scoparia* switch places in the nuclear and chloroplast analyses between the helianthemoid and Galeana clades, along with some integration of *M. scoparia* into the broader scabroid group.

If hybridization is responsible for the apparent mobility of these two species in trees resulting from different phylogenetic analyses, then the hybridizations must be ancient ones involving the ancestors of the helianthemoid and Galeana clades. Based on the chloroplast data, each hybrid species would have resulted from reciprocal crosses involving a different maternal parent (assuming maternal inheritance of plastids). This seems rather straightforward in the case of *M. intricata*. However, the apparent ties of *M. scoparia* to the larger scabroid group suggest that there are some problems with this interpretation, and several alternative hypotheses are possible. Since the scabroid and helianthemoid groups are closely related, perhaps the hybridization that resulted in *M. scoparia* occurred prior to their divergence, i.e., the cross was between a proto-Galeanoid maternal parent and an ancestor of the collective helianthemoid-scabroid clade; this ancestor may have possessed molecular characters that were sorted differently between the two lineages. *Menodora scoparia* may thus reflect the ancestral condition, and subsequently the alternative placements of the species may be due to lineage sorting of these characters. However, we would actually expect *M. scoparia* to appear as sister to the entire helianthemoid-scabroid clade, and it does not appear in this position in any analysis. Another option is that *M. scoparia* is indeed derived from a hybrid cross between helianthemoid and Galeanoid ancestors, but this cross later quite promiscuously hybridized and perhaps introgressed with a proto-scabroid as well. If this cross involved allopolyploidy, then modern *M. scoparia* could have components of all three genomes, and this could account for the results we see. Yet a third possibility is that any of the alternative placements of *M. scoparia* in the phylogenetic trees is really just an artifact of homoplasy. For example, if *M. scoparia* resulted from a cross between proto-Galeanoid and proto-scabroid parents, then the placement with the helianthemoids could be just convergence in the data. Unfortunately, sorting these questions out will require a great deal more study.

Morphology

Habit

Menodora, like most of the Oleaceae, is a primarily woody genus, although it differs from the family in that most of its species are essentially suffrutescent but range from those that are nearly herbaceous to true shrubs. In form, the group can be classified into four loosely-defined classes: the large mound-forming shrubs, the more or less erect, fastigiate shrubs, the small mostly mound-forming shrublets, and the more herbaceous suffrutescent perennials. As individuals age, there can be quite a bit of intergradation between most of these forms, such that rather than the four distinct classes, there is really more of a continuum, particularly between the latter three forms.

The large, mound-forming shrubs include only basal clade members *Menodora robusta* and *M. spinescens*, which also happen to be the only members of the genus that are armed. Each also forms a very dense, intricately branched, impenetrable mound, and it can be almost impossible to discriminate if a particular mound represents one or more individuals. *Menodora robusta* can form large, globose mounds over a meter tall, but more commonly is much lower and spreading. *Menodora spinescens* usually takes the latter form. Observation of dead plants of *M. spinescens* in the Mojave Desert reveals that these often have relatively massive short woody trunks or caudices ranging from 4—8 cm in diameter. Given the slow dynamics of growth in a desert environment, it is reasonable to assume that these plants are probably long lived.

The species categorized as fastigiate shrubs can be broken into two subclasses, those that are more woody and shrub-like, and those that are at least slightly more suffrutescent and somewhat herbaceous. The former category includes the shrubs *M. juncea*, *M. decemfida*, arguably *M. longifolia* and probably *M. jaliscana*, though it is poorly known. The more suffrutescent category of fastigiate shrubs is quite large and variable, and individuals of species that I place in this category may fall out as woodier shrubs or even subherbaceous perennials depending on the variety or their state of development. This class includes *M. integrifolia, M. intricata, M. laevis, M. linoides, M. longifolia, M. mexicana, M. scabra* and its generally woodier varieties*, M. scoparia,* and *M. yecorana.* Most of these (*M. integrifolia, M. laevis, M. linoides, M. mexicana, M. intricata, M. scoparia* and *M. scabra*) often appear to be more subherbaceous.

Menodora coulteri, *M. henricksonii* and *M. muellerae* have both somewhat fastigiate and more mound-forming forms (*M. coulteri* var. *minima* has been traditionally recognized in the past, but grades almost completely into the species; *M. henricksonii* var. *confusa* morphologically resembles *M. helianthemoides*) but are probably better placed within the small mound-forming shrublet group. The latter group includes most of the North American species not mentioned above (*M. gypsophila, M. helianthemoides,* and *M. tehuacana*) and the high elevation species *M. pulchella* of Argentina. These form rather dense relatively small mounds, sometimes appearing caespitose or even matforming, though generally somewhat taller. These are also characterized by a reduced, few-flowered inflorescence, and flowers often appear as solitary until the plants are more closely examined.

Menodora heterophylla and *M. africana* are the most consistently subherbaceous or suffrutescent perennials in the genus, although again, particularly the latter species, they may sometimes appear a little more suffrutescent than herbaceous. Both species are often decumbent, but on occasion specimens with more fastigiate forms have been observed, particularly in *M. africana* and its subspecies *australis*. In Texas, *M. heterophylla* has been observed to often die back completely in hot dry summers, and is also subject to browsing, thus making it difficult for this species to achieve a more arborescent habit.

Roots and stems

All species, no matter the habit, are subtended by a woody caudex and taproot. In all species that have been observed, the taproot has been simple and sparingly branched, and is often quite substantial. A qualification for this is that in the case of the larger, woodier shrubs (e.g., *M. decemfida, M. juncea, M. robusta,* and *M. spinescens*), roots are rarely collected even for smaller individuals, and the majority of specimens may not even represent the woodier parts of the individual. However, Roig (1973) found the taproot in *M. decemfida* to be at least 8—10X the length of young plants, but was never able to determine the actual complete length due to technical difficulties. Steyermark (1932) remarked that occasionally some specimens indicate root growth occurs in a horizontal orientation rather than a vertical due to growth on a steep slope. This may also be the case when growing over a shallow, hard pan.

Plants grow from the woody caudex, with many axes branching from the usually fairly reduced woody crown. Often these will be somewhat decumbent and spreading, and lignify with age. Roig (1973) noted that new stems in *Menodora decemfida* remain green and photosynthetic for three years, beginning lignification during the third year and completely lignified by the fourth. Branches rise from these major axes, and it is from these that in general the plant takes its form, with new growth appearing from axils. All axes are terminated by either a flower or a thorn, thus growth of the plant is generally anthelate in form, with lateral axes often exceeding the major, central axis of each branch.

Growing stems are almost always subherbaceous in nature, and can be classified into two categories, those that are fluted with 4—6 well developed costae and thus are at least somewhat angled in cross-section (the intercostal regions or sulcae are often not very deep, giving a more terete section), and those that lack well-defined costae. The former class includes all but two species, while the latter includes only *Menodora robusta* and *M. spinescens*.

The condition in the former class has been variously described as ribbed, striate, fluted, sulcate, or furrowed, depending on whether the author sees the glass as half-empty or half-full (that is, emphasizing the ribs or costae versus the intercostal region, furrows, or sulcae; see Fig. 8). Species of *Menodora* with this form of stem have decurrent leaves with the leaf bases confluent with costae of the stems. Additional costae are usually present, and these are confluent with the usually abaxially prominent midvein of the leaves; these costae may not be as prominent or well-developed as the decurrent costae. *Menodora intricata* and *M. mexicana* serve as extreme examples where costae are very prominent and furrows relatively deep (Fig. 8); in most other species, the fluting is less dramatic. In some species, the costae of adjacent decurrent leaf bases may be particularly closely spaced, with a deep furrow between them, forming a notable transverse (between the axils) canaliculate groove running the length of the internode. In some cases, as commonly found in *M. decemfida* and *M. juncea*, this groove may be a distinctive feature of the stem in that the other intercostal regions will be significantly shallower. It is not a uniform feature, however. Böcher and Lyshede (1972) noted that this groove may serve to funnel water to the axils for uptake.

This form of stem has been anatomically studied in *Menodora. decemfida* (Böcher and Lyshede 1972), *M. scabra* var. *glabrescens* (as *M. scoparia*; Carlquist and Hoekman 1985), *M. scabra* (Record and Hess 1943; Baas et al. 1988) and *M. coulteri* (Baas et al. 1988). Böcher and Lyshede (1972) found that the costae are supported by collenchyma, and that inside the hypodermis are several layers of chlorophyllous palisade-like cells. The endodermis features large plasmodesmatal pits and perivascular fibers surrounding the phloem and xylem; the pith features large, lignified cells. Vessels were small and scattered. Similar results are reported by Carlquist and Hoekman (1985), though their study was comparative and aimed at identifying characters that correlate with ecological circumstance. In their study, *Menodora* is plainly a xeromorphic species, with a large number of vessels per mm^2 (about 700), small, mostly solitary vessels (averaging 169 mm long by 18.9 mm diameter), true tracheids, helical sculpturing on both early and latewood and ring-porous growth rings. Baas et al. (1988) and Record and Hess (1943) provided more detailed descriptions with similar observations (but see below) and noted the presence of distinct growth rings with radially flattened latewood fibers and marginal parenchyma, uniseriate rays, and the presence of parenchyma in "discontinuous, uniseriate, marginal bands" (this not noted by Record and Hess), but also noted the wood as being only "weakly semi-ring-porous" rather than simply ring-porous.

In their study of wood anatomy, Baas et al. (1988) also examined a third specimen, *Menodora* spec., of Liberia (specimen Fobes 1954 (WIS), wood voucher MADw 16689, USDA Forest Products Laboratory), which was radically different in several ways from the two North American examples. Since tropical Liberia is quite out of the known range for *Menodora*, I contacted Regis Miller of the USDA Forest Products Laboratory – Madison and Ted Cochrane of the University of Wisconsin Herbarium (WIS) for verification of the specimen. Cochrane (pers. comm.) determined the specimen to be a species of *Ixora*, of the Rubiaceae, and Miller (pers. comm.) confirmed that the wood is consistent with the Rubiaceae. While the conclusion by Baas et al. that "the generic identity of the wood sample studied is not suspect" is reasonable given the variability found in other genera of their study (*e.g.*, *Jasminum*), this points out the importance of both organismal knowledge and voucher specimens.

Representing the other, smaller class of stem morphology, the wood anatomy of *M. spinescens* has also been examined (Gibson 1983). Although not fluted, the stout, terete stems are striate, with many irregularly, longitudinally confluent striae separated by very shallow furrows. Striations are spaced more or less regularly in cross-section, and conform to Gibson's type 3 classification of cortical organization, with chlorenchyma concentrated around furrows and fibers localized in the costae (Gibson, 1983). A layer of gelatinous fibers is also found in the hypodermis. Another important feature noted by Gibson (1983) is that the occurrence of stomata on the stem is limited to stomatal crypts found only in the furrows (Fig. 9c). Crypts are relatively widely spaced (appearing in a density of 4—5 per μm^2) somewhat densely puberulent and deep, with randomly oriented stomata, and the hypodermis is lacking (Gibson, 1983). On the stem, these appear as white, lenticel-like dots in the shallow furrows of chlorophyllous stems (Fig. 9c), but turn black on older wood (Fig. 9d). Cortical chlorenchyma are not regularly palisade-like due to distortions caused by the crypts.

The chlorophyllous stems of *Menodora robusta* are superficially very similar in appearance to those of *M. spinescens*, though more robust. Closer examination, however, shows that the stout, terete stems of *M. robusta* lack any form of striation, and instead the surface is rather roughly irregular. *Menodora robusta* does, however, share the occurrence of stomatal crypts on the stems with *M. spinescens* (Correa, 1999). These two species are also the only two in the genus which are armed, and both appear to be armed by similar modifications of the terminal apex or axis of the branches, forming thorns (as opposed to spines). Steyermark (1932) referred to the situation in *M. robusta* as being pseudo-spinescent, apparently in the belief that this is a secondary feature that develops with age. Observation of young stems indicates, however, that this is a primary feature of stem development.

Stem vestiture (Fig. 10) is highly variable in the genus, and is not necessarily diagnostic in terms of species recognition by itself. For example, *M. longiflora* appears in more or less glabrous or glabrate, densely hispidulous and canescent, and more or less sparsely pilose forms, and these have been described as different species (*M. pubens, M. hispida*) though they often occur within the same population growing next to each other, *e.g.*, as found growing in a road cut above the Pecos River in west Texas (pers. obs.). Trichomes are unicellular, terete, simple and unbranched, usually hyaline or appearing white, with acute apices; occasionally the trichomes appear flat and deltoid (as in *M. africana*, and rarely in *M. heterophylla*) or rarely with somewhat broader, subpustulate bases. In plants that appear glabrous, trichomes are usually papillose, being quite reduced and rudimentary, but may be longer and better developed in the leaf axils and nodes, and occasionally along the transverse groove. Stems are often moderately hispidulous with short, recurved (usually retrorse) trichomes in many species, occasionally more densely so as in the canescent forms of *M. longifolia* and *M. coulteri*. Longer trichomes are common in the magniflora form of *M. helianthemoides*, the related M. *tehuacana*, *M. gypsophila*, and *M. henricksonii* var. *confusa*. Examples of stem vestiture are shown in Fig. 10.

Leaves

Leaf arrangement is highly variable in the genus, but at the basalmost nodes along a branch leaves are usually opposite. For most species, this arrangement is maintained along the axis up (or a few nodes prior) to the point where branching for the inflorescence begins. In the majority of species, at that point leaves grade into alternately arranged bracts subtending flowering pedicels or branches, although in *Menodora. coulteri, M. decemfida, M. henricksonii, M. longifolia, M. muellerae,* and *M. robusta*, the bracts remain opposite throughout, rarely becoming alternate only at the most distal parts of the inflorescence. In *M. africana, M. laevis, M. scabra* and *M spinescens*, the leaf arrangement is primarily alternate throughout, though in *M. scabra* var. *glabrescens* the leaves are usually opposite to near mid-branch. In other species, e.g., *M. heterophylla*, *M. integrifolia, M. juncea*, *M. pulchella* and *M. linoides*, the leaf and bract arrangement is predominantly opposite but can be quite irregular, moving from opposite or sub-opposite to alternate and back again.

Leaf attachment is mostly sessile or subsessile, with the leaf bases attenuating to the point of attachment, with the decurrent margins and midvein forming the ridges or striations of the stem fluting. In some species, *e.g.*, *M. helianthemoides*, the leaves may appear to be somewhat more petiolate due to the generally broader blades, but the base is still cuneate. Only in *M. africana* subsp. *africana* can the leaf be described as petiolate, but even in this case, the petiole is scarcely differentiated (other than by its location) from the majority of the highly dissected leaf blade.

The leaves of *Menodora* are simple, although Green (2004) cited them as being "simple, pinnatisect or *imparipinnate*." The latter may be a matter of interpretation, perhaps referring to the highly reduced, linear leaf segments found on the trifid leaves of *M. intricata* or the multifid leaves of *M. africana* subsp. *africana*. As the leaf segments do not appear as well-differentiated rachises, pinnules and petiolules, this interpretation seems to be superfluous.

Leaf shape is variable, occasionally even within a single individual (especially in *Menodora. integrifolia*), but for the most part is consistent within species. In most species, the leaves are entire and unlobed, and in some variation of linear to elliptic, lanceolate to oblanceolate (usually narrowly) or less commonly somewhat broader and ovate to obovate, with a single prominent nerve (rarely trinervate, as in *M. muellerae* and *M. gypsophila*). Even within taxa with leaves that are predominantly of these entire forms, however, some form of lobed leaf may be very rarely observed, as in *M. spinescens, M. helianthemoides, M. scabra, M. intricata,* and *M. decemfida*.

Species that commonly or predominantly have some form of lobed (bifid to pinnatifid) or pinnatisect leaf include the multifid-leaved *M. africana* subsp. *africana,* its subspecies *australis, M. heterophylla*, the highly variable *M. integrifolia,* and *M. pulchella*. *Menodora integrifolia* frequently appears throughout its distribution in an entire-leafed form, and *M. heterophylla* occurs rarely with only lanceolate leaves.

Leaf vestiture generally follows that of the stem, though usually not quite as dense, and often only on the adaxial surface, particularly along the margins or base. Both surfaces are usually punctate, the darker punctae apparently representing multicellular estipitate glands as found in *M. decemfida* (Böcher and Lyshede 1972). These are usually more apparent on the abaxial surface, where any other vestiture is usually limited to the prominent midvein, and may be obscure or absent adaxially.

Leaf anatomy has been studied in *M. decemfida* by Böcher and Lyshede (1972). They noted the presence of silica crystals in the epidermis, and a general sclerification of cells along the leaf margins and surrounding the vascular traces. Palisade layers appear to be bi-or triseriate.

Inflorescence

Characterization of the inflorescence of *Menodora* is a fairly difficult task due to variability. The broadest interpretation would be to describe inflorescences to range from solitary and terminal on the branches to a racemose or paniculate, rarely thyrsoid cyme. The inflorescence is determinate, as a single flower always terminates a major growth axis (except in the special cases of *M. robusta* and *M spinescens*, discussed below). In many of the smaller, typically mound-forming species (*M. coulteri, M. helianthemoides, M. henricksonii, M. gypsophila, M. pulchella, M. heterophylla, M. africana*) the inflorescence often appears solitary, but closer examination will usually identify at least some axillary branching below the terminal flower. In better-developed inflorescences, flower development is clearly centrifugal, moving from the center out, and often anthelate, with secondary, tertiary, or quaternary lateral cymules exceeding the main axis; branching for the inflorescence usually begins in the top half or one-third of a branch. Since branching for the inflorescence occurs fundamentally on at least two axes, the cyme is perhaps best described as a dichasium, although for the most part branching is alternate rather than the equal, opposite branching normally associated with that term.

Both *Menodora robusta* and *M spinescens* exhibit a divergent form of inflorescence in the genus. Major axes in these species are terminated not by flowers but by thorns, and the flowers terminate short, axillary shoots, forming a few-flowered, racemose, open thyrse (*M. robusta*) or a dense, compact, many-flowered, paniculate thyrse (*M. spinescens*).

Flowers

The flowers of *Menodora* are uniformly complete and perfect, and except for a few species follow a generic pattern with little variation (Fig. 11). The calyx is united into a turbinate tube with 5—10 usually linear or subulate calyx lobes, the tube being about 2 mm long and about as wide in flower, flattening and broadening horizontally about 2X as the fruit develops. Externally, the tube generally shares the vestiture of the pedicel, and is most often prominently nerved, the nerves continuing into the lobes. Lobes are usually sparsely hispidulous, and often punctate on the inner surface. In *M. africana* subsp. *africana*, the lobes are trifid, and in *M. pulchella*, *M. linoides*, and *M. africana* subsp. *australis*, individual lobes may be bifid. In some North American species such as *M. scabra* and *M. helianthemoides*, two adjacent lobes are occasionally fused, forming a broad, bifid structure. The calyx lobes often appear to be accrescent, growing longer as the fruit matures.

The corolla is typically infundibuliform, a light or bright yellow, with a tube usually of 2—7 mm, the length of the tube generally more or less coinciding with the apices of the calyx lobes. The tube is usually pilose with long, flat, hyaline trichomes within, and begins to flare to the throat at about half to two-thirds of its length, and this usually coincides with the point of attachment for the filaments; the diameter at the orifice is usually about 3-4 times the width of the tube at the base. There are usually five (rarely four to eight) ovate to obovate limbs, generally 3—10 mm by 2—6 mm, with obtuse to acute apices; just after opening, the apex may appear mucronate, but the mucro is ephemeral.

The two stamens are epipetalous, usually with flattened filaments attached at about one-third to half the length of the tube below the throat and holding the dorsifixed anthers exserted 2—4 mm above the throat. Anthers are yellow, often with a yellow or golden tan connective, and two longitudinally dehiscing thecae. Often a small linear, conical or deltoid process may exceed the connective apically, but is often obscure or missing; it is probably best observed in fresh material.

The ovary is superior, and in flower appears small, green and loaf-shaped, about 1 mm by 0.5 mm, divided in two equal-sized lobes by a medial, transverse suture and appearing apically subcordate. Each lobe represents a single carpel with a single locule, and contains two or more commonly four ovules with axile placentation.

The single style rises from between the two lobes of the ovary, and is terete, usually glabrous (sparsely pubescent only in *M. henricksonii* and some individuals of *M. gypsophila*) and terminates in a capitate, usually bilobed stigma. The stigma is usually equal to or can exceed the anthers by up to 4 mm.

In bud, the corolla is imbricate, and the outer petals are often a bright red in many species (e.g., *Menodora heterophylla, M. helianthemoides, M. integrifolia, M. scabra, M. spinescens*). The red usually fades quickly as the flower opens. In many species, flowers open in the late afternoon or evening, but fall by noon of the following day. Many, if not most, of the species are also pleasantly scented in flower.

In *Menodora coulteri, M. decemfida*, *M. helianthemoides, M. juncea,* and rarely *M. integrifolia,* I have observed populations containing individuals with both relatively small and large flowers, the larger being about 2X the smaller. In North America this size dimorphism has resulted in taxonomic recognition of *M. helianthemoides* vars. *parviflora* and *magniflora,* and *M. coulteri* var. *minima*. Rzedowski and Rzedowski (2004) cite a similar size disparity in *M. intricata* for the few specimens collected within the Bajío region of central Mexico. Roig (1974) also noted this dimorphism in *M. decemfida*. From observations of herbarium specimens, most species of *Menodora* have a similar size differential at the extremes, and for the most part, these represent the extremes of a normal frequency distribution (Table 2; Fig. 12).

Departures from the standard *Menodora* flower pattern include the flowers of *M. longiflora*, *M. muellerae*, and *M. spinescens*. Both *M. longiflora* and *M. muellerae* feature more or less salverform corollas, with the tube being 10—18 mm long in *M. muellerae* and an extraordinary 20—50 mm in *M. longiflora*; the corollas are the usual shades of yellow found in the genus. *Menodora longiflora* is also unusual in that the stamens are included within the tube (this also very rarely occurs in specimens determined as *M. muellerae*), and are almost sessile with the filaments very short; the apices of the anthers usually just reach the orifice. While stamen position is more or less standardized in *M. longiflora*, the length of style varies, and the stigma can be found positioned well-below the anthers, equaling the anthers or just exceeding them at the orifice, or well-exserted above. Except for the position of the anthers, this is suggestive of heterostyly, and is worthy of further research.

Menodora spinescens is the only species of *Menodora* in which the corollas are not yellow. The corollas are instead a white or cream-color, often with a rubescent-purpurescent tinge externally remaining from the red buds. These are uniformly among the smallest flowers of the group. Stamens are included (though in variety *spinescens* the anthers are often half-exserted above the throat). There are floral differences between the varieties of the species, as well. The corollas of variety *spinescens* are smaller and explanate, with short (3—5 mm) almost cylindrical tubes, with limbs 1.5—3 mm long; in variety *mohavensis*, the tube is essentially twice as large, and is ampliate, rapidly swelling and broadening. Flowering specimens from Baja California similarly have a corolla tube of about twice the length of the species, but narrower; corollas are salverform (Jon Rebman, pers. comm.). In the species, stamens are almost sessile, while in variety *mohavensis*, filaments are much longer (6—9 mm). The species also appears to be gynodioecious, with individuals that appear to have solely functionally female flowers (the included anthers are small, green, and appear rudimentary, style and capitate stigma exserted), and individuals with probably hermaphroditic flowers, with large, half-exerted, yellow, pollen bearing anthers, rarely with a visible style and stigma (the style and stigma are often trapped by the cohesive anthers, and rarely escape them, and the stigma is usually merely terminate or bifid; while this may limit pollination opportunities, these individuals do not seem to be female sterile; for further information, see discussion under the species treatment). The female flowers are generally smaller (tube 2.5-3.8 mm long, 1.3—2.2 mm at throat, limbs 1.2—2.2 mm long; versus tube 4.3—5 mm long, 1.8—2.8 mm at throat, limbs 2—2.9 mm long in the male/hermaphroditic corollas) and fewer in the inflorescence. Similar conditions are observed rarely in the variety *mohavensis*, but most specimens appear to have well developed anthers; however, the variety is poorly collected in flower.

Fruit

The capsular fruit of *Menodora* is its most distinctive character. It develops from the bicarpellate, bilobed ovary into two seemingly separate, ovoid to obovoid (often globose or ellipsoid) cells or cocci; these are connected only near the base (Fig. 13). These have been variously referred to as valves, cells, locules, cocci, mericarps or even as separate capsules. Typically the cocci occur in somewhat testiculate pairs, but rarely are single by abortion, and even more rarely as a trio as observed in *M. decemfida* (pers. obs.) or *M. africana* (Rohwer 1995a).

In most species, the pericarp of each coccus is thin, glabrous, somewhat membranaceous, green becoming a translucent papery golden tan in maturity, though often with a rubescent or purpurescent tinge. The coccus opens by circumscissile dehiscence around an equatorial suture, and the amphora is usually persistent; when mature, the calyptra is quite easily removed. The suture is often marked by a thickening of the pericarp on both surrounding sides. Each coccus typically contains two or four seeds; most start with four ovules, so fewer seeds develop through abortion. Seed dispersal may depend upon an elastic whipping motion of the flowering stem to catapult the seeds to some distance from the parent; otherwise gravity seems to be the only alternative.

Two species, *Menodora robusta* and *M. spinescens*, deviate from the common generic pattern of the capsule by having cocci that are indehiscent or more properly with irregularly loculicidal dehiscence; the ovary of both also contains only two ovules per carpel, as opposed to the usual four (Bentham 1846; Steyermark 1932; Correa 1999). In both cases, the cocci lack the circumscissile suture, and simply break open or shatter to release the seeds. The fruit of *M. spinescens* appears to be intermediate between the atypical form of *M. robusta* (see below) and that of the majority of species. The pericarp of the coccus is similarly papery and translucent when mature, though often hispidulous, and while it does lack the circumscissile suture, a vertical furrow is commonly observed, and is possibly but certainly not strictly correlated with dehiscence. It appears to have some similarity to the manner of dehiscence described for *Jasminum mesnyi* by Rohwer (1997), but is probably more like that of *J. nudiflorum* (Rohwer 1993).

The fruit of *Menodora robusta* is unusual in that the nearly independent cocci are quite fleshy and much more berry-like than most *Menodora* until maturity. The pericarp is quite thick and leathery, becoming dry, hard, opaque and black with age; internally it is often tan and quite lustrous. At maturity, the coccus is fragile, and shatters quite readily under a minimum of mechanical stress. While not quite identical in aspect, this seems to be similar to dehiscence of the papery capsule as reported for *Jasminum nudiflorum* by Rohwer (1993).

Rohwer (1997) examined in detail the fruit and seed development of *Menodora. africana*. As the ovary grows, the septum separating the two unilocular carpels fails to develop apically, allowing the cocci to develop independently in an almost balloon-like fashion. As the fruit develops in *M. africana*, the pericarp thickens gradually to the suture line, and then becomes very thin, and on drying, separates at this point; it lacks any lignified elements or stone cells, except at the base.

Seed

The seeds of *Menodora* are fairly uniform in their appearance, with most species having a somewhat spongy more or less deeply reticulate exotesta. Seeds are usually obovate in outline, with an obvious hilum at the base. In cross-section, the shape depends on how many seeds have developed within the locule; the exterior face (antiraphal) is usually convex, but the interior (raphal) face(s) will be shaped by the adjoining seeds. In a locule with a single developing seed, the seed will appear clavate, and somewhat elliptic in section. If two seeds develop, as is very common, the seed will appear plano-convex (with a flat raphal face) or somewhat meniscoid (raphal face concave, mirroring the antiraphal surface), usually with a prominent raphal rib. When three or more seeds develop (typically four), the seed will be trigonal in section, with two raphal faces separated by a raphal rib. The margins of the seeds often appear somewhat winged due to the enlarged spongy testa extending well around the enclosed embryo. Mature seed color is usually light to golden tan, but has been notably more castaneous to black in a few species (*M. robusta, M. decemfida, M. linoides,* and often *M. scabra*).

In *Menodora spinescens*, the seed is somewhat different in appearance, lacking the spongy testa found on most other species. The seed coat is relatively smooth, finely and regularly reticulate under magnification. The seeds are plano-convex and without a raphal rib.

Menodora laevis also has a somewhat different seed coat, in which the reticulate testa is covered by a more or less continuous coat, being irregularly foveolate (with small, usually circular foveolae) rather than alveolate-reticulate. The coat is chartaceous in appearance, and is usually quite light in color.

Rohwer (1995a) examined the seed anatomy of *Menodora africana* and *M. spinescens*. In the former, in which the seed resembles those of the majority of the group, the exotesta is essentially lost in during development, and the spongy, reticulate testa is formed by a middle layer of cells that has undergone an extreme anticlinal elongation. The outer seed coat is almost always separate from the inner layer, and in contrast to Steyermark (1932) two to three layers of endosperm are present until maturity. The embryo is large and straight with flat cotyledons and an inferior radicle (Steyermark 1932; Rohwer 1995a). The structure of the seed of *M. spinescens* is similar, but the enlargement of the middle layer of cells is by no means as extreme.

Chromosome number

Menodora has a unique base chromosome number for the family, with $x = 11$, based upon six counts representing probably four North American taxa in my classification. At the time of publication, however, these represented three species – *scabra* (three counts), *scoparia* (two counts), and *longiflora* (Bowden 1945; Taylor 1945; Lewis, Stripling, and Ross 1962; Reveal and Spellenberg 1976). Since taxon circumscriptions in the *scabra-scoparia* group have changed in my treatment, the identity for most of the counts is uncertain, though there is little reason to question the identity of the *M. longiflora* voucher (2n = 22; Taylor 1945) as this species is quite distinctive. Unfortunately, of the others, I have only seen the voucher for one, *Ross 52* (TEX), and have determined it as *M. laevis* (*n* = 11; Lewis, Stripling, and Ross 1962). The locality for one of the other *scabra* collections strongly suggests that it is probably *M. laevis* as well (*2n* = 22; Reveal and Spellenberg 1976). Taylor (1945) does not explicitly cite the origin of the remaining scabroid sample, but presumably it may have been obtained locally by the Soil Conservation Service in Tucson, from whom Taylor received all of his *Menodora* material. If so, then this sample probably represents *M. scabra* var. *sonorensis*, and is a polyploid with *2n* = 44. The identity of the *scoparia* samples can be estimated with some certainty from their provenance. Both counts were from stock grown from the same seed accession, and thus represent independent counts of either one individual or two individuals of one population. Being a western scoparioid form, it is probably *M. scabra* var. *glabrescens*, and its collection locality of Payson in Gila County, Arizona is certainly consistent with that determination (*2n* = 22; Taylor 1945).

Ecology

Menodora has been described as a plant of arid lands (Steyermark 1932; Goldblatt 1978), and this is true of the majority of species. In the highly generalized Köppen-Geiger world climate classification (Kottek et al. 2006), these species inhabit arid steppes and desert regions. From a physiographic viewpoint these are remarkably similar in appearance worldwide, and in the case of northwestern Argentina and the southwestern North America even share many genera in the composition of the flora.

However, a few species, namely, *Menodora africana*, *M. heterophylla,* and *M. integrifolia*, occur in more temperate, humid conditions. In the Köppen-Geiger scheme (Kottek et al. 2006), these species inhabit regions that are categorized as warm temperate, humid or winter-dry, with hot or warm summers (Cfa, Cfb, Cwa, Cwb in the classification). However, as noted by Meyer (1957) in South America, these species do tend to occupy drier habitats, and in particular are plants of grasslands or savannas, preferring open, sunny exposures. In North America, the greater part of the range of *M. heterophylla* is in the relatively moist coastal plain and grassland savannas of central Texas, but does extend westward into more arid climates classified as hot arid steppes in west Texas and northeastern Mexico (classified as matorral xerófilo in the vegetation scheme of Rzedowski 1981). In South America, the range of *M. integrifolia* is almost entirely within climate characterized as warm temperate with hot summers, although in northwest Argentina and Bolivia conditions are at least winter-dry, and in Bolivia, summers are cooler. In South Africa, the grassland-savannas of northeastern South Africa and southeastern Botswana are classified as temperate and winter-dry, with hot or warm summers.

One aspect of these grassland species that is unexplored is their relationship with fire. In both South America and South Africa, *Menodora integrifolia* and *M. africana* subsp. *africana* were observed to resprout vigorously from the caudex in places that had recently burned. Low intensity grassland fires may serve to limit competition from other species and keep habitats relatively open and unshaded; the perennial habit of *Menodora* in these grasslands would seem to be well adapted to resprouting, and the generally subherbaceous aspect of these species may reflect an adaptation to fire.

Menodora, as noted by Roig (1973) in *M. decemfida*, is largely a social species, and can form extensive colonies. It may be locally quite common, but is often absent from nearby, and to the eye, identical habitats; the distribution of most species is often therefore quite patchy. In the case of *M. robusta*, *M. spinescens*, and *M. decemfida*, populations can be dominant or co-dominant elements of the landscape. In *M. decemfid*a, Roig (1973) also notes a varying age structure centered around older, presumably maternal individuals, in one instance counting 52 probable progeny; despite this, plants maintain a 1—2 meter spacing between them. This seems to be true of most species, with the only exceptions being *M. robusta* and *M. spinescens*. While these commonly appear as isolated individuals, they can be occasionally found in groups of densely intertwined two or three.

Roig (1973) further noted the occurrence of *Menodora decemfida* in bands of more or less equal mid-elevations along rocky slopes, and suggests that the lack of individuals above or below may be to due lack of water accumulation above and erosion on lower slopes. In general, most arid-land species of *Menodora* also occur predominantly on exposed, rather rocky or gravelly slopes, and are often limited to the mid-to-lower elevations on a given slope; rather rarely they may be present in the sandy bottoms of washes, but are almost completely absent from desert basins unless some topographic feature is present. The limiting factor below may be more associated with a combination of soil texture and the greater availability of water with accompanying competition from other species. The lack of water accumulation on higher slopes may be a limiting factor in the upward expansion of the colony, but gravity may also be a factor. Lacking a better vector, seed dispersal is probably initially due mostly to gravity as seeds fall from the mother plant, and may also be aided by sheet flow of water over the surface (in the downhill direction, of course) once propagules are on the ground. Thus, it may be somewhat difficult for a population to move upward except by action of wind or animal dispersal.

The pollination ecology of *Menodora* has not been studied systematically. The general syndrome (light-colored, scented, night-blooming) is highly consistent with moth pollination, and in particular the long corolla tube of *M. longiflora* may be especially adapted for pollination by hawk moths (Faegri and van der Pijl 1978). During daylight, a species parade of flies (including long-tongued species), small wasps, bees, butterflies and moths can be observed visiting flowers.I have observed this in a number of populations of *M. heterophylla*, *M. integrifolia*, *M. scabra*, and *M. spinescens* var. *spinescens*. In flowering populations of the last, in the evenings I have found individuals loaded with large groups of an undetermined (and presumably single) species of moth, although I've never been able to see if they are visiting flowers or just otherwise engaged on the plants (e.g., mating or laying eggs). In fruiting populations, though, it is quite common to find fruit with a small circular hole in the pericarp and a small green caterpillar inside, and thus some form of interaction seems likely. The differing floral forms of the variety *mohavensis* and the Baja populations may indicate selection for different pollinators than the species.

Flowering in most species appears to be tied more to precipitation than daylight or night duration, and many species (particularly those that have been well collected) have been found in flower in almost every month of the year. Roig (1973) further correlates the occurrence (or lack) of precipitation with the appearance and disappearance of leaves in *M. decemfida*, and this certainly seems to hold true with other species that often appear aphyllous (*e.g.*, *M. intricata, M. juncea, M. robusta* and *M. spinescens*).

Life expectancy, survivorship and recruitment have been studied in a few North American species. Summarizing the results of a more than seventy-year long term study of plots on Tucamoc Hill at the Desert Laboratory in Tucson, Arizona, Goldberg and Turner (1986) found that densities of *M. scabra* have routinely declined since 1906 even in grazing-excluded plots, and in particular crashed after 1950 coinciding with a protracted period of drought between 1948—1967, with a steady decline since. They found only 25% of plants survive to their seventh year, with a maximum age lying between 30 and 50 years. Over a fifteen year period, Cody (2000) studied survivorship and recruitment of desert perennials in an 18 x 20 meter plot in the Granite Mountains of California. In his study, he noted a 10% average increase in size, only two mortalities and a single recruitment among the population of *M. spinescens*, and estimated the lifespan to lie between 99 to 426 years (though the latter, due to low mortality, should be potentially regarded as an overestimate). Each of these studies suggest that population recruitment may be fairly low (despite the fact that seedset is usually fairly heavy in most species), and that individual plants may be relatively long-lived. The data suggest that once a population crashes it may be difficult for it to recover, and moreover that establishment of new populations may be difficult.

Ethnobotanical and Human Uses

Menodora has not been noted historically to have been widely utilized by indigenous peoples. The only recorded usage is by the Navajo of the southwestern United States, where *Menodora scabra* was used medicinally to treat several ailments or conditions. A Navajo name for the plant, *Tinétc'il* (Elmore 1943) or *diné C'il* (Wyman and Harris 1941), is translated as "Navajo plant" although this appellation seems to have been applied to a wide range of genera and species (Wyman and Harris 1941); similarly, another name, *wolaci ilbez*, meaning “red ant decoction,” is also used for a potion made from a large and variable list of plants including *Menodora* (Wyman and Harris 1941). Vestal (1952) noted that a decoction of the root was used as a general analgesic for back pain, a decoction of the plant was used as an aid in labor, an infusion of the plant was used to treat heartburn, and that the plant in general was used as a tonic or “life medicine.”

Although often quite showy in flower and pleasantly scented, *Menodora* has not traditionally been cultivated as a garden flower. Beginning perhaps in the late 1980s or early 1990s, there has been interest in cultivating *M. longiflora*, and it is with some regularity available from native plant vendors. Most interest in the plant has been in its utility as a forage plant for wildlife and livestock.

MATERIALS/METHODS

This work is based upon experience gained from field collection of specimens and review of herbarium material. Field collections were undertaken between 2001 and 2004 in the southwestern USA, Mexico, Argentina, and South Africa, and resulted in the collection of 77 specimens. Loans of herbarium specimens were requested from the Harvard University Herbaria (A/GH), New York Botanical Garden (NY), Missouri Botanical Garden (MO), United States National Herbarium (US), University of California at Berkeley (UC/JEPS), Universidad Nacional Autónoma de México (MEXU), University of Michigan (MICH), Museo de La Plata (LP), Herbario Nacional de Bolivia (LPB), Herbier National de Paris (P), Conservatoire et Jardin botaniques de la Ville de Genève (G), Göteborg University (GB), University of Michigan (MICH), and the

National Herbarium of South Africa (PRE). Additional specimens were reviewed at the Plant Resources Center of the University of Texas at Austin (TEX/LL), Rocky Mountain Herbarium (RM), Instituto de Botánica del Nordeste (CTES), Fundación Miguel Lillo (LIL), Universidad Nacional de Salta (MCNS), Instituto Argentino de Investigaciones de las Zonas Áridas (MERL), Instituto de Botánica Darwinion (SI), Museo Nacional de Historia Natural (SGO), Herbier National de Paris (P), Conservatoire et Jardin botaniques de la Ville de Genève (G/G-DC), the Royal Botanic Gardens at Kew (K), National Herbarium (PRE), Bews Herbarium (NU), KwaZulu-Natal Herbarium (NH) and Compton Herbarium (NBG/SAM). In total, about 3,283 specimens were reviewed in this study.

Label data from field and herbarium collections were routinely entered in an Access 97 database (Microsoft Corp., Redmond, WA). Locality data were georeferenced if possible for mapping and analysis using ArcView version 3.1 (ESRI, Redlands, CA). The database was used to compile lists of exsiccatae and collectors, and to compile morphological, ecological, elevational, and phenological information for each specimen.

Detailed observations and measurements of morphological characters were taken from 492 herbarium specimens, representing 1 to 98 specimens per species, with a median of 14.5 per species. Initially, all measurements were taken by hand using a ruler or optically with a reticle in a stereo microscope, and recorded in a Microsoft Access 97 database (Microsoft Corp., Redmond, WA). Later macromeasurements were made using a Fowler Sylvac UltraCal IV electronic caliper (Fred V. Fowler Co., Inc., Newton, MA), which with the accompanying GageWedge software (TAL Technologies, Philadelphia, PA; distributed by Fred V. Fowler Co.) allowed for direct input of measurement data into the database. Figure 14 shows how most measurements were made, and an elaboration follows.

Plant height (Fig. 14a) was measured from the apparent ground line on the caudex to the tallest extremity; if label information included the height, this superseded any measurements. Height was not recorded on specimens that were obviously fragmentary, as most of the larger shrubs usually were, unless this information appeared on the label. Caudex diameter was measured at the widest point, which typically was near the top of the caudex. Internodes were measured at the first full internode below the branching for the inflorescence (Fig. 14b); in cases where an entire branch could be considered the inflorescence, internodes were measured at midbranch. Specimens were surveyed to find what best might represent a subjective average internode length; a single value was recorded in this range, and minimum and maximum values were also recorded. Stem trichome length was surveyed in a similar fashion, but only a single measurement was recorded.

Leaf measurements (Fig. 14c and 14d) are straight forward, with length being measured from the point of attachment to the apex, and width being measured at the widest point. In lobed leaves (Fig. 14d), width was measured from the widest apex to apex of the lateral lobes, and additional observations were recorded for the width of the ultimate segment of the central lobe and at the base of departure for the lower lobes.

Floral measurements are similarly straight forward. Length of the calyx and corolla tubes and the style were measured from the base of the receptacle. These were found from dissection to vary less than 1 mm from actual lengths, and thus extensive dissection was felt to be unnecessary. Similarly, the point of attachment for the filaments was found through dissection to coincide with the point where the corolla tube in most species began to flare dramatically, thus making dissection unnecessary, though this was checked frequently. Tube diameter was recorded only at the throat of the calyx, while for the corolla, tube diameters were recorded for the base and throat. Widths for the calyx lobes and petals were recorded from the widest parts of the appendage. Generally, floral measurements were relatively uniform throughout a specimen, and only a single flower was measured per specimen unless there were marked differences.

Fruit and seed measurements are also straight forward. Each coccus of the deeply bilobed fruit was measured independently, with length and diameter being recorded for each (Fig. 14g); one to ten fruit were measured per specimen, depending on the number of available mature fruit. Length, width and height were recorded to a maximum of ten mature seeds per specimen if available (Fig. 14h).

Once specimen observations were complete, character data were exported by taxon from the Access database to an Excel 2003 spreadsheet (Microsoft Corp., Redmond, WA). Qualitative characters were summarized by hand, and quantitative characters were summarized by computing the median and standard deviations along with minimum and maximum values. The summarized data for each taxon was copied to a single worksheet, which was used to generate the taxon descriptions. These were finally edited by hand into their final forms.

Species Concept

Species within *Menodora* are recognized as monophyletic groups, and I use a phylogeny based upon molecular evidence (see previous chapter) to inform this systematic treatment. In this regard, my species concept thus requires that a species be not only distinctive morphologically (*i.e.*, is distinctive in at least one character but usually by a suite of character differences) but also represented in the phylogeny as a monophyletic group. For infraspecific taxa, I have used both subspecies and variety, with the implied hierarchical superiority of the former rank over the latter. For both ranks, I have looked for distinctive morphologies that also have a distinctive geographic component. The major difference between these lower categories is chiefly in the range of morphological intergradation observed along geographic boundaries. Monophyly is desired at these lower ranks, but may not be strictly observed, as the molecular markers used in the phylogenetic analyses may simply lack the necessary information to provide resolution at this level, and there is also the possibility (or even high probability) of reticulation between sympatric or peripatric populations as well. Problems with recognizing species, subspecies, or varieties are discussed in detail in the taxon descriptions below.

SYSTEMATIC TREATMENT

***Menodora* Bonpl. in Humb. & Bonpl.**, Pl. Aequin. 2: 98, tab. 110, 1812. TYPE: MEXICO: HIDALGO: *Menodora helianthemoides* Bonpl.

Bolivaria Cham. & Schltdl., Linnaea 1:207, 1826. TYPE: URUGUAY: *Bolivaria integrifolia* Cham. & Schltdl. *Calyptrospermum* A. Dietr., Sp. Pl., 6 ed., 1:227, 1831.

Menodoropsis (A. Gray) Small, Fl. S.E. U.S. 917, 1903. Basionym: Sect. *Menodoropsis* A. Gray, Amer. J. Sci. II 14: 45, 1852. TYPE (Steyermark, Ann. Missouri Bot. Gard: 19:143, 1932.): USA:TEXAS: [Comal Co.]: *Menodora longiflora* A. Gray.

Shrubs or more typically erect or spreading ***suffruticose or subherbaceous perennials***, branching from a woody caudex and taproot, rarely armed. ***Leaves*** simple and entire or variously lobed to pinnatisect or multifid; if entire, linear to suborbicular, usually narrowly lanceolate to narrowly oblanceolate; attachment sessile, subpetiolate or rarely petiolate; arrangement opposite, approximate or alternate; leaves are quite reduced in some species and may only be seasonally present in others. ***Inflorescence*** determinate, usually a centrifugal, anthelate, simple to compound dichasium with either opposite or alternate branching, but in some species more thyrsoid and racemose or paniculate; flowers also often appearing solitary and terminal. ***Flowers*** complete, perfect, imbricate in bud and often bright red before flowering, hermaphroditic (apparently functionally gynodioecious in one species), pedicellate. ***Pedicels*** usually axillary from leaf-like bracts, erect in flower, erect or cernuate in fruit. ***Calyx*** gamosepalous, persistent; tube typically short, turbinate or campanulate, broadening to 2X in fruit; 5-10 (rarely more) linear or subulate lobes, these bifid or trifid in some species. ***Corollas*** gamopetalous bright or pale yellow (white in one species); tube usually at or just exceeding calyx lobes (much longer in some species), usually pilose or rarely glabrous within; limbs typically 5 (rarely 4-8), imbricate, outer often red in bud. ***Stamens*** 2, epipetalous, filantherous (though nearly sessile in two species); filaments inserted, typically adnate below throat of corolla tube, free above, usually holding the anthers exserted except in two species (rarely in another); anthers with two thecae, dorsifixed, erect, dehiscing longitudinally, often with a small process extended above the connective. ***Ovary*** superior, bicarpellate, bilobed, each carpel represented by a lobe and with a single locule and 2-4 ovules with axile placentation; style single, filiform, usually exserted and equaling or more commonly exceeding the anthers; stigma capitate or bilobed. ***Fruit*** a deeply divided, didymous capsule with two nearly independent globose to obovoid cocci, these attached (usually quite obscurely) only near the base on the receptacle; rarely with only a single coccus and even more rarely with three; each coccus irregularly dehiscent or more typically circumscissile, the amphorae of the circumscissile cocci usually persistent. ***Seeds*** 1-4 per carpel/coccus, with minimal endosperm, usually trigonal or somewhat plano-convex or meniscoid in section, typically with a spongy reticulate outer seed coat and a smooth hard, inner seed coat, the latter often green and chlorophyllous in younger seeds. ***Base chromosome number*** $x = 11$, $2n = 22, 44$.

Key to taxa

1\. Plants armed, thorny; obovoid cocci of capsules irregularly dehiscent
2\. Corolla yellow; capsules glabrous; pericarp thick, dark and opaque when mature ……………………………………………1. ***M. robusta***
2\. Corolla white (often reddish or purplish on exterior); capsules scabrid (rarely glabrous); pericarp thin, appearing membranaceous and translucent when mature ……………………………………2. ***M. spinescens***
1\. Plants unarmed; each globose or obovoid coccus of capsules with circumscissile dehiscence
3\. Internodes elongate, greatly exceeding the subtending leaves with total length approximately 1.5x the leaves or more, leaves not appearing crowded
4\. Leaf attachment below inflorescence predominantly alternate, opposite usually only at basal nodes on branch ……………21. ***M. laevis***
4\. Leaf attachment below inflorescence predominantly opposite, becoming alternate only distally near the inflorescence if at all
5\. Stems punctate, often hispidulous at nodes and leaf axils ……………………………23. ***M. yecorana***
5\. Stems glabrate to strigillose, often hispidulous at least at nodes and axils, but never punctate
6\. Plants often spreading (occasionally twining in dense vegetation) to erect; stems prominently fluted with relatively deep sulcae, strongly angled in cross section
7\. Leaves highly reduced, linear to linear-lanceolate or linear-oblanceolate, usually less than 1 mm wide, glabrate (though often hispidulous at base); fruit held strictly erect .....11. ***M. intricata***
7\. Leaves lanceolate to elliptic or slightly oblanceolate, rarely narrower to linear but usually greater than 1 mm wide, notably punctate especially abaxially, otherwise glabrate (though often hispidulous at base and along

margins above and nerve below); fruit held erect, pendant, or both ....15. ***M. mexicana***

6. Plants strictly erect, fastigiate; stems merely somewhat striate to moderately fluted (often more so above) with shallow furrows, terete to moderately angled in cross section
    - 8. Plants subherbaceous to suffrutescent shrubs; upper leaves much reduced in size versus the lower; internodes relatively short and crowded basally but lengthening dramatically to midstem
        - 9. Leaf arrangement below inflorescence mostly opposite; leaf blades never punctate; corolla tube glabrous internally ....20. ***M. scoparia***
        - 9. Leaf arrangement below inflorescence usually opposite to near midbranch and alternate above; leaf blades occasionally punctate below; corolla tube pilose internally .... 24b. ***M. scabra* var. *glabrescens***
    - 8. Plants suffrutescent shrubs; leaves above basal nodes relatively uniform in size, largest at midstem but not markedly different in size from those at surrounding nodes; internodes relatively uniform in length
        - 10. Stem leaves lanceolate to oblanceolate, usually greater than 1 mm wide, rarely bifid or trifid below; flowering pedicels glabrous; 5—10 calyx lobes, prominently nerved ....5. ***M. decemfida***
        - 10. Stem leaves linear or subulate, usually less than 1 mm wide, plants often appearing aphyllous; flowering pedicels hispidulous; 5—6 calyx lobes, nerved but not prominently .... 3. ***M. juncea***

3. Internodes short, scarcely if at all exceeding the subtending leaves or with total length less than 1.5X the leaves, leaves appearing relatively crowded on branch
    - 11. Calyx lobes usually fewer than 8 (typically 5-6).
        - 12. Leaves mostly trifid with obtuse apices; plants dense, short mound-forming shrubs less than 10 cm tall ....7. ***M. pulchella***

12. Leaves simple or variously lobed (bifid to pinnatisect) with acute apices (occasionally obtuse); plants erect fastigiate shrubs or subshrubs greater than 10 cm tall

13. Leaves predominantly variously lobed, if simple, these usually at and in inflorescence.............8. ***M. integrifolia***

13. Leaves predominantly simple, if lobed, these usually limited to lowest nodes on branch

14. Leaves linear to narrowly lanceolate or oblanceolate, usually greater than 3 mm wide and greater than 10 mm long, usually punctate below, rarely hispidulous especially at base ....8. ***M. integrifolia***

14. Leaves mostly elliptic to oblanceolate, usually less than 3 mm wide and less than 10 mm long, hispidulous....................................6. ***M. linoides***

11. Calyx lobes usually 8 or more, rarely fewer

15. Fruit held both erect and pendant …................15. ***M. mexicana***

15. Fruit held strictly erect or pendant but not both [18]

16. Fruit held erect

17. Corolla salverform, tube greater than 25 mm long; stamens included; calyx lobes usually 10 mm long or more ....10. ***M. longiflora***

17. Corolla infundibuliform, tube less than 8 mm long, stamens exserted; calyx lobes usually less than 10 mm long

18. Leaves below inflorescence predominantly opposite

19. Stems prominently fluted with deep sulcae; leaves often becoming alternate just prior to inflorescence, bracts in inflorescence usually alternate; calyx lobes usually greater than 4.5 mm long ....15. ***M. mexicana***

19. Stems fluted with shallow to moderately deep sulcae; leaves and bracts predominantly opposite, bracts becoming alternate only in most distal portions of inflorescence; calyx lobed usually less than or equal to 4.5 mm long ....22. ***M. longifolia***

18. Leaves below inflorescence predominantly alternate, opposite only at basal nodes (though rarely to inflorescence)

20**.** Seeds with a continuous chartaceous rugulose-foveolate outer coat**,** pitted with small, irregularly circular openings (foveolae), an underlying larger reticulate pattern sometimes visible ....21. ***M. laevis***

20**.** Seeds with a deeply and somewhat coarsely reticulate outer coat, alveolae usually somewhat quadrangular in outline ....24. ***M. scabra***

16. Fruit pendant

21. Leaves predominantly bifid, trifid, pinnatifid or pinnatisect (upper leaves and bracts may be entire)

22. Leaves deeply pinnatisect, with ultimate segments less than 1 mm wide; calyx lobes usually trifid... 4a. ***M. africana* subsp. *africana***

22. Leaves primarily bifid, trifid or pinnatifid, ultimate segments 2 mm or more wide; calyx lobes usually simple and entire (rarely one or a few bifid or trifid)
    23. Plants suffrutescent, spreading or erect; corolla tube usually less than 5 mm long; anthers 2—3 mm long by 0.6—0.9 mm wide; style exceeding the anthers by 2 mm or more; stem trichomes deltoid ....4b. ***M. africana*** **subsp.** ***australis***
    23. Plants subherbaceous, commonly spreading or decumbent but occasionally more erect; corolla tube usually 5 mm or more long; anthers 1—2.5 mm long by 0.4—0.5 mm wide; style equaling or exceeding the anthers by 2 mm or less; stem trichomes more or less linear, rarely broader and deltoid ....9. ***M. heterophylla***
21. Leaves predominantly entire, obovate or elliptic or linear to oblanceolate, rarely bifid or trifid
  24. Stems prominently fluted with deep sulcae ....15. ***M. mexicana***
  24. Stems merely somewhat striate or fluted with shallow to moderately deep sulcae
    25. Leaves relatively broad throughout, elliptic or ovate to obovate, 2.5—9 (11) mm wide, (1) 2.5—4 (5) times long as wide
      26. Leaf blades not at all punctate; stem trichomes less than 0.1 mm long; leaf length to width ratio 2 or less; plants usually taller than 50 cm ....16. ***M. jaliscana***
      26. Leaf blades punctate, often more notably below; leaf length to width ratio 2 or more; plants usually less than 30 cm
        27. Leaves strictly opposite throughout, even in inflorescence; uninervate, nerve not prominent below; style sparsely pubescent ....13b. ***M. henricksonii*** **var.** ***confusa***
        27. Leaves becoming alternate, bracts alternate in inflorescence; uninervate (lateral nerves may be visible but not prominent in one species), nerve prominent below at least basally, though often attenuating to apex; style naked
          28. Stem trichomes mostly less than 0.3 mm in length; lateral nerves on leaf blade not apparent ....19. ***M. helianthemoides***
          28. Stem trichomes mostly greater than 0.3 mm in length; lateral nerves on leaf blade often visible though not prominent below ....18. ***M. tehuacana***
    25. Leaves relatively narrow, narrowly elliptic or linear-lanceolate to linear-oblanceolate, often broader below, usually 1-3 (5) mm wide, (2) 3—9 (15) times long as wide
      29. Corolla tube 9—18 mm long, glabrous within; anthers rarely included ....12. ***M. muellerae***
      29. Corolla tube less than 7 mm long, pilose within; anthers always exserted
        30. Leaves trinervate, (lateral nerves occasionally obscure but often prominent), narrowly elliptic or lanceolate to oblanceolate; stems

and leaves mostly pilose with long spreading trichomes 0.2 mm long or more ....14. ***M. gypsophila***

30. Leaves uninervate, linear-lanceolate to linear-oblanceolate, occasionally broader; stems and leaves moderately to densely scabrid; trichomes short, mostly retrorse-appressed, less than 0.15 mm long but rarely longer
    31. Styles sparsely pubescent near stigma .... 13a. ***M. henricksonii* var. *henricksonii***
    31. Styles glabrous ....17. ***M. coulteri***

Species descriptions

1. *Menodora robusta* (Benth.) A. Gray

Amer. J. Sci. 14:43, 1852. Basionym: *Bolivaria robusta* Benth., London J. Bot. tab. 5, 1846. Holotype: ARGENTINA: Patagonia, *Capt. Middleton s.n.* (K!)

Common name: *manca potrillo*

Illustrations: Lilloa 28: 216, Fig. 1 (Meyer, 1957); Fl. Patagonica 6: 39, Fig. 23 (Correa, 1999)

Plants large, densely mound-forming and armed ***frutescent perennials***, (30) 73.7—150 (180) cm tall, with a woody taproot, basal trunk up to 5 cm or more with many branches; often appearing aphyllous. ***Stems*** stout, spreading, intricately and densely branched throughout, branching opposite, rarely alternate, divaricate, branches and branchlets terminating in a thorn; older wood tan to gray to black, atratous, often with black spots, glabrous, rimose; younger stems green, rugose or warty, pitted, terete in cross section, glabrate, trichomes rudimentary, minutely papillate under magnification, (0.03) 0.05—0.08 (0.09) mm; appearing jointed at nodes with a transverse suture connecting the opposite leaves, internodes at midbranch (3) 5—16 (23) mm; often appearing aphyllous.

Leaves opposite, sessile or rarely more or less subpetiolate, divaricate, subcoriaceous, elliptic to obovate or ovate, occasionally linear to lanceolate or oblanceolate, (1.2) 2.5—6.3 (9) by (0.4) 0.8—2.1 (3) mm, length to width ratio (1) 2—4.9 (6.4), glabrous to hispidulous, apices obtuse or acute, margins entire, base attenuate, decurrent, uninervate, nerve obscure, not prominent, swollen at node; after falling, remnant leaf bases often appear as dry cuneate scales at nodes. ***Inflorescence*** a terminal, loose, open racemose or paniculate cyme of 1—12 flowers, individual flowers terminating unbranched axillary short shoots or longer branchlets. ***Flowers*** fragrant, on short pedicels. ***Pedicels*** (0) 0.2—1.9 (3.4) mm long, 0.5—1 (1.1) mm in diameter, densely puberulent, holding fruit erect, subtended by an opposite pair of reduced, densely hispidulous leaf-like bracts. ***Calyx*** tube turbinate to campanulate, glabrous to hispidulous, (2) 2.2—3.4 (4) by (1.7) 1.8—2.8 (3) mm, broadening in fruit to 4.6—7 mm; lobes 5—6, (0.5) 0.6—1.7 (2.3) by (0.3) 0.6—1.2 (1.5) mm, thick, not nerved, deltoid, occasionally linear or broadly subulate, hispidulous, apices acute, margins entire, occasionally appearing reflexed. ***Corolla*** infundibuliform, yellow, tube (8) 10—13.8 (15.4) mm, (0.9) 1—1.8 (2.2) mm at base, opening to (4.7) 4.8—7.2 (8) mm at throat, pilose within; limbs (4) 5 (7), ovate, apices obtuse or mucronate, rarely broadly acute, (3.7) 5—7.8 (8.6) by (3.5) 4.4—6.2 (6.4) mm, glabrous. ***Stamens*** filantherous; filaments adnate ca 4—6 mm below throat, (6) 7.4—10.3 (10) mm long, pilose to sparsely pubescent, rarely glabrous; anthers plump and yellow (rarely appearing rudimentary), exserted ca 3—5 mm, (1.3) 1.5—2.5 (3.2) by (0.7) 0.8—1 (1.1) mm, lacking any process from the connective. ***Pollen*** yellow, 60—70 µm. ***Ovary*** bicarpellate, bilobed, each carpel with a single locule and 2 ovules. ***Style*** (13.7) 14.4—21.8 (24) mm, glabrous. ***Stigma*** capitate, equalling to exceeding the anthers 3—6 mm. ***Fruit*** with cocci globose or more commonly ellipsoid or obovoid, fragile on maturity and irregularly dehiscent, glabrous, ca (6) 6.7—8.1 (8.4) by (4) 4.5—6.3 (6.9) mm in diameter; pericarp thick, coriaceous, a mottled light green becoming darkly castaneous or atratous with maturity, interior a light, lustrous tan; not persistent; each coccus containing usually 2 seeds. ***Seeds*** obovate, more or less plano-convex to lenticular, 4.5—5.2 (5) by 2.3—2.5 —3 by 0.7—1.7 (2) mm shallowly faveolate with a more or less prominent adaxial rib.

Distributed along the coast in northern and central Patagonia from Rio Negro south to central Santa Cruz province in Argentina, and rarely at a few isolated localities in the interior of southern La Pampa, Neuquén, Rio Negro and Chubut (Fig. 3) at 0—360 m elevation. Flowering (Sep) Oct to Nov (through Feb), with fruit Nov to Dec (through Feb).

This species is one of the most distinctive in the genus, and is unusual in its truly shrubby habit, its armed character, and the indehiscent nature of its fruit. *Menodora robusta* is vegetatively very similar in its habit, structure and branching pattern to the North American *M. spinescens*, and these two are also the only species which are armed, feature stomatal crypts on the stems and lack circumscissile dehiscence of the cocci of the capsule.

Along the coast, this species can form extensive co-dominant stands (with *Chuquiraga* (Asteraceae) and various spinescent legumes, especially *Adesmia*) on stabilized sand dunes. The largest individuals were on the lee side of the largest dunes closest to the water and beyond this were uniformly low (circa 30 cm) and spreading for the extent of the dune field. The occurrence of this species is patchy, however, and often is found only in small groups (pers. obs., Correa 1999).

Inland populations are found at relatively isolated localities in Neuquén, Río Negro, and Chubut (*Correa et al. 4839* (CTES, P); *Leal 5601* (MERL); *Cabrera 18645* (CTES); *Fabris 821* (LP); and probably *Fischer 28* (GH, MO, NY, SI, US)). Correa (1999) documented other inland localities in this region, including a collection from departmento Puelén, La Pampa, close to the Río Negro and Neuquén localities. In these localities, it occurs on dry, rocky ground (Correa, 1999).

Correa (1999) also noted that these shrubs are often heavily browsed by goats and sheep, and in obviously browsed populations I have seen, plants are quite reduced and sculpted into rather improbable topiary. No young plants are seen in these localities.

SPECIMENS EXAMINED:

ARGENTINA: without exact locality: Travesia de Rawson a la Cordillera, 1/30/1903, Nicolas Illin 74 (SI, UC). **CHUBUT: Dpto. Biedma:** Peninsula Valdez. Punta Norte; 1/4 km from shore, 11/22/1972, Jane Frick s.n. (GH); Punta Norte, en proximadades de Ea. La Ernestina (Península Valdés), 10/30/1969, Juan Daciuk 798 (LP); Istmo C. Ameghino, camino a Isla de Pájares, 11/11/1988, M. N. Correa et al. 9650 (CTES); Peninsula Valdez: Isthmus Ameghino. On road to Isla de los Pajaros, ca 2 km off paved road at entrance station to the Peninsula, ca 2.5 km from the shore, 12/26/2002, Timothy W. Chumley 7422a (TEX); Peninsula Valdez: Isthmus Ameghino. On road to Isla Golfo San Jose, ca 10 km from entrance station to the peninsula, ca 1 km from shore, 12/26/2002, Timothy W. Chumley 7422b (TEX); **Dpto. Escalante:** Astra, Pico de Salamanca, Comodoro Rivadavia, 11/19/1945, C. A. O'Donell 3459 (K, LIL); Patagonia. Port St. Elena, Capt. King s.n. (K). **Dpto Florentino Ameghino:** Punta Tombo, alrededores de la pinguinera, 11/20/1970, Juan Daciuk 800 (LP); Presso la Estancia La Perla a NE de Punta Tombo, 1/3/1974, R. E. G. Pichi Sermolli & P. Bizzarri 7342 (SI). **Dpto. Paso de Indios:**

Paso de Indios, 11/8/1972, M. N. Correa et al. 4839 (CTES, P). **Dpto. Rawson:** Trelew, 10/28/1945, C. A. O'Donell 3281 (LIL); Río Chubut, 1/1/1900, Carlos Burmeister 121 (LIL); Ruta [Nacional] 3 - 10 km al N de Trelew, 11/23/1976, J. A. Ambrosetti s.n. (MERL); Playa Santa Isabel, 12/18/1994, Renée H. Fortunado et al. 4799 (G, NY); Entre Puerto Madryn y Punta Ninfas, Soriam 2770 (SI). On road to Playa Santa Isabel, ca 2.5 km N of Playa, ca 13.5 rd km S of Rawson. Common from Playa Bonita S to Playa Santa Isabel, 12/24/2002, Timothy W. Chumley 7422 (TEX). **NEUQUEN: Anelo:** Sierra Auca Mahuida, 11/1/1953, Humberto A. Fabris 821 (LP). **RIO NEGRO:** [Locality on labels given as either “Rio Negro, F.C.S.” or “Vicinity of General Roca, Rio Negro,” but Hicken in Physis 2:10: 112 cites locality only as Chubut], 10/20/1914, Walter Fischer 28 (GH, MO, NY, SI, US). **El Cuy:** Camino de a Neuquén a Cerro Policía, 11/13/1967, A. L. Cabrera 18645 (CTES). **San Antonio:** Bajo de la Bombilla, 11/20/1928, A. Castellanos s.n. (LIL). **Valcheta:** 40 km al N de Valcheta, 12/18/1967, A. Ruiz Leal 5601 (MERL). **SANTA CRUZ: Dpto. Deseado:** Lobería, 10/19/1929, A. Donat 182 (K, MO, SI, UC); Deseado, 1/1/1899, Carlos Ameghino 20 (BA); Golfo San Jorge, 11/1/1899, Carlos Ameghino s.n. (LP); Pico Truncado, 2/7/1966, Estela D. M. Kreibohm 267 (SI, US).

2. *Menodora spinescens* A. Gray

Proc. Amer. Acad. Arts 7:388; Holotype: USA: NEVADA: C. L. Anderson s.n. (GH).
Common name: spiny menodora, spiny desert olive

Plants low, densely mound-forming and armed ***frutescent perennials***, 20-50 (60) cm tall, spreading 30-100 (200) cm, with no roots seen, but the major above ground axis observed to be sometimes 5—6 cm in diameter, and with some adventitious rooting rarely on larger woody lateral branches; often appearing aphyllous except when flowering, and then leaves often absent from the main axis and present only on short, flowering shoots; hermaphroditic or gynodioecious (or perhaps polygamodioecious). ***Stems*** spreading, branching densely intricate thoughout, more or less divaricate, alternate, branches and branchlets terminating in sharp thorns, often appearing forked at ends of branches; older wood tan or gray, often with black spots or pits, glabrous, rimose, often becoming fibrous or somewhat exfoliating; younger stems green, shallowly and irregularly fluted, often appearing pitted with small, white, densely pubescent cavities in the sulcae between costae, terete in cross section, densely puberulent, often hispidulous in leaf axils, trichomes short, white, appressed, 0.03—0.08 (0.09) mm; internodes at midbranch (1) 4—11 (18) mm. ***Leaves*** alternate or appearing fascicled (the latter on short flowering shoots, thus more properly considered as bracts), rarely nearly opposite, sessile, thick, almost succulent, linear-oblanceolate to oblanceolate, very rarely trifid, (2) 4-10 (16) by (0.7) 1—1.8 (2.5) mm, length to width ratio (2) 3.5—6.1 (7.8), densely puberulent, apices acute or apiculate, commonly obtuse, margins entire, base attenuate, nerves obscure or absent. ***Inflorescence*** a dense, compact many-flowered compound or paniculate thyrse, with flowers terminating short, usually branching axillary shoots. ***Flowers*** perfect but with androecium appearing rudimentary in some individuals of one variety, on short pedicels. ***Pedicels*** 0—3.4 (8) mm long, 0.4—0.6 (0.8) mm in diameter, glabrous to densely puberulent, holding fruit erect, subtended by often reduced and linear or otherwise leaf-like bracts. ***Calyx*** tube turbinate, puberulent, rarely glabrous, (0.7) 1—1.9

(2.5) by (0.7) 1.1—2 (2.5) mm, broadening in fruit to 2.5—4 (4.2) mm; lobes (4) 5—6 (8), (1.8) 2—4 (5) by 0.3—0.6 (0.8) mm, thick, not nerved, linear or subulate, apices obtuse to acute, margins entire. ***Corolla*** explanate, ampliate, or salverform, white, often tinged red or purple on outside, tube (2.5) 3.5—8.9 (11) mm, (0.7) 0.8—1.4 (2) mm at base, opening to (1.2) 1.8—4.3 (5.3) mm at throat, sparsely pilose below attachment of filaments, rarely glabrous within; limbs 4—5 (6), obovate, apices obtuse, (1) 1.7—4 (2.8) by (0.9) 1.4—3.4 (4.8) mm, glabrous, rarely hirtellous. ***Stamens*** included or mostly so, filantherous or nearly afilantherous in one variety; filaments reduced, often much less than 1 mm, anthers often appearing sessile, or filaments (0.4) 0.6—1.7 (2) mm, adnate ca 1-2 mm or ca 5 mm below throat, 0—1.4 (2) mm long, glabrous; anthers fertile or rudimentary, included at throat (or 1-2 mm below) or half-exserted, (0.6) 1—3.4 (4.3) by (0.2) 0.3—0.8 (0.9) mm, rarely with a conical or cylindrical extension of the connective, dorsifixed, latrorse. ***Pollen*** bright yellow, 30—50 (60) µm. ***Ovary*** bicarpellate, each carpel with a single locule and 2 ovules. ***Style*** (3.3) 3.7—9.2 (12) mm, glabrous. ***Stigma*** either simply terminate or bifid, or capitate, bilobed or trilobed. ***Fruit*** with cocci obovoid or rarely ovoid, irregularly dehiscent, not persistent, often with a vertical suture above, glabrate to scabrid, (5) 6.3—7.9 (9) by (4.3) 5.3—7.1 (8.2) mm in diameter; pericarp thin, membranaceous, more or less translucent; each coccus containing 2 seeds, fewer by abortion. ***Seeds*** elliptic to obovate, plano-convex to lenticular, (5) 5.7—7.2 (8) by (4) 4.5—6 (7) by (2.1) 2.6—3.7 (4.6) mm, very finely and regularly cancellate, somewhat lustrous, appearing smooth.

Distributed on desert hillsides in the Mojave Desert of California and Nevada (peripherally in Arizona and Utah) and in central Baja California (Fig. 7) at (390) 690—1985 (2307) m elevation. Flowering Mar to May (Jul), with fruit Apr to Jun (Aug).

This species has two varieties, and probably a third (pending examination of authentic flowering material, but I have included it here) based upon distinct flowering characteristics. The varieties are indistinguishable vegetatively or in fruit, but can be distinguished by the following floral characters:

1. Calyx tube usually less than 1.5 mm in length; corolla explanate, tube less than 5 mm long ....2a. ***M. spinescens*** **var.** ***spinescens***
1. Calyx tube usually 1.5 mm or more in length; corolla ampliate or salverform, tube 7 mm or more long
    2. Corolla ampliate, tube diameter at throat 3.5 mm or more ....2b. ***M. spinescens*** **var.** ***mohavensis***
    2. Corolla salverform, tube diameter at throat 2.5 mm or less ....2c. ***M. spinescens*** **var.** ***bahensis***

2a. *Menodora spinescens* A. Gray var. *spinescens*

Illustrations: Intermountain Fl., 4: 345

Plants gynodioecious or possibly polygamodioecious. ***Flowers*** are perfect, but anthers are rudimentary in functionally female plants, stigmas appear to be relatively rudimentary in the male or hermaphroditic plants, but ovary seems well developed; the relative abundance of fruit set has not been established**.** ***Inflorescence*** a dense, compact many-flowered compound thyrse or thyrsoid panicle, with flowers terminating short, usually branching axillary shoots; female plants with fewer, smaller flowers, males (or hermaphroditic) with more, larger flowers. ***Pedicels*** 0—2.1 (6) mm long, 0.4—0.6 (0.8) mm in diameter, glabrous to densely puberulent, holding fruit erect, subtended by often reduced and linear or otherwise leaf-like bracts. ***Calyx*** tube turbinate, puberulent, rarely glabrous, (0.7) 0.9—1.4 (1.6) by (0.7) 1—1.6 (1.8) mm, broadening in fruit; lobes (4) 5 (6), (1.8) 1.9—3.9 (5) by 0.3—0.6 (0.8) mm, thick, not nerved, linear or subulate, apices obtuse to acute, margins entire; calices of female plants tend to be larger, but within the range of variation found in those of the male/hermaphroditic plants. ***Corolla*** explanate, white, often tinged red or purple on outside. ***Male/hermaphroditic flowers:*** *corollas* larger, tube (4.0) 4.3—5.1 (5.2) mm, (1.6) 1.8—2.8 (3.1) mm at throat, 0.7—1.1 (1.2 mm) at base, sparsely pilose within, lobes (1.9) 2.0—2.9 (3.0) by (1.3) 1.6—2.6 (2.9), glabrous or rarely sparsely hispidulous externally; *stamens* half-exserted, sessile or with very short filaments to ca 1 mm, glabrous; *anthers* yellow, exserted half-way beyond the throat, (1.4) 1.9—2.1 (2.3) by (0.4) 0.5—0.7 (0.9) mm, usually cohesive and capping the style and stigma; *pollen* yellow, 30-60 microns; *style* (3.3) 3.7—5.9 (6.0) mm, very rarely exceeding the anthers 0.5—1.5 mm; *stigma* bifid or merely terminate. ***Female flowers:*** *corollas* smaller, tube (2.5) 2.6—3.7 (3.8) mm, (1.2) 1.3—2.2 (2.3) mm at throat, 0.8—1.2 (1.3) mm at base, glabrous or sparsely pilose within, lobes (1.0) 1.2—2.2 by (0.9) 1.1—1.8, glabrous or rarely sparsely scabrid externally; *stamens* included; *anthers* sessile, green, (0.5) 0.7—0.9 (1.0) mm by 0.1—0.3 mm, without pollen; *style* 3.5—4.6 mm, exceeding throat of corolla 0.5—2 mm; *stigma* capitate, often bilobed, always exserted to 2 mm.

Distributed on desert hillsides in the central and northern Mojave Desert of eastern California and Nevada and adjacent regions of the Great Basin to the north in Nevada, rarely in adjacent southwestern Utah and northwestern Arizona (Fig. 7) at (390) 708—1985 (2307) m elevation. Flowering (mid-Mar) Apr to mid-May (through early Jul), with fruit (Apr) May to Jun (through Aug).

This variety of *Menodora spinescens* is the most widespread, and is quite common and often dominant. It appears to be gynodioecious, which has not been previously reported, and individual plants appear to be either functionally female (inflorescence with fewer flowers, these with slightly smaller corollas, small green and apparently rudimentary anthers without pollen, and an exserted style and capitate stigma) or hermaphroditic (inflorescence with more flowers, corolla larger, with a pair of well-developed, pollen bearing anthers, style and terminate or bifid stigma rarely visible without dissection).

I first made this observation while surveying a flowering population near Tonopah, Nevada in 2001 (*Chumley 7347* (TEX)). I first noticed there were a number of plants with markedly fewer flowers in their inflorescence, and on closer examination found that they lacked the large, half-exserted, yellow and obviously pollen bearing anthers of the more floriferous plants. Choosing an arbitrary transect line, I counted the first 100 plants within roughly a meter of either side of the line, and found that the two phenotypes were present in about a 50/50 ratio. Similar results were found at two other localities (represented by *Chumley 7348, 7349a,* and *7349b*). Fruiting populations in Death Valley (at the base of Dante's View; unvouchered) and other localities in Inyo County, California (*Chumley 7351* and *7352*) showed a similar division between individuals with heavy fruitset and those much more moderately with fruit. No individuals were observed lacking fruit, thus suggesting that the hermaphrodites are not female sterile, or at least not completely so. I surveyed two additional populations in 2003 (vouchered by *Chumley 7435* and *7436* (TEX); unfortunately, these were the only flowering populations found that year). In this case, five randomly selected, 10 m radius circular plots per site were surveyed, and for each plot five plants were counted as male or female, the number of flowers along an arbitrary branch was recorded, and the presentation (diameter across the face) of three randomly-selected flowers was measured per plant. Results (data not shown) for both sites were consistent, with the female to hermaphrodite ratio being slightly skewed towards the hermaphrodites (4.4: 5.6). Females consistently had slightly smaller floral presentations (4.7 mm average (range 3—6 mm) vs. 7.2 mm (range 5—9 mm)) and generally fewer flowers per inflorescence branch, though with considerable overlap (19 ± 10 vs. 32 ± 16).

One of the unanswered questions about this variety is whether it is truly gynodioecious or possibly polygamodioecious. In fruiting populations, it is not clear whether the plants in heavy fruitset represent the females or the hermaphrodites. The hermaphroditic plants could be functionally male and only occasionally set fruit. In these plants, the style and stigma is often trapped between the large cohesive anthers, and on a given specimen, the styles may only rarely escape them (on a given specimen at the time of harvesting or observation, this has usually been observed only one to three times). Over the flowering period, this could add up to a moderate fruitset. If the anther cap does not effectively prevent pollination, though, then fruitset might be expected to be heavier in the generally more floriferous hermaphrodites. Potentially, the hermaphrodites may also be predominantly self-pollinating, thus insuring a heavy fruitset as well. More study will be required to solve these issues.

This condition has likely escaped notice before this primarily due to the fact that 85% of the herbarium specimens reviewed in flower are predominantly of the often much showier hermaphrodites.

SPECIMENS EXAMINED:

U. S. A.: ARIZONA: Mohave County: Detrital Valley, 21 mi SE of Boulder Dam, Black Mountains, 3/29/1940, Lyman Benson 10153 (UC); **CALIFORNIA: Inyo County:** About 3 mi W of Laws, 5/8/1906, A. A. Heller 8202 (GH, MO, NY, US); Dante's View, Black Mts., 3/27/1940, Alice Eastwood & John Thomas Howell 7759 (UC); Saline Valley Road 5/1/1942, Annie M. Alexander & Louise Kellogg 2751 (A, NY, UC); In Titus Canyon, at N end of Death Valley 4/4/1939, Aven Nelson & Ruth Nelson 3396 (UC); Below Dante's View, Death Valley 4/6/1935, Bonnie C. Templeton & I. W. Clokey 5763 (NY); Funeral Mountains, Death Valley National Monument, 1/1/1985, C. Annable s.n. (UC); Near Dante's View 4/17/1932, C. L. Hitchcock 12335 (A, MO); 7 mi W of Death Valley Junction, on road to Fenmore [Furnace] Creek 3/21/1962, C. L. Hitchcock & C. V. Muhlick 22265 (MO); Ca 5 mi S of Lee's Camp 4/16/1983, C. R. Annable 481 (NY); head of Furnace Cr Wash (E Branch), c. 13 mi E of Travertine Springs, Death Valley drainage, 3/22/1954, C. W. Sharsmith 6128 (SJS); near head of E branch Furnace Cr Wash, Death Valley drainage. 3500 ft, 4/12/1968, C. W. Sharsmith 7554 (SJS); Death Valley region, W side of Funeral Range, Boundary Canyon, Daylight Spring 5/1/1935, Carl B. Wolf 6676 (GH, NY); Owen's Valley: N of Warm Springs Rd, 7/16/1995, Carol R. Annable et al. 2568 (NY); Black Mountains, Death Valley National Monument, 1/1/1982, D. R. Schramm (UC); Chloride Cliff, Funeral Mts., 5/8/1920, Edmund C. Jaeger 66 (US); Death Valley: Near Greenwater, upper

Furnace Creek valley 4/18/1931, Frederick V. Coville & M. French Gilman 87 (US); Argus Mts. w slope 5/19/1906, H. M. Hall H. P. Chandler 7096 (UC); below Dante's View, Death Valley National Monument 4/6/1935, I. W. Clokey B. C. Templeton 5763 (NY, UC); On the Bishop side of Sherwin grade along Hwy 395 6/6/1962, Jack L. Reveal 98 (NY); 0.5 mi W of Willow Spring, Last Chance Mountains 5/15/1955, John C. Roos 6369 (GH); Lee Flat, 15 mi N of Darwin, 9/28/1917, Joseph Grinnell s.n. (UC); Boundary Cañon 5/3/1937, Lester Rowntree s.n. (A); On road to Saline Valley 4/1/1978, Margaret J. Williams 78-3-3 (NY); Inyo Mountains, Waucoba Road, 16 km (10 mi) from CA Hwy 168 (Westgard Road), 17 km (10.5 mi) airline distance ESE of Big Pine 5/16/1978, Noel Holmgren & Patricia K. Holmgren 8690 (NY); Darwin 5/6/1932, P. A. Munz 12479 (MO, UC); Road to Greenwater, E side of Funeral Range, Death Valley region 4/24/1937, Percy Train s.n. (US); Westgard Pass, 3.8 mi w of White Mountain Road, White Mountains 6/20/1963, Robert M. Lloyd 2743 (NY, UC); About 1 mi E of summit between Monument and Death Valley Jct, CA Hwy 190 3/14/1961, Roxana S. Ferris 13520 (TEX); W side of Westgard Pass 4/18/1932, Roxana S. Ferris & Rimo Bacigalupi 8060 (UC); 7 mi E of Dante's View, Black Mts. Death Valley region 4/5/1928, T. Craig 907 (MO); Along California Hwy 168 ca 4 air mi NW of Deep Spring 5/10/2001, Timothy W. Chumley 7351 (TEX); On Death Valley Road, ca 2 rd mi S of intersection with California Hwy 168, ca 5 air mi E of Big Pine 5/11/2001, Timothy W. Chumley 7352 (TEX); Mouth of Black Canyon, White Mountains 7/2/1927, Victor Duran 1931 (UC); Hwy 190, 2 mi NW of Darwin turnoff 5/7/1979, W. Burkhardt & S. Dean s.n. (NY); Road to Dantes View, Death Valley 3/28/1939, W. C. Muenscher & M. W. Muenscher 14842 (A). **Mono County:** About 1 mi up Coldwater Canyon in side drainage, 1.5 mi N 18E of Belle Mine. Owens Valley Drainage 4/17/1986, James D. Morefield & Douglas H. McCarty 3439 (GH, MO, NY, TEX, UC). **San Bernardino**

County: Mountain Pass 5/7/1941, Alice Eastwood & John Thomas Howell 8917 (GH); [NE part of county], Clark Mt Range, 5.3 mi NNE of Mt Pass, 1/4 mi E of Ivanpah Springs 4/23/1974, Barry Prigge 1360 (TEX); Clark Mountain Range, 7 air mi NWW of Mountain Pass, in Cactus Canyon 4/21/1973, Barry Prigge & John Prigge 641 (NY); NE part of county, Clark Mt. Range, 6 mi NNW of Mt Pass in Fir Canyon. 4/29/1973, Barry Prigge 798 (TEX); Kingston Mts. 10 mi NW of Kingston 4/20/1940, C. L. Hitchcock 6155 (NY, UC); Mojave Desert, S sides of Old Dad-Granite Mountain Range. E fork (near summit) of Willow Spring Canyon 4/29/1941, Carl B. Wolf 10145 (NY); Mojave Desert, W slope of Providence Mts., 2 mi W of Columbia Mine, 5/26/1941, Carl B. Wolf 10736 (UC); Eastern Mojave Desert, E base of Ivanpah Mt., 1 mi S of Lakeview service station, 5/3/1932, Carl B. Wolf 3302 (UC, US); Mojave Desert, Clark Mt. Coliseum [Colosseum] Mine (1 mi W of), 5/26/1940, Carl B. Wolf 9616 (NY); Mojave Desert, W side of Ivanpah Mts. about 7 mi N of Kessler Spring on rd to Mexican Well, 5/29/1940, Carl B. Wolf 9686 (TEX, UC); Wheaton Springs, 5/3/1937, Howard S. Reed & F. M. Reed 832 (P); 2.5 air mi SE of Cima , 1 mi NW of Burro Spring, 6/3/1973, James Henrickson 10426 (TEX); 9.5 mi NE of Kelso, 2.8 rd mi W of Wild Horse Canyon Rd along Macedonia Canyon in Mid-Hills, 7/7/1973, James Henrickson 11162 (LL); 21 air mi ESE of Cima along trail 8 mi N of Hart Mine Road, NW of Castle Buttes. 4800 ft, 4/29/1973, James Henrickson 9481 (NY, TEX); Barnwell, 5/1/1911, Katharine Brandegee s.n. (UC); 1 mi S of Excelsior Talc Mines, Kingston Mountains, Mojave Desert, 5/13/1941, L. R. Abrams 14101 (GH); Cima, eastern Mohave Desert, 5/5/1935, P. A. Munz 13747 (UC); On E side of Ivanpah Mts., 12 mi W of Nipton, 4/7/1947, Philip A. Munz 11686 (NY); 16 mi E of Baker on road to Las Vegas, 5/30/1952, Philip A. Munz 17408 (NY); Horse [Thief?] Spring below; along road and E of road summit over the mountains, ne slopes of Kingston Mountains, 4/18/1952, Rimo Bacigalupi et al. 3646

(JEP); E. Mojave Desert, Kingston Mts.: ca 1/2 mi E of Horsethief Springs, 6/1/1972, Robert F. Thorne 43822 (NY); Government Holes-Cima road, 6 mi from Cima, 4/25/1928, Roxana S. Ferris 7325 (NY); Leastalk, 6/3/1915, S. B. Parish 10361 (UC); Mojave Desert between Baker and Mexican Wells, 4/30/1932, Susan Delano McKelvey 2733 (A); On Kelbaker Road ca 36 air mi SE of Baker, 8/26/2000, Timothy W. Chumley and Micheal J. Moore 7317 (TEX); Yucca Grove [on US Hwy 91] road station, [6 mi] E of Halloran Spring [ca 12-1/2 mi NE of Baker], 6/2/1931, W. L. Jepson 15805 (JEPS); Willow Springs Canyon, Old Dad Mts., Mohave Desert, 4/29/1941, W. L. Jepson 20430 (JEP); New York Mts., 5/10/1913, W. L. Jepson 5467 (JEP). **NEVADA: Clark County:** Eldorado Mts., N end of Ireteba Peaks, 5/26/1999, Ann Pinzl 13252 (); Near Charleston Mts., 4/5/1939, Aven Nelson & Ruth Nelson 3437 (UC); Clark Canyon, Clark Mts., 5/7/1936, I. W. Clokey & E. G. Anderson 7233 (NY, UC); Wilson's Ranch, 4/30/1938, I. W. Clokey 8058 (A, NY, UC); Charleston Mts. Old Kyle Canyon Fan, 4/26/1938, I. W. Clokey 8059 (A, GH, MO, NY, UC, US); Goodsprings, 4/19/1919, Ivar Tidestrom 8907 (US); Jean, 5/15/1915, Katharine Brandegee s.n. (UC); Las Vegas, 5/8/1905, Leslie N. Goodding 2340 (MO); E side of Sheep Range, 8 km (5.1 mi) from US Hwy 93 on Mormon Wells Road, 41 km (25.5 mi) airline distance W of Glendale, 5/27/1979, Noel Holmgren et al. 9197 (NY); 5 mi E of Crescent, 4/21/1938, Percy Train 1456 (NY); Eldorado Canyon, Opal Mts., NE of Searchlight, 4/26/1938, Percy Train 1496 (A, UC); 10 mi NW of Valley of Fire, 4/4/1937, Philip A. Munz 14904 (GH, MO); Bajada at southwest base of Spring Mts., along NV Rd 16, 3.9 mi W of Mountain Springs Summit, 8/11/1968, Rimo Bacigalupi & L. R. Heckard 9166 (JEPS); Rte 68 ca 16 mi W of Searchlight, jct rtes 68 & 95, 4/27/1974, T. Reeves & D. J. Pinkava 12026 (NY, US); On Clark County Road 604, ca 16.5 air mi NW of Las Vegas, ca 1.5 air mi SE of Apex, 8/25/2000, Timothy W. Chumley & Micheal J. Moore 7315 (TEX); Off Blue Diamond

Road or Nevada Hwy 159 ca 1 rd mi W of entrance to Blue Diamond Mine, ca 2 air mi NW of Blue Diamond, ca 17 air mi SW of Las Vegas, 8/26/2000, Timothy W. Chumley & Micheal J. Moore 7316 (TEX); Blue Diamond Junction, at intersection of NV 159 and NV 160, ca 20 rd mi W of Las Vegas, 5/8/2001, Timothy W. Chumley 7344 (TEX). **Esmeralda County:** Silver Peak Range, Coyote Spring, 7/17/1990, Ann Pinzl & J. Schwuyhart 9194 (NY); Rte 266, wash/draw N of road, (believe ca 2-1/2 mi NW of Palmetto site), 4/20/1992, Ann Pinzl 9914 (NY); Along the road from Silver Peak to Lida, 4/29/1977, Arnold Tiehm & Lyn Wise 3049 (NY); Gold Mt., 6.1 rd mi SE of Hwy 93 on dirt rd, which is 4 rd mi S of jct of hwys 3 & 93;, 5/4/1985, Arnold Tiehm 9372 (TEX); 7 mi S of Goldfield, 5/25/1945, Bassett Maguire 25165 (GH, MO, NY, UC, US); Silver Peak Range, 7 mi W of Pigeon Springs, on W side of range, 6/2/1945, Bassett Maguire & Arthur H. Holmgren 25266 (GH, NY, UC, US); Palmetto Range, C. A. Purpus 5903 (NY, UC); 5 mi W of Tonopah, 7/5/1981, D. Atwood 7989 (NY); Silver Peak Mts., 9/29/1915, E. A. Goldman 2547 (US); Montezuma Mountains, near Goldfield, 6/4/1919, Ivar Tidestrom 9775 (P, US); Sand Spring Canyon 2 mi N, 3 deg w of Pinyon Hill summit. Fishlake Valley drainage, 5/13/1987, James D. Morefield et al. 4399 (MO, NY, TEX, UC); 5 mi E of Basalt, on Mt. Montgomery-Tonopah hwy. Mineral-Esmeralda county line, 6/8/1940, Percy Train 3972 (NY); Ca 3 rd mi S of Tonopah, off US Hwy 95 along old highway, 5/9/2001, Timothy W. Chumley 7347 (TEX); On road to Gilbert, at intersection with road to Crow Springs, ca 22 air mi NW of Tonopah, 5/9/2001, Timothy W. Chumley 7348 (TEX); Emigrant Pass, ca 9 air mi SW of Blair Junction, ca 37 air mi WSW of Tonopah, 5/10/2001, Timothy W. Chumley 7349a & 7349b (TEX); White Wolf Canyon, ca 7 air mi E of Dyer airport, ca 12 air mi ESE of Dyer, 5/10/2001, Timothy W. Chumley 7350a (TEX); In the Goldfield Hills, along road to Railroad Pass ca 1 rd mi W of jct with US Hwy 95, ca 6.3 air mi S of Goldfield, 5/4/2003, Timothy W. Chumley

7436 (TEX); Old Davis Ranch, Chiatovitch Creek, White Mt USGS quad, 7/11/1929, Victor Duran 2527 (UC); W. H. Shockley 105 (JEPS); Candelaria, W. H. Shockley 17 (UC); Candelaria, 5/15/1881, W. H. Shockley s.n. (GH). **Lincoln County:** 14 mi N of Glendale, 4/6/1934, Bassett Maguire et al. 4905 (GH); 20 mi N of Glendale, 4/6/1934, Bassett Maguire et al. 4907 (GH, MO); Mormon Mts., 7/15/1906, P. B. Kennedy & L. N. Goodding 134 (NY, UC, US); Between Crystal Springs and Ash Springs, 5/7/1986, R. C. Barneby 18109 (NY); Bajada W of 4405 hill; East Pahranagat Range; 3.2 mi N on rd to Pahranagat Refuge from Old Corn Creek Road junction, 5/12/1983, T. L. Ackerman 83-445 (NY); Kane Springs Valley Road, ca 7 air mi NE of intersection with US Hwy 93, ca 20 air mi W of Elgin, ca 28 air mi NNW of Moapa, 5/12/2001, Timothy W. Chumley 7354 (TEX); Along US Hwy 93, across road from Pahranagat National Wildlife Refuge, ca 4 air mi S of Alamo, 5/12/2001, Timothy W. Chumley 7355 (TEX). **Mineral County:** Huntoon Mountains, 3.4 rd mi E of state line on the road from Mono Valley to Huntoon Spring, 6/16/1998, Arnold Tiehm & Jan Nachlinger 12414 (NY); 3 rd mi NW of Rawhide on road to Hwy 50, 6/17/1980, Arnold Tiehm & Pat Lott 5961 (NY); Hawthorne, 6/23/1882, Asa Gray 9 (P); On Thorne-Frenchman road between Ryan Canyon & Nugent Wash in the Gillis Range, ca 7.5 mi SW of jct w/Luning-Frenchman Rd., 6/15/1979, B. Ertter & J. Strachan 2792 (NY); Historic site of Belleville, 5/24/1979, Kenneth R. Genz 9130 (NY); Candelaria, 6/22/1982, Marcus E. Jones s.n. (NY); Sodaville, S. B. Parish s.n. (UC); 3 mi S of Hawthorne, near mouth of Corey Creek, 8/29/1938, W. Andrew Archer 6808 (A, NY, UC). **Nye County:** 6.5 mi NW of Springdale, 5/9/1963, Arthur Cronquist 9845 (GH, NY); 20 mi N of Beatty, 3/26/1964, C. L. Hitchcock & C. V. Muhlick 23319 (MO); Base of Mount Montgomery near Queen Station, 6/20/1919, Ivar Tidestrom 10034 (P, US); Amargosa Desert, State Hwy 58, ca 4 mi E of Daylight Pass, 3/31/1958, J. C. Tothill s.n. (UC); US Atomic Energy

Commission Nevada Test Site, Thirsty Canyon drainage, along rd 20-02, NW Pahute Mesa, Nellis Air Force Range, ca 0.5 mi N of Ribbon Cliffs, 7/28/1968, J. L. Reveal & J. C. Beatley 1669 (NY); Paradise Range, Sheep Canyon, 6/8/1979, Ken Genz 9169 (NY); E side of the Paradise Range, near Toiyabe National Forest Boundary, 7/6/1980, Margaret J. Williams 80-188-1 (NY); NW side of Big Smokey Valley, 24 mi due W of Tonopah, 5/31/1980, S. White & E. Neese 173 (NY); On Ashford Meadows Road, ca 13 air mi NW of Pahrump, ca 12 air mi E of Death Valley Junction, California, 5/11/2001, Timothy W. Chumley 7353 (TEX); Off US Hwy 95 ca 38 rd mi S of Goldfield, just before Nye Co. mile marker 88, 5/3/2003, Timothy W. Chumley 7435 (TEX); Tonopah, 5/15/1907, W. H. Shockley 106 (UC); Amargosa Desert, 5/3/1940, W. L. Jepson 19822 (JEPS). **Washoe County:** 14 mi N of Glendale, 4/6/1934, Bassett Maguire et al. 4905 (UC). **UTAH: Washington County:** 5.5 airline mi S Lytle Ranch, Beaver Dam Wash. W 1.2 mi up jeep trail to Initial Mesa, 4/17/1986, D. Atwood & K. Thorne 12015 (NY); Ca 2 mi S of Beaver Dam well, along W side of Beaver Dam Wash and side draw, 4/12/1997, D. Atwood et al. 21712 (NY); Near 3 Corners Monument, south end of Initial Mesa, 4/20/1985, J. Chandler et al. 245 (RM); Beaver Dam Wash, ca 2 mi SW of Beaver Dam Well, 3/28/1984, K. Thorne et al. 3165 (NY); NE Initial Mesa, 4/20/1985, K. Thorne et al. 3700 (NY); 2 mi S of Beaver Dam Well, 3/29/1984, R. Kass & E. Neese 1578 (NY).

2b. *Menodora spinescens* A. Gray var. *mohavensis* Steyerm.

Ann. Missouri Bot. Gard. 19:155, 1932. Holotype: USA: CALIFORNIA: San Bernardino Co.: 14 mi N of Barstow, 4/23/1915, *S. B. Parish 9795* (UC!).

Plants hermaphroditic or rarely with flowers appearing functionally as the species. ***Inflorescence*** a dense, compact few-flowered compound or paniculate thyrse, with flowers terminating short, usually branching axillary shoots; with generally fewer, much larger flowers than the species. ***Pedicels*** (0) 0.3—4.9 (8) mm long, 0.5—0.6 (0.7) mm in diameter, glabrous to densely puberulent, holding fruit erect, subtended by a linear or linear-oblanceolate bract. ***Calyx*** tube turbinate, glabrous to puberulent occasionally densely so, 1.5—2.1 (2.4) by (1.4) 1.6—2.2 (2.5) mm, broadening in fruit to 2.6-4.2 mm; lobes (4) 5-6 (8), 2.3—4.1 (4.9) by0.4—0.6 (0.7) mm, thick, not nerved, linear to subulate, apices obtuse to acute, margins entire. ***Corolla*** ampliate, white, often tinged red on outside, tube (7.5) 7.9-10.2 (11) mm, (0.8) 1—1.7 (2) mm at base, opening to (3.6) 3.7—4.9 (5.3) mm at throat, sparsely hispid to sparsely pilose within; limbs (4) 5 (6), obtuse, 2.9—4.9 (5.8) by (2) 2.4—4.2 (4.8) mm, glabrous. ***Stamens*** filantherous, included; filaments adnate ca 5 mm below throat, (0.4) 0.6—1.7 (2) mm long, glabrous; anthers included 1-2 mm below throat, (1.1) 2—4.3 by (0.3) 0.5—0.9 mm, rarely appearing rudimentary or cohesive. ***Pollen*** 30—60 µm. ***Style*** (5.8) 6.9—11.1 (12) mm, glabrous. ***Stigma*** slightly to broadly capitate, bilobed or occasionally trilobed, usually exceeding the anthers 3—4 mm.

Distributed in the southern Mojave Desert in Riverside and San Bernardino counties, California (Fig. 7) at 615—1385 m elevation. Flowering late Mar to early May (early Jun).

This taxon was not recognized in the floras of California (Munz 1959; Wilken 1993) nor by Turner (1991), however, I agree with Steyermark (1932) that it is a distinct varietal worthy of recognition. The specimens I have examined that possess a larger, ampliate corolla uniformly form a geographically distinct group in the southern Mojave, and are slightly isolated from the more common species form found along the Nevada border in California; the species seems absent from the range of this variety. In floral size and presentation, this variety is larger than the species (see Table 2, Fig. 12), with no overlap in size between the two varieties. Not only are the corollas larger, but the filaments are longer. The anthers are usually larger as well and are well developed in all but one of the specimens reviewed (*Jepson 5415* (JEP, GH, US)), and are usually free (though coherent and capping the style in *Thorne 34707* (MO)).

SPECIMENS EXAMINED:

U. S. A.: CALIFORNIA: Riverside County: Twenty-nine Palms Fan, near boundary, Joshua Tree National Monument, 4/10/1941, James E. Cole 517 (UC). **San Bernardino County:** Ca 2 mi S of 29 Palms, Joshua Tree National Monument, 4/1/1983, E. Neese & R. Kass 12765 (NY); Ord Mts. Mohave Desert, 4/30/1906, H. M. Hall & H. P. Chandler 6780 (UC); Barstow, Mohave Desert, 4/23/1921, Mary F. Spencer 1776 (GH); Joshua Tree National Monument: ca 1 mi S of entrance of Twentynine Palms, 6/1/1965, Robert F. Thorne and S. T. Blake 34707 (MO); 14 mi N of Barstow, 4/23/1915, S. B. Parish 9795 (Holotype UC); Calico Wash, Calico Mountains, 5/6/1913, W. L. Jepson 5415 (JEP, GH, US); Calico Mts., Coolgardie Yucca Mesa, Mohave Desert, 3/27/1916, W. L. Jepson 6635 (A, GH, JEP, US).

2c. *Menodora spinescens* A. Gray var. *bahensis* Chumley, *var. nov.* (proposed)

Menodorae spinescens *A. Gray similis sed corolla hypocrateriformis brevis, tubo 8—9 mm, fauce 2—2.5 mm, limbae 3—4 mm longis et 1.5—2.5 mm latis.*

Corolla salverform, white; tube 8—9 mm, 1—2 at base opening to 2—2.5 mm at throat; limbs 3—4 by 1.5—2 mm. ***Stamens*** filantherous, included.

Distributed in southern Baja California Norte on isolated, rocky hilltops (Fig. 7). Flowering in March.

Menodora spinescens has only been collected relatively recently and fairly infrequently in Baja California. The specimens I have reviewed are purely vegetative, and these are indistinguishable from the species. Jon Rebman of the San Diego National History Museum reviewed a few flowering specimens in their collection, and provided the information used in the brief diagnosis above.

SPECIMENS EXAMINED:

MEXICO: BAJA CALIFORNIA NORTE: SE of El Rosario: just N of km marker 99 of MEX Rte 1 between El Rosario and Cataviña, and 5.4 mi E of Rte 1 on road to Rancho Los Martires, 5/18/1994, Jon P. Rebman & Paul Vincent 2726 (TEX); 1.5 mi SE of Sauzalito 8/11/1968, Reid Moran 15386 (LL, UC, US).

3. *Menodora juncea* Harv.

Gen. S. Afr. Pl., 2nd ed., 220, 1868; Lectotype (*fide* Verdoorn, Bothalia 6:3: 603, 1956): SOUTH AFRICA: NAMAKWA: Kamiesberg: Modderfontyn, Namaqualand, *Rev. H. Whitehead s.n.* (K!).

Common name: blombiesie

Illustrations: Fl. S. Africa 26:126, Fig. 14.2 (Verdoorn, 1963).

Plants fastigiate ***frutescent perennials***, (0.3) 0.6—1.6 (1.8) cm tall, with roots unkown. ***Stems*** strict, branching throughout, opposite to subopposite or alternate; older wood tan, gray to black, atratous, glabrous, rugose, rimose; younger stems green, shallowly fluted, terete to slightly angled in cross section but often with a decurrent canaliculate groove, appearing glabrous to the eye, but papillose to densely hispidulous or strigillose under magnification particularly along decurrent groove; trichomes minute, retrorse, white or hyaline, 0.04—0.1 (0.15) mm; internodes at midbranch (2) 14—38 (48) mm, greatly exceeding the subtending leaves; if leaves are alternate, internodes length alternates short and long. ***Leaves*** opposite or subopposite, often alternate bracts in inflorescence, sessile, submembranaceous, linear or subulate, (2) 4—14 (28) by (0.4) 0.6—1.2 (3.5), length to width ratio (4) 5—10 (12), often significantly larger below, glabrous or densely hispidulous, apices acute or obtuse, margins entire, base attenuate, decurrent, uninervate, usually obscurely so. ***Inflorescence*** a simple to compound dichasium of 1—5 (12) flowers usually with alternate branching. ***Pedicels*** (2) 4—13 (23) mm long, 0.5—0.8 (0.9) mm in diameter, moderately to densely strigillose-hispidulose, holding fruit erect, subtended by a linear or linear-lanceolate, glabrous to densely hispidulous leaf-like bract. ***Calyx*** tube turbinate, glabrous to densely hispidulous, (1) 2—3 (5) by 2—3 (4) mm, broadening in fruit; lobes 5 (6), (1.5) 3—5 (7) by 0.5—1 mm, thin, linear to broadly subulate, apices acute or acuminate, margins entire. ***Corolla*** infundibuliform, yellow, tube 4—7 mm, 0.7—1.8 mm at base, opening to (2) 3.5—6.3 (7) mm at throat, pilose within; limbs (4) 5, oblong or obovate, apices mucronate, (6) 10—16 (18) by (3) 5.6—9 (10) mm, glabrous, occasionally hirtellous in bud. ***Stamens*** filantherous; filaments adnate ca 1—2 mm below throat, (3) 3.6—9.4 (10) mm long, glabrous or pilose below; anthers exserted (1.5) 2—5 (7) above throat, (2) 3—5 by (0.5) 0.7—1 mm, often with a short, conical process above the connective, dorsifixed, latrorse. ***Pollen*** 60—70 (80) µm. ***Ovary*** bicarpellate, bilobed, each carpel with a single locule and 4 ovules. ***Style*** (8) 12—18 (20) mm, glabrous. ***Stigma*** capitate, bilobed, just exceeding to 1—5 mm beyond or rarely equalling the anthers. ***Fruit*** with cocci obovoid or globose, circumscissile, glabrous, (5) 6.8—9.4 (11) by (4) 4.6—6.6 (8) mm in diameter; pericarp thin, membranaceous, more or less translucent; each coccus containing 4 seeds, fewer by abortion. ***Seeds*** elliptic or obovate, trigonal or rarely clavate, (4.5) 6.6—8.2 (9.5) by (2.5) 3.6—4.8 (6) by (1) 1.6—2.3 (3), testa golden or light tan, regularly reticulate with a prominent raphal rib.

Distributed discontinuously in the karroid regions of Namakwa in the Northern Cape and in the Great and Lesser Karoo in the Western Cape at (0) 230—990 (1191) m elevation. Flowering late Aug to mid-Nov, with fruit Sep to Nov (early Dec).

Menodora juncea is found on dry, rocky slopes, forming small, localized colonies. It seems to be widely distributed within two disjunct regions of Namakwa and the Karoo, but its occurrence is very patchy. As noted by Verdoorn (1956), it is quite distinct from the subherbaceous subspecies of *M. africana*. At Karoo National in Beaufort West, I observed it to be quite heavily browsed by wildlife, and reduced to quite compact, dense mounds, but without such grazing pressure, it was found on roadsides outside the park as large, upright shrubs. In form and habitat, this species is very reminescent of *M. decemfida* of South America.

SPECIMENS EXAMINED:

SOUTH AFRICA: without locality: W. Scully s.n. (SAM); **EASTERN CAPE: Willowmore:** 6-1/2 mi E by S of Strydomsvlei P.O., 10/19/1956, J. P. H. Acocks 19080

(PRE); **NORTHERN CAPE: NAMAKWA: Kamiesberg:** Modderfontyn, Namaqualand, H. Whitehead s.n. (Holotype, K); Namaqualand: Kamieskroon. 13 mi SSW of Kamieskroon, 9/25/1948, J. P. H. Acocks 14996 (K, PRE); Soebatsfontein Road, Namaqualand, 11/1/1939, F. W. Thorns s.n. (NBG); **Karoo Hoogland:** Jongenshoek, in Tanqua Karoo. W. Mt. K. 2 of steep stony W side of spur of Kodesberg, 11/17/1955, J. P. H. Acocks 18643 (PRE). "Layton" Leeu—Gamka—Fraserburg, 9/22/1967, D. Shearing 132 (K, PRE); Beaufort West distr., farm Layton. Tontelkop, 10/18/1983, D. Shearing 235 (PRE); Fraserburg; Layton, Tontelkop/Rooiwal Road Reserve, 10/7/1992, D. Shearing A160 (NBG, PRE). **Nama Khoi:** Helskloof, Richtersveld, 10/15/1988, G. Williamson 3974 (NBG); Hellskloof, Namaqualand, 9/19/1953, H. Hall 782 (NBG); Goldmine, Helskloof, Richtersveld, Namaqualand, 9/23/1933, H. Herre 18995 (NBG); Richtersveld: Helskloof South, 8/23/1987, N. Jürgens 22466 (PRE); Richtersveld: Helskloof, 8/29/1987, N. Jürgens 22525 (PRE); 20 km W of Springbok at foot of Spektakelburg Pass, 10/14/1974, P. Goldblatt 3045 (MO, NBG, PRE); **Richtersveld:** Namaqualand on farm "Taiboskraal" at Springbok-Wildepaardehoek Pass, 10/3/1980, A. le Roux 2839 (NBG, PRE); O'biep. Richtersveld, 9/6/1959, D. S. Hardy 208 (PRE); 2 mi S of Mesklip, Springbok & Khamieskroon Road, 11/7/1962, D. S. Hardy 1123 (K, PRE); Richtersveld. Ridge leading to summit of Numees Peak, 9/22/1981, D. McDonald 727 (NBG, PRE); Fand ich bishes nur in Karachub [Karagap] Flues Richtersveld, 9/15/1925, G. Meyer 9092 (NBG); 3 mi NE from Stinkfontein, 12/6/1910, H. H. W. Pearson 5639 (K); Klipbokbergrivier, Richtersveld, Namaqualand, 9/11/1929, H. Herre 12080 (NBG); Arragab, Richtersveld, Namaqualand, 9/14/1929, H. Herre 12195 (NBG); Kalkfonteinberg, Namaqualand, 9/14/1929, H. Herre 12200 (NBG); Sabiesies. Last plateau before the summit of the Ploegberg complex, 9/20/1989, M. Viviers 2087 (NBG); Numees, Namaqualand, 10/15/1926, N. S. Pillans 5108 (K); Karuchabpoort. Lekkersing, 8/26/1979, Oliver 138 (MO, NBG, PRE, US); Namaqualand: Lekkersing, 8/24/1925, R. Marloth 12282 (NBG); Little Namaqualand: Kloof at Kubus, 8/29/1925, R. Marloth 12282b (A, NBG, PRE); Namaqualand, Stinkfontein, T. W. Matthews s.n. (NY, PRE); Ploegberg, eastern end above Perdewater, 11/24/1981, Van Jaarsveld 12081 (PRE). **WESTERN CAPE: CENTRAL KAROO: Beaufort West:** Karoo National Park, Beaufort West. Opposite Fonteintjie on Wagenpad road, 10/1/1983, A. Braack 39 (PRE); Below Rosesburg Pass [N of Beaufort West], 5/16/1950, J. P. H. Acocks 15885 (PRE); On Molteno Pass Road (R381) 6.4 km N of intersection with the N1, 2/12/2001, Timothy W. Chumley 7341a (TEX); On Molteno Pass Road (R381) 7.2 km N of intersection with the N1, 2/12/2001, Timothy W. Chumley 7342 (TEX). **Laingsburg:** Grootfontein near Laingsburg, 10/15/1908, R. Marloth 8347 (A, PRE). **Prince Albert:** 7-1/2 mi N of Prince Albert, 9/13/1956, J. P. H. Acocks 19008 (K, PRE). **EDEN: Kannaland:** 5 km E of Van Wysksdorp on southern foothills of Rooiberg, 1/20/1989, J. H. J. Vlok 2081 (MO, PRE); 2 mi ENE of Van Wyksdorp, 7/31/1959, J. P. H. Acocks 20559 (PRE); 20.7 mi SW by W of Ladismith, 10/9/1959, J. P. H. Acocks 20633 (PRE); Floriskraal, Wittepoort N of Prinsberg, 9/6/1982, M. Viviers 68 (NBG, PRE); Rooiberg Pass, ca 10 km from Van Wyksdorp, 11/22/1983, Mauve 23 (MO, PRE); Along the road to Rooiberg Pass, E of Van Wyksdorp, 10/28/1986, Peter Goldblatt 8034 (MO, NBG, NY, PRE); Majiesvlei. Huis River, 11/13/1971, R. D. A. Bayliss 5020 (A, MO, NY, PRE, UC, US); 5.5 km E of Van Wyksdorp on road to Rooiberg Pass, 1/28/2001, Timothy W. Chumley 7324 (TEX). **Mossel Bay:** Clearings of Gooritz River Georg [Near Herbertsdale, *fide* Verdoorn 1956], 12/15/1894, Ecklon 5 [94-12] (MO).

4. *Menodora africana* Hook.

Hooker's Icon. Plant. t. 586, 1842. Holotype: SOUTH AFRICA: FREE STATE: Fat River. [Great Vet River, Orange River Colony], *Burke 134* (K!)

Bolivaria africana (Hook.) Benth., London J. Bot. tab. 5, 1846.

Plants fastigiate or occasionally decumbent and spreading ***subherbaceous to suffrutescent perennials***, (6) 8.7—22.4 (40) cm tall, with a woody taproot, caudex 4—18 mm diameter at ground with few branches. ***Stems*** erect or spreading, branching approximately and remotely in inflorescence, opposite basally, alternate in inflorescence; older wood straw-colored, terete in cross section, glabrous or rarely densely hirsute, rugose; younger stems green, moderately to deeply fluted, angled in cross section, glabrous or glabrate to hirsute, often becoming glabrate with age, trichomes short, stout, deltoid, white or hyaline, (0.05) 0.10—0.33 (0.46) mm; internodes (2) 4—15 (24) mm at midbranch, alternating long and short. ***Leaves*** predominantly alternate, usually opposite basally but quickly becoming alternate; petiolate or subpetiolate, subcoriaceous, multifid or variously more broadly lobed, bifid to pinnatifid, rarely entire below, lobed leaves (3) 5.3—12.1 (19) by (2) 5.1—10.6 (15), length to width ratio (0.7) 0.8—1.6 (2.7), ultimate segments 0.2—2 (3) mm wide, glabrous or sparsely hirsute especially on margins and nerves, often punctate especially below, apices acute, rarely obtuse or mucronate, margins entire, or if broadly lobed, often with a few smaller apical dentiform lobes, base truncate or attenuate, decurrent, nervose, prominent abaxially. ***Inflorescence*** a compound dichasium with alternate branching, of 1—7 flowers, flowers often appearing solitary. ***Pedicels*** (2) 2.9—9.7 (15) mm long, (0.36) 0.43—0.72 (0.84) mm in diameter, glabrous or glabrate to densely hirsute, holding fruit pendant, subtended by a binnpinnatisect or entire and linear or lanceolate bracteiform leaf. ***Calyx*** tube turbinate, prominently nerved, broadening to 2X in fruit, hirsute, especially at base and along nerves, lobes sparsely hirtellous, (1) 1.5—2.7 (5) by (1.5) 1.8—2.6 (3) mm, broadening in fruit to (2.5) 3—5.2 (6) mm; lobes (7) 10 —12), (2) 3.7—6.6 (9) by (0.1) 0.2—0.5 (0.6) mm, thick, usually nerved, linear, apices acute, margins entire or bifid or trifid. ***Corolla*** infundibuliform, yellow, outer petals usually red in bud, tube (3) 3.4—4.8 (5) mm, (0.6) 0.8—1.3 (2) mm at base, opening to (2) 2.2—4 (6) mm at throat, pilose within; limbs 4—5 (6), mucronate, (6) 7.2—10.1 (11) by (2.5) 3.2—5.2 (7) mm, glabrous. ***Stamens*** filantherous; filaments adnate at or 0.6—1.9 (2.1) mm below throat, (1) 2—4.2 (5) mm long, glabrous; anthers exserted (0.5) 1.1—3.1 (5) mm, (2) 2.5—3.2 (3.5) by (0.5) 0.6—0.9 (1) mm, with a thin, short, cylindrical extension of the connective, dorsifixed, latrorse. ***Pollen*** 50—60 (80) µm. ***Ovary*** bicarpellate, bilobed, each carpel with a single locule and 4 ovules. ***Style*** (7) 8.5—12.2 (15) mm, glabrous. ***Stigma*** capitate, bilobed, exceeding the anthers (1) 2—4 mm. ***Fruit*** with cocci ovoid to obovoid, circumscissile, glabrous, (5) 6—8.5 (10) by (4.5) 5—7.5 (10) mm in diameter; pericarp thin, membranaceous, more or less translucent; each coccus containing 2—3 (5) seeds, fewer by abortion. ***Seeds*** ovate or obovate, trigonal though often flattened and plano-convex or meniscoid with a prominent raphal rib, (5) 5.7—7.7 (8) by (2) 3—5.7 (6) by 1—2.1 (3) mm, testa reticulate.

Distributed in South Africa from northern KwaZulu Natal northwest to Botswana at (615) 1000—1599 (1825) m elevation. Flowering mid-Sep to Jan (through May), with fruit (from late Sep) Nov to Jan. (through May).

A molecular phylogeny of the genus (see previous chapter) made a realignment of some taxa necessary, and as a result, this species is recognized with two morphologically distinct subspecies, subspecies *africana* and *australis*. The latter was formerly recognized as variety *australis* of the North American species *M. heterophylla*, but the two taxa were not closely related. Instead, *australis* is firmly imbedded within *M. africana* as sister to a northern clade of the species. Since the two taxa are morphologically quite distinct, showing no intergradation between the two forms, inhabit distinct geographical ranges with little evidence of mixing (Fig. 4), and the molecular phylogeny clearly shows one imbedded within the other, I have recognized them as a single, monophyletic species consisting of two subspecies.

The two subspecies can be separated by the following characters:

1. Leaves multifid, ultimate divisions linear, less than 1 mm wide ....**4a. *M. africana* subsp. *africana***

1. Leaves variously lobed, bifid to pinnatifid, ultimate segments greater than 1 mm wide and not linear ....**4b. *M africana* subsp. *australis***

4a. *Menodora africana* Hook. subsp. *africana*

Illustrations: Hooker's Icon. Plant. t. 586, (Hooker 1842); Fl. S. Afr. 26:126, fig. 14.1, (Verdoorn 1963).

Common name: balbossie

Leaves alternate, opposite basally but quickly becoming alternate, terminal leaves appearing clustered or whorled on very short internodes; petiolate, multifid, (3) 5—10 (15) mm (including petiole) by 5—11 (15) mm, length to width ratio (0.7) 0.8—1.1 (1.3), width at departure of lowest lobes 0.2—0.4 (0.5) mm, ultimate segment 0.2—0.4 (0.5) mm wide, glabrous or sparsely hirsute along margins and nerves, occasionally punctate sometimes obscurely so, apices acute, margins entire, base truncate, pinnanervate, nerves usually prominent abaxially. ***Calyx*** tube turbinate, prominently nerved, hirsute especially at base and along nerves, (1) 1.5—2.8 (5) by (1.5) 1.8—2.4 (3) mm, broadening in fruit to 2.5—5.3 (6) mm; lobes 10—12, (2) 3.7—6 .4 (9) by (0.1) 0.2—0.4 (0.5) mm, thick, nerved, linear, bifid or trifid, apices acute, margins bifid to pinnatifid, sparsely hirtellous. ***Stamens*** with filaments adnate 1.4—2.1 mm below throat, (2) 2.6—4.5 (5) mm long, glabrous (perhaps pilose at base, difficult to distinguish from that of corolla tube); anthers exserted (1.3) 1.4—3.5 (5) mm, occasionally with a conical process extending above the connective. ***Pollen*** 50—60 µm. ***Style*** (7) 9—11 (12) mm.

Rare in southern Botswana, and occasional but widespread in grasslands of bordering South Africa from southern Limpopo to northern KwaZulu-Natal, west to the eastern Northern Cape and Free State, though exclusive of the region inhabited by subspecies *australis* (Fig. 5) at (615) 1037—1599 (1825) m elevation. Flowering mid-Sept to Jan. (through Apr), with fruit (from late Sep) Nov to Jan. (through Apr).

These are plants of Highveld grasslands or mixed bushveld.

In the molecular phylogeny, subspecies *africana* is not a monophyletic group, in that the northern populations group with what is recognized here as subspecies *australis*. Geographically, the populations from which the exemplars of *africana* were drawn are separated by the northward extension of the Drakensberg, with the southern populations following the eastern slope of the Great Escarpment and the northern populations on the Highveld inner plateau. To be properly monophyletic in this context, the northern populations would require their own unique subspecific (or varietal) designation, but they are indistinguishable morphologically from the southern populations. More work is needed to determine if the separation of these clades is an artifact of sampling or perhaps has a cytological basis. Better sampling could integrate the northern populations into the species while making it as a whole sister to the *australis* clade; on the other hand, chromosome races are often cryptic morphologically, and its possible that the northern populations represent a polyploid race that is itself, as shown, sister to *australis*.

SPECIMENS EXAMINED:

BOTSWANA: NGWAKETSE: Pharing, 11/13/1948, Hillary & Robertson 480 (PRE); Pelotshethla, 45 km W of Lobatse. [nr. Kanye], 11/12/1983, D. C. H. Plowes 7004 (PRE).

SOUTH AFRICA: without exact locality: Zeyher 1132 (SAM); Transvaal: Doornkloof, 11/23/1928, J. B. Gillett 2547 (K); Transvaal: Rooikop, 12/6/1928, Mrs. A. B. Gillett M232 (K); Panfontein Game Reserve, 10/10/1951, W. J. Louw 1977 (PRE); Cutvir's Pass, William Tuck s.n. (SAM). **FREE STATE:** Gr. Vetrivier, Bechuanaland, [No collector] s.n. (SAM); Fat River. [Great Vet River, Orange River Colony], Burke 134 (K); **Lejweleputswa dist.: Tokologo:** Kromrant c. 20 km SW von Boshof, 11/27/1985, P. C. Zietsman & L. Zietsman 1361 (PRE). **Motheo dist.: Mangaung:** Wintervalley N of Bloemfontein, 12/11/1968, D. B. Muller 400 (PRE); Bloemfontein, 9/15/1894, Otto Kuntze s.n. (NY); Plaas Wolfkop, c 20 km Oos van Blomfontein Dreineringslyn, 2/6/1985, P. C. Zietsman & L. Zietsman 141 (PRE). **Northern dist.: Mafube:** Mandyville, Terblanche's farm on banks of Vaal River. SW hillside near river, 1/28/1988, M. Crosby 616 (PRE). **Ngwathe:** Heilbron, 1/20/1931, A. P. Goossins 410 (PRE). **Moghaka:** Kroonstad, 10/15/1929, F. W. Port 228 (A, A, PRE); Vaal River near Hebron, 12/15/1892, H. G. Flanagan 1472 (SAM). Farm Naseby Thorns 288. (Kroonstad), 4/2/1968, J. C. Scheepers 1715 (K). **Metsimaholo:** Sasol Game Park: near Vaalpark, 2/22/1995, N. V. Kroon 11624 (PRE); Rietfontein 123, as crow flies 7 km WNW of Sasolburg, 10/10/1996, N. V. Kroon 12013 (PRE). **GAUTENG:** Transvaal. Uitkomst 499 JQ. Vlakte by Picadilly Circus, 11/23/1970, B. J. Coetzee 492 (PRE). **Ekurhuleni Metropolitan:** Pretoria, Transvaal. Witfontein, 9/8/1928, A. Leeman s.n. (PRE). **Johannesburg Metropolitan:** Ruimsig Roodepoort, 10/29/1984, C. M. Bebr 788 (PRE); 26 km NNW of Johannesburg, on the farm Zandspruit. (91) 191IQ, 10/19/1997, R. A. Reddy et al. 986 (PRE). **Metsweding dist.: Nokeng tsa Taemane:** Near Pretoria, 9/20/1925, Alice M. Ottley & C. E. Moss 2227 (NY); 20-30 meilen nordöstlich von Pretoria, 12/6/1958, E. Werdermann & H.-D. Oberdieck 1302 (A, A, PRE, US). **Sedibeng dist.: Midvaal:** Transvaal: Suikerbosrand Hek by Wetter, 10/9/1971, G. J. Bredenkamp 105 (PRE); Meyerton District. Brakfontein 425 IR farm. Karma Game Farm, 1/20/1991, H. F. Glen 2518 (MO, PRE). **Lesedi:** N Heidelberg, Transvaal: Lower slopes of Kopjie on Plaas Hagenspoort, 12/17/1951, Du Prosser 1650 (PRE); Heidelburg. Lower slopes of kopje on farm Lagerspoort, 11/17/1951, L. N. Prosser (JNBG) 831 (PRE). **Tshwane Metropolitan:** Rustenburg, seen from Pretoria to Woodstock. [Note in Verdoorn's hand: "Probably from near Pretoria"], 9/17/1903, A. Pegler 950 (SAM); Moreleta Spruit Nature Trail, Pretoria, 3/2/1985, B. Clarke 1098 (PRE); Pretoria Dist. +/- 6 mi S of Pretoria on Kempton Park road, 10/21/1954, D. M. Comins 860 (PRE); Groenkloof Valley (Pretoria), 9/25/1925, I. B. Pole-Evans 452 (PRE); 6 mi S of Pretoria on Delmas Road, 11/2/1953, I. C. Verdoorn 28544 (MO, PRE); Eldoraigue [Eldoraigne], S of Pretoria, 11/4/1973, J. Lavranos 11062 (MO); Wonderboom Reserve. South slope, 11/9/1945, J. E. Repton 2765 (PRE); Near Pretoria, 11/15/1905, J. T. Janse 170 (SI); Faerie Glen [Pretoria]. Manitoba Drive. Valley bottom S of junction of Moreletaspruit tributaries, 11/27/1971, SAGP/SAAB 1/87 (PRE); Faerie Glen [Pretoria]. Oregon Road 474-488, 11/27/1971, SAGP/SAAB 2/59 (PRE); Faerie Glen [Pretoria], 11/27/1971, SAGP/SAAB 3/66 (PRE); Faerie Glen [Pretoria]. Copervlakte, onderkant kwartsietkoppie, 11/27/1971, SAGP/SAAB 4/77 (PRE); Rietondale Pasture Research Station, Pretoria Transvaal, C. G. Trapnell 628 (K). **West Rand dist.: Mogale City:** Sterkfontein Caves, NE section, Isaac Stegmann Nature Reserve, portion of farm Zwartkrans 67, dist Krugersdorp, central Transvaal, 9/28/1969, A. O. D. Mogg 34403 (K); [Note in I.C. Verdoorn's hand: "loc. Magliesburg."], Burke 134 (SAM); Transvaal, Johannesburg Distr., Witpoortjie Falls, 18 radial mi NW, 9/12/1962, K. Å. Dahlstrand 1081 (GB). **Xhariep dist.:** Sudafrika, Kapkolonien, Innsmark via Mosterts Hoek, Paardeberg Road, 10/16/1936, Adolf Hafstrom 972 (A); [Innsmark] vir Mostert's Hoek, Paardeberg Road, 10/16/1936, Adolf Hafstrom 992 (A); At Mosterts Hoek on Paardeberg Road, 10/16/1936, Hafstrom & Acocks H992 (PRE). **KWAZULU-NATAL: Amajubi dist.: Dannhauser:** Fairbreeze Farm. Local grazing land, 12/28/1992, A. M. Ngwenya 1100 (NH, PRE). **Umzinyathi dist.: Endumeni:** Farm Uithoek B, 12/31/1955, Elizabeth Shepherd 60 (NH); 1/2 mi from Syndicate farm. Indumeni Mt., 10/3/1926, D. Gordon Truscott 157 (PRE); **Uthukela dist.: Emnambithi-Ladysmith:** Ladysmith Airport, 10/9/1971, H. B. Nicholson 961 (PRE); Near Ladysmith, 2/14/1895, J. Medley Wood 5506 (MO); Harts Hill near Colenso, 10/18/1960, R. G. Strey 9960 (NU, PRE). Wagon Hill, Ladysmith, 2/6/2001, Timothy W. Chumley & William M. M. Eddie 7339 (TEX). **Indaka:** Waschbank, 11/2/1964, M. E. Shirley s.n. (NU). **Okhahlamba:** Spioenkop Dam Nature Reserve, 10/15/1975, A. C. van Rensburg 75 (NU); Spioenkop, 9/15/1974, S. van Rensburg s.n. (NU); Spioenkop Nature Reserve, on hills near dam, 2/5/2001, Timothy W. Chumley & William M. M. Eddie 7338 (TEX). **Umtshezi:** Estcourt district, 11/15/1985, D. M. Green 322 (NH); Banks of the Tugela River, Weenen, 1/2/1886, J. Medley Wood

3336 (NH); Near Estcourt on Est. Natal: Estcourt district: Weenen Rd., 10/15/1961, K. D. Gordon-Gray 3999 (NU); Adruper flum. Tugelarivier, Natalise, 10/23/1888, J. Medley Wood s.n. (SAM); Bank of the Tugela River near Colenso, 10/23/1888, J. Medley Wood 758 (SAM); Bank of the Tugela River near Colenso, 10/23/1888, J. Medley Wood 758 (US); Colenso, 1/15/1956, P. B. 22 (NU); nr. Colenso, 11/27/1893, R. Schlechter 3369 (G). Natal. Weenen Nature Reserve, 3/15/1999, T. Edwards 1636 (NU). **Zululand dist.: Abaqulusi:** 18 km from Nkongolane to Louwsberg, 10/18/1982, B. Schrire 1156 (NH); 21 km from Louwsburg on road to Ngome forest, 10/17/1982, G. Germishuizen 2164 (PRE). **LIMPOPO: Capricorn dist.: Polokwane:** Pietersburg Nature Reserve, between gate and Aalwyn Koppie, 1/8/1979, Bredenkamp & van Vuuren 45 (K, MO, PRE); Pietersburg, Transvaal, F. v. d. Merwe 2272 (PRE); Pietersburg, 1/15/1903, Henri A. Junod 1737 (G). Moletsi; Mmadikoti; on bank of Mohlapetsi River, SE of Mountain Mmadikoti, 1/3/1994, M. C. Makgakga 35 (PRE). **Sekhukhune dist.: Greater Marble Hall:** Farm Doornpoort (Rehmann's "Klippan") +/- 2 mi from Grass Valley on road to Roedtan, 1/19/1955, A. D. F. Meeuse 9573 (K, PRE). **Waterberg dist.: Bela-Bela:** Kransberg, 1/6/1959, E. Werdermann H. D. Oberdieck 1665 (PRE); Transvaal: Rust de Winter, 9/24/1945, J. Gerstner 5527 (PRE); Warmbaths, 9/30/1908, R. Leenderlz 5555 (PRE). **Modimolle:** +/- 12 km from Nylstroom on Naboomspruit road, 10/17/1953, A. D. J. Meeuse 9733 (PRE); Transvaal: Waterberg, 10/19/1956, Meeuse 9733 (K); Sterkrivier Dam Nature Reserve, 1/11/1973, N. Jacobsen 2554 (PRE). Waterberg. Riverside 6 mi on Palala road, 1/2/1936, Smuts & Gillett 3371 (PRE). **Mogalakwena:** 10 mi S of Limburg, 1/25/1962, H. J. Schlieben 9192 (PRE). **Mookgopong:** Delftzyl Trust Farm near Roedtan on Springbok Flats, 2/9/1993, C. Reid 1970 (PRE). **MPUMALANGA: Ehlanzeni dist.: Thaba Chweu:** Transvaal: Lydenburg: Bei der Stadt Lydenburg, 9/15/1895, F. Wilms 1068 (G). **Umjindi:** Plains near Crocodile Poort, 9/28/1890, E. E. Galpin 1071 (SAM, US); Crocodile Valley near Barberton, 9/28/1890, E. E. Galpin 1071 (K, PRE); Near Barberton, 10/15/1906, G. Thorncroft 646 (NH); Transvaal: Barberton, 7/15/1916, R. Pott 5593 (G). **Gert Sibande dist.: Albert Luthuli:** Stolzberg Syncline, on farm Groenvaly 701 JT, on the border of farm Doyershoek, 10/10/1997, K. Balkwill et al. 9868 (K). **Lekwa:** Spruit near Val Station, 10/15/1932, J. C. Smuts 397 (PRE). **Nkangala dist.: Emalahleni:** Leeuwpoort, 10/15/1918, F. A. Rogers 22393 (NH). **Steve Tshwete:** Klein Oliphants River near Middelsburg, 11/6/1933, R. G. N. Young A95 (PRE). **NORTHERN CAPE: Frances Baard dist.: Sol Plaatjie:** Bank beside Transvaal Road at Kenilworth, 10/13/1936, A. Hafstrom H902 (PRE); Kimberley, S. S. Oliver s.n. (SAM); Barkley West: Vaalbos Nasionale Park, 10/20/1988, P. C. Zietsman 436 (PRE). **Siyanda dist.: Tsantsabane:** Postmasburg M.W., Ehul s.n. (SAM); Griqualand West, 4/15/1914, M. Wilman s.n. (SAM). **NORTHWEST: Central dist.: Mafiking:** Mafeking, Appleyard s.n. (SAM); Mmabatho - NW of Unibo [University of Bophutswana] campus, 11/11/1982, S. D. Phalatse 47 (PRE). **Tswaing:** Delareyville (on side of Schweizer-Reneke) at entrance of auction area, 1/22/1987, E. Retief 1813 (PRE). **Bophirima dist.: Greater Taung:** Between Kuruman and Vryberg, 11/15/1939, G. Lhome s.n. (SAM); Vryburg. Farm Zoet Vley. [Zoetvlei], 11/22/1988, J. G. Speedy 231 (PRE). **Lekwe-Teemane:** Armoes Vlakte. Bechuanaland. [Armoedsvlakte], 10/7/1920, A. O. D. Mogg 8024 (PRE); Bloemhof: town commonage, Christiana, Joseph Burtt-Davy 12480 (PRE); S. A. Lombard Nature Reserve, 12/15/1985, L. F. Jeffers 413 (PRE); S. A. Lombard Nature Reserve, 4/3/1955, O. A. Leistner 81 (PRE). **Naledi:** Mafeking div., "Moshesh.", 12/4/1945, A. Brueckner 420 (PRE); Cape. Stella. 30 mi N of Vryburg, 11/18/1962, D. S. Hardy Bayliss 1243 (K). **Southern dist.: Maquassi Hills:**Transvaal: Wolmaransstad Distr., ad urbem W, 10/11/1930, Th. C. E. Fries Tyco Norlindh & Henning Weimarck 1855 (MO, PRE). **Merafong:** Carletonville, A. Bailey Nature

Reserve, 4/15/1983, S. Van Wyk 262 (PRE); Welverdiend (Potchefstroom district), 10/19/1938, W. J. Louw 72 (PRE). **Potchefstroom:** Dassierant. Potch., 10/6/1976, A. E. Van Wyk 1741 (PRE); Noyjons - SW von Potchefstroom, 11/9/1983, D. J. Botha 3350 (PRE); 13.4 mi W of Potch [Potchefstroom] on Klerksdorp Road, 2/5/1946, R. Story 760 (PRE); Boskop (Potchefstroom), 9/27/1939, W. J. Louw 355 (PRE).

4b. ***Menodora africana*** **Hook. subsp.** ***australis*** **(Steyerm.) Chumley**, *comb. nov.*

Basionym: *Menodora heterophylla* Moric. *ex* A. DC. var. *australis* Steyerm., Ann. Missouri Bot. Gard. 19:127, 1932. Holotype: On grassy turf, near Rustenburg, alt. 1220 m, Aug., 1903, *Pegler 950* (B), destroyed. Lectotype (designated here): SOUTH AFRICA: NORTHWEST PROVINCE: nr. Rustenburg, Aug. 1903, *Alice Pegler 950* (K!).

Illustrations: Hook. J. Bot. t. 1459 (Oliver, 1884); Fl. S. Africa 26:126, fig. 14.1, (Verdoorn 1963); Fl. Zambes. 7:1:319. Tab. 72 (Kupicha 1983).

Leaves alternate, opposite basally but quickly becoming alternate, sessile to subpetiolate, subcoriaceous, trifid to pinnatifid, the lower often entire, spatulate to oblancelate or lanceolate, occasionally entire throughout, lobed leaves (3) 7.2—14.4 (19) by (2) 4.7—10.4 (12), length to width ratio (1) 1.2—2 (2.7), ultimate segment (1) 1.4—2.8 (3) mm wide, entire leaves or bracts similar in length and one-third to one-half as wide as long; apices acute, rarely obtuse or mucronate, margins thickened and somewhat revolute, major lobes often with a few smaller dentiform lobes, base attenuate, decurrent, densely hirsute, glabrous or sparsely hirsute especially on margins and nerves, often punctate especially below, uninervate, nerve prominent abaxially often attenuating to apex, rarely trinervate. ***Calyx*** tube turbinate, prominently nerved, hirsute especially at base and along nerves, 1.5—2 (2.5, rarely to 4) by (1.5) 1.8—2.8 (3) mm, broadening in fruit to 4—5 mm; lobes (7) 10 (12), (3) 4—6.6 (8) by (0.1) 0.4—0.6 mm, thin, sometimes thickened with a prominent nerve, linear, occasionally broadly subulate, rarely bifid or trifid, apices acute, margins entire, sparsely hirtellous. ***Stamens*** with filaments adnate at or 0.6—1.5 mm below throat, (1) 1.4—3.4 (3.6) mm long; anthers exserted (0.5) 0.9—2.3 mm, with a thin, short, linear or cylindrical extension of the connective. ***Pollen*** 50—70 (80) µm. ***Style*** 9—14 (15) mm, glabrous. ***Stigma*** capitate, bilobed, exceeding anthers 2—4 mm.

In savanna-bushveld east of the Kalahari in southern Botswana and adjacent South Africa (northeastern Northwest Province and adjacent Limpopo, around the Waterberg district; Fig. 5) at (1000) 1100—1300 m elevation. Flowering and with fruit mid to late Sep to Dec (through May).

This taxon was first reported from Africa by Oliver (1884) from a collection made by Holub in the "Matebe Valley" (Verdoorn (1956) states that this is near the village of Linokana, a few miles west of Zeerust) and as determined by N. E. Brown, it was recognized as conspecific with the North American *M. heterophylla*. Though indeed poorly discriminated from the species, Steyermark (1932) recognized it as variety *australis* based largely on it s geography (citing but not elaborating "morphological differences"), and it was often cited afterwards as evidence of a land bridge connecting the continents or of continental drift. In fact, as anticipated by Cockerell (1932), the African taxon is not closely related to the North American species, and thus represents a striking example of morphological convergence. The two can be very difficult to distinguish within the range of variation in each of them; Verdoorn (1956) notes that the principal difference seems to be leaf size, but I have not noted this in my observations.

In habit and stem and trichome characters, *australis* is close to *M. africana*, with a usually upright habit, deeply fluted stem, and moderately to densely hispid with coarse deltoid trichomes. Both *africana* and *australis* are occasionally somewhat decumbent, however, and conversely, the usually decumbent American *heterophylla* can sometimes be more erect, and also occasionally has broadly deltoid trichomes. Herbarium specimens of *australis* tend to be a little more glaucous than the American material, and occasionally, an individual calyx lobe may be bifid or trifid.

Other than the similarities noted above, this taxon is morphologically distinct from *M. africana*, and is probably worthy of recognition at the species level. Verdoorn (1963) notes that variation in leaf size and shape can make determinations between the two difficult at first glance, but I have not noted such in material I've examined.

The holotype for this taxon at Berlin was destroyed by fire in 1943 after a bombing raid. Choosing a lectotype is a bit complicated since Pegler seems to have used the same collection number for at least two collections made in 1903, bearing slightly different localities and collection dates, a fact noted by Verdoorn (1963). Specimens at G, P, SAM and PRE are dated 17 Sept. 1903, and the locality noted as "Rustenburg ... seen from Pretoria to Woodstock" or alternatively "Occurs from Pretoria to Woodstock," on "turf and sandy loam." Sheets at G, SAM and one of the two at PRE also represent mixed collections with *M. africana*, and Verdoorn notes on the specimen at SAM that the locality for the latter is "probably from near Pretoria" and that *M. africana* is unknown from the vicinity of Rustenburg (Verdoorn, 1956). Of the sheets reviewed at K, one is dated only Sept. 1903 and the locality noted as "Woodstock, Rustenburg." The label on a second sheet, however, agrees with that of the type selected by Steyermark (1932), and is a composite specimen with Holub s.n. (see Oliver, 1884). Since this specimen appears to be of the authentic collection named by Steyermark (1932), I therefore designate it as the lectotype.

SPECIMENS EXAMINED:

BOTSWANA: CENTRAL: 93 km NW of Serowe [+/- 1/2 Serowe: Lothlekane [Letlhakane], W of Macloutsie [Motloutse], Francistown], 3/24/1965, H. Wild R. B. Drummond 7273 (K, PRE); **KGATLENG:** Mochudi, Bechuanaland Protectorate, South Africa. [Botswana], 4/15/1914, F. A. Rogers 6900 (G, K, NH); Mochudi, 1/15/1915, W. A. H. Harbor 17012 (PRE); **SOUTH EAST:** Lobatsi, 10/15/1913, F. A. Rogers 6225 (K, PRE); 6 mi NE of Gaborones, 12/2/1954, L. E. Codd 8937 (K, PRE); Gaborone District: Near St. Jospeh's College (Khale), 9/22/1978, O. J. Hansen 3464 (K, PRE).

SOUTH AFRICA: LIMPOPO: Waterberg dist.: Bela-Bela: Pienaars River Rail, 10 km further N on road leading to Warmbaths, 12/16/1966, A. O. D. Mogg 37262 (PRE); **NORTHERN CAPE: Kgalagadi dist.: Moshaweng:** Bophuthaswana: N of Heuningsvlei. [Heuningvlei], 12/8/1977, C. Peeters et al. 261 (MO). **NORTHWEST: Bojanala dist.: Kegetlengrivier:** Zwartruggens, 7/11/1936, J. D. Sutton 1113 (PRE); Zwartruggens. [Swartruggens], 5/24/1934, J. D. Sutton 852 (PRE); **Madibeng:** Near P.O. Assen, near the Farm Welgwonder Crocodile River, 12/15/1932, J. J. van Nouhuys 31047 (PRE); Pretoria Portland Cement Game Reserve ("Beestekraal") approx 40 km N of Brits, 10/2/1988, N. P. Barber 443 (PRE). **Moses Kotane:** Saulspoort: Kwa-Ramoga. [Ga-Ramoga], 11/28/1977, G. Germishuizen 484 (PRE); Buffelskloof farm, Buffelskloof, 12/1/1977, G. Germishuizen 612 (PRE); Bophutswana: Pilanesberg National Park. New road between main road and Mankwe Loop, ca 1-1.5 km from main road, 1/6/1991, H. F. Glen 2493 (MO). **Rustenburg:** near Rustenburg, Aug. 1903, A. Pegler 950 (Lectotype, K); Pretoria, Woodstock, Sept. 1903, A. Pegler (K); Rustenburg, seen from Pretoria to Woodstock [occasionally as “occurs from Pretoria to Woodstock”], 9/17/1903, A. Pegler 950 (G, P, PRE, SAM); Rustenburg, 11/6/1928, E. E. Galpin 9668 (PRE); **Central dist.: Ramotshere:** On the border between Marico and Rustenburg districts near Wonderfontein, 10/25/1907, C. E. Gray 4131 (PRE); Doornfontein, 2/19/1986, H. Bezuidenhout 127 (PRE); Matebe Valley, Holub s.n. (K, PRE); Rooderand Farm 41 JP Marico District, 12/22/1969, J. H. Carter 808 (PRE); Rooikoppiesfontein Farm. Marico District, 12/14/1969, J. H. Carter 834 (PRE); 4 mi S of Zeerust, 2/6/1946, J. P. H. Acocks 12415 (PRE); Zeerust, 12/31/1927, J. Thode A1442 (GH, NH, PRE); Zeerust, 1/15/1912, R. Heenderly 11325 (PRE); Skvinsdrift, E. Marico. Along 'Rode Sloot.', 4/25/1927, S. Liebenberg 106 (PRE); Skvinsdrift, E. Marico, 4/23/1927, S. Liebenberg 15 (PRE); On Skuindrif Road ca 7 km N of Groot Mavica. Opposite entrance to J. J. Stein Boerderie-Doornkraal, 2/8/2001, Timothy W. Chumley & William M. M. Eddie 7340 (TEX); **Southern dist.: Matlosana:** Near Klerksdorp, 10/3/1935, J. Philips 53 (PRE). Wolwerand, Klerksdorp, 1/2/1971, W. J. Hanekom 1514 (PRE).

5. *Menodora decemfida* (Gill. ex Hook. & Arn.) A. Gray

Amer. J. Sci. II 14: 44, 1852. Basionym: *Bolivaria decemfida* Gill. ex Hook. & Arn., Hook. J. Bot. 1: 284, 1834. Lectotype (designated here): ARGENTINA: MENDOZA: Valleys of the Andes of Mendoza [ms. included on the sheet cites “Found at Cerro Maya above Mendoza & near Villavicenzio, both in the valleys at foot of mountains. Nov 2, 1822.”], *L. Gillies s.n.* (K!). Probable Isolectotype: Valleys of Mendoza, without collector (GH), but noted as “collector Gillies in Fielding Herbarium by I. M. Johnston” in Steyermark (1932).

Illustrations: Lilloa 28:219, Fig. 2 (Meyer, 1957).

Plants usually large, fastigiate ***suffrutescent to frutescent perennials,*** (20) 26—43 (60) cm tall, with a woody taproot, branching from caudex with many branches. ***Stems*** erect, branching remote, opposite; older wood tan to gray, glabrous, rugose, rimose; younger stems green, moderately to deeply fluted, often with a strongly defined decurrent, caniculate groove, terete below, more strongly angled above in cross section, glabrate, often hispidulous in leaf axils or nodes, trichomes rudimentary and minutely papillose, or short, white or hyaline, 0.02—0.07 (0.11) mm; internodes longest at midbranch often just above largest leaves, (5) 12—35 (45) mm, usually exceeding the subtending leaves. ***Leaves*** opposite, occasionally becoming alternate bracts in inflorescence, sessile, submembranaceous, lanceolate to oblanceolate,often narrowly so, very rarely bifid or trifid, basalmost often obovate, entire leaves (3) 5.4—15 (20) by (0.7) 1—2.3 (3), length to width ratio (2) 4.2—8.1 (10), apices acute, acuminate or apiculate, thickened, often obtuse below, margins entire, base attenuate, decurrent, glabrous to minutely hispidulous, often hispidulous at base adaxially, uninervate, prominent abaxially, not swollen at nodes, if lobed laterals not prominent. ***Inflorescence*** a compound dichasium with mostly opposite but irregularly alternate branching, rarely solitary, of 1—9 (21) flowers. ***Pedicels*** (0) 0.5—14 (33) mm long, (0.4) 0.5—0.9 (1) mm in diameter, glabrous, holding fruit erect, subtended by a linear or linear-lanceolate, glabrous or hispidulous bract, bracts often occurring in opposite pairs but irregularly variable. ***Calyx*** often tinged red; tube turbinate, glabrous externally, prominently nerved, (1.7) 1.9—3.7 (5) by (1.5) 2—3 mm, broadening in fruit to (2.4) 3—4.6 (5.5) mm; lobes 5—10 (11), (1.7) 1.9—4.3 (7) by (0.2) 0.3—0.5 mm, thin, prominently nerved, linear to narrowly deltoid, hispidulous on internal faces, apices acute, margins entire. ***Corolla*** infundibuliform, yellow, red in bud, tube (4) 5—8 (9.6) mm, 1—1.6 mm at base, opening to 3—4.5 mm at throat, glabrous to densely pilose within; limbs (4) 5 (6), acute or obtuse, (4.7) 6.3—12.7 (15) by (2.8) 3.1—4.5 (5.2) mm, glabrous. ***Stamens*** filantherous; filaments adnate ca 1.5—2 (3) mm below throat, (3) 3.9—7.2 (7.5) mm long, glabrous; anthers exserted (1.5) 3—5 mm above throat, (2.3) 2.7—4.9 (5.7) by (0.5) 0.6—1 mm, with a short, linear or cylindrical process extending above the connective, dorsifixed, latrorse. ***Pollen*** 50—70 µm. ***Ovary*** bicarpellate, each carpel with a single locule and 4 ovules. ***Style*** (4.7) 8.9—18.3 (22) mm, glabrous. ***Stigma*** capitate, equalling or exceeding the anthers to 3 mm beyond. ***Fruit*** rarely with 3 cocci; cocci obovoid, circumscissile, glabrous, (3.3) 4.7—6.3 (6.7) by (2.9) 3.5—4.9 (5.5) mm in diameter; pericarp thin, membranaceous, more or less translucent; each coccus containing 2 seeds, occasionally 3 or 4. ***Seeds*** obovate or elliptic, somewhat flattened and plano-convex with a strong adaxial rib, to trigonal, (4.2) 4.7—5.5 (5.9) by (2.2) 2.4—3.1 (3.3) by 1—1.5 (1.7) mm, testa regularly alveolate-reticulate.

Distributed in the shrub-steppe pre-cordillera of Mendoza, San Juan, La Rioja and Catamarca in Argentina at (800) 1300—1700 (3200) m elevation. Flowering (late Oct) Nov to Feb, in fruit (mid-Nov) Dec to Apr (early May).

Meyer (1957) noted that this species was cited erroneously by Steyermark (1932) for Chile, and Muñoz et al. (2006) noted that it was again erroneously placed in Chile by Zuloaga and Morrone (1999). The rediscovery of *Menodora linoides* in Chile does raise the possibility that it is a peripheral isolate of *M. decemfida*, but superficially it appears to be closer to *M. integrifolia*. However, the range of variation between the two species is such that *M. linoides* could be close to or possibly even conspecific with either.

Variation within many characters of *Menodora decemfida* and *M. integrifolia* can make it difficult to make a determination, as a small *M. decemfida* can look very much like *integrifolia* with entire leaves. Vegetatively, *M. decemfida* is more frutescent than *M. integrifolia*, but it may be difficult to assess this character in a small or young plant, or the usual fragment found in a herbarium specimen. Usually, the internodes at midbranch will be longer than the leaves subtending them, whereas in *M. integrifolia* they are usually (but not always) shorter or approximate. The number of calyx lobes is diagnostic if there are ten, but fewer are quite common, putting this into the range of variation for *M. integrifolia*. Flower size is generally larger in *M. decemfida*, but again, this character also overlaps with *M. integrifolia* on the small side of the range of variation.

Even more remarkable is the apparent convergence between the Argentine species and the North American variety *longifolia* described by Steyermark (1932). Turner (1991) was essentially correct in placing this variety in a cohort of *Menodora scabra*-like species in North America, but the morphological parallels are striking, nonetheless.

In the protologue of the original description, no type is designated, but two specimens are mentioned, one collected by Dr. Gillies, and the other, with no locality given, collected by Mr. Cruckshanks. At K, the former specimen can be readily identified, but the second is something of a mystery. However, another collection by Mr. Cruckshanks is referenced for *Bolivaria trifida* on the "Plains of Mendoza." One composite specimen at K, consists of two specimens numbered 67 and 68 but without a collector, determined as *Bolivaria decemfida* and *B. trifida*, respectively, with the locality for the former given as "Plains of Mendoza" and for the latter "Found in the same place as No. 67." Both specimens are *Menodora decemfida* (No. 68 represents a small-flowered individual), and I believe No. 67 to be the Cruckshanks syntype. However, since we can with certainty recognize the Gillies specimen, it is preferable to designate it as the lectotype for the species.

SPECIMENS EXAMINED:

ARGENTINA: without locality: 11/1/1912, Renato Sanzín 16 (SI);11/1/1912, Renato Sanzín 29 (SI). **CATAMARCA: Dpto. Las Abritas:** Quebrada de Sta. María al Cajón, Las Abritas, 1/1/1915, Castillón 3739 (LIL); Quebrada de Sta. María a San Antonio, Las Abritas, 1/1/1915, Castillón s.n. (GH). **Dpto. Tinogasta:** El Vallecito, 2/7/1930, Castellanos s.n. (BA); Coipita a Vallecito, 2/6/1930, R. Schreiter 6247 (LIL). **LA RIOJA:** Sierra de Famatina; Ciénega de Cosme, 1/19/1928, Castellanos s.n. (BA). **Dpto. General Belgrano:** Entre Olta y el Dique, a 2 km de la primera. Sector de ingreso al paraje llamado El Bosque Petrificado, 11/29/2001, F. Biurrun & D. González 6749 (CTES). **Dpto. General La Madrid:** Entre Jaqué [Jagüe] y la Salina del Leoncito, a 23 km del cruce con el camino a Chile. Paraje llamado Agua de Cándido, 2/5/1999, F. Biurrun & J. Molina et al. 5489 (CTES). **General Sarmiento:** Entre Jaqué y la Salina del Leoncito, a 43 km de la primera. Paraje: Agua Quemada, 3/28/1998, F. Biurrun & J. Molina 5327 (CTES). **MENDOZA:** Valleys above Mendoza, 10/30/1829, L. Gillies s.n. (GH). **Dpto. Godoy Cruz:** Gobernador Benegas, 3/1/1945, A. Ruiz Leal 9997 (LIL). **Dpto. La Valle:** Paramillo de Mendoza, Tolliers 592 (G). **Dpto. Las Heras:** Pampa de Los Ñangos. Salto de La Cabra, 12/28/1979, A. Dalmasso & C. Passera 31847 (MERL); Quebrada de la Mina Atala, 12/24/1937, A. Ruiz Leal 4697 (LIL); Entre Vistalba y La Crucesita, 4/17/1938, A. Ruiz Leal 5080 (HRL); Cerro Melocotón, 12/18/1938, A. Ruiz Leal 5521 (HRL); Parque General San Martín (Zanjón Frías), 1/18/1944, A. Ruiz Leal 8761 (LIL); El Challao, 1/29/1933, A. Ruiz Leal 969 (HRL); Uspallata, Qda. del Telégrafo, 1/11/1982, Andrada et al. 378 (SI); Villavicencio, 1/21/1944, C. A. O'Donell

1107 (A, UC); Camino de Villavicencio a Chile, proxímo a Villavicencio, 2/2/1946, E. G. Nicora 4329 (K, SI); Estación Canota, 3/20/1947, E. M. Garcia s.n. (LIL); Challao, 12/24/1949, F. A. Barkley & L. Orlando Melis 19Ar892 (NY); Villavicencio, 12/25/1949, F. A. Barkley 19Ar940 (NY); Quebra. de Santa Elena, 1/21/1960, F. Roig 3730 (MERL); Uspallata Co. Agua de la Tinaja, 11/20/1982, F. Roig s.n. (MERL); Villavicencio, 12/25/1949, Fred A. Barkley 19Ar940 (NY); Canota. [Est. Villevicencio], 11/13/1944, G. Covas 3068 (SI); Villavicencio, 1/18/1943, G. Covas 874 (SI); Path leading up to ridge from Hotel at Villavicencio, 1/18/1943, H. H. Bartlett 19391 (MICH, SI, US); entre Uspallata y Los Homillos, 3/1/1954, Humberto A. Fabris 1205 (LP, US); Cordón de Las Higueras, 12/23/1980, J. A. Ambrosetti & L. A. Del Vitto 31104 (MERL); Los Puertezuelos, on the international road to Chile, 1/4/1966, J. G. Hawkes J. P. Hjerting & K. Rahn 3153 (K); San Ignacio, 5/1/1944, J. Semper 101398 (NY); Agua de los Chilenos, 12/12/1949, Manuel R. Cárceres et al. 362 (NY); Immedaciones del Cerro del Arco, 4/28/1981, R. H. Brown et al. 31763 (MERL); Lomas de Vistalba, 11/21/1981, Rdrg.-Mendez s.n. (MERL); Entre Vistalba y La Crucesita, 4/17/1938, T. Meyer 5080 (MERL); Cerro Melocoton, 12/18/1938, T. Meyer 5524 (MERL); San Ignacio, 5/7/1944, T. Meyer 9309 (MERL); 5 km east of Villavicencio, 1/6/1956, T. W. Böcher et al. 2107 (MO); Caracolos de Villavicencio, 1/12/1969, Theodor Meyer 22.805 (LL); Dpto. Las Heras. On Ruta Provincial 52 ca 31 air km E of Villavicencio, on hills above paved road at entry to mountains, 12/15/2001, Timothy W. Chumley et al. 7377 (TEX). **Dpto. Luján de Cuyo:** Entre Cacheuta y Potrerillos, 12/20/1951, A. Ruiz Leal 14508 (HRL); Estancia El Salto, Cerro el Medio, 12/4/1938, A. Ruiz Leal 5488 (LIL); Potrerillos, 1/25/1944, C. A. O'Donell 1041 (A); Distrito Chacras de Coria, 12/5/1942, H. H. Bartlett 19183 (MICH, SI, US); Vicinity of red sandstone outcrop, Potrerillos, 1/10/1943, H. H. Bartlett 19321 (GH, MICH, SI, US); Potrerillos, Qda. del Salto. prox. Co. Cabras, 11/29/1977, J.

A. Ambrosetti & L. A. Del Vitto 29182 (MERL); Potrerillos, Co. Cabras, 11/28/1977, J. A. Ambrosetti & L. A. Del Vitto 29208 (MERL); Lujan de Cuyo, 11/26/1913, Renato Sanzín 195 (SI); Márgenes del R. Mendoza en las tomas del Canal Naciente, 11/16/1934, Ruiz Leal 2658 (LIL); Cachueta, 1/1/1926, Señorita Negrete s.n. (SI); Dpto. Lujan. On Ruta Nacional 7 from Mendoza to Uspallata at km marker 1085, 12/13/2001, Timothy W. Chumley et al. 7371 (TEX); Dpto. Lujan. On Ruta Nacional 7 near km marker 1088 ca 3 rd km E of Potrerillos, 12/13/2001, Timothy W. Chumley et al. 7375 (TEX). **Dpto. Maipú:** Médano de los Morritos (El Tapon), 11/27/1945, A. Ruiz Leal & Oliverio Paci 475 (NY); Las Barrancas, 1/15/1943, G. Covas 824 (SI); Médanos de los Morritos, 11/27/1949, Paci 475 (LIL). **Dpto. San Carlos:** Laguna del Diamante, 1/15/1952, Lidia Serra 82 (LP). **Dpto. San Rafael:** Las Picasas, 1/23/1941, A. Ruiz Leal 7301 (LIL); Cuadro Benegas: Sierra Pintada, 9 km al sur del Dique Galileo Vitali, 2/21/1984, J. A. Ambrosetti et al. s.n. (MERL). **Dpto. Tupungato:** San José, Estacion Meterológica, 11/19/1982, A. Ciccarelli & S. Marqués s.n. (MERL); Tupungato, immediaciones de la villa mismo nombre, 3/3/1933, A. Ruiz Leal 1242 (LIL); Entre Anchoris y Zapata, 4/26/1944, G. Covas 1672 (SI); Lomas cerca del Tupungato, 12/27/1949, H. Sleumer 347 (LIL). **SAN JUAN: Dpto. Calingasta:** Mina Castaño Viejo, 2/23/1967, A. L. Cabrera et al. 17940 (LP); Quebrada del rio Calingasta, 1/15/1974, A. L. Cabrera et al. 24325 (LP); Los Morillos, detrás del campamento, 1/25/1997, R. Kiesling et al. 8860 (NY). **Dpto. Iglesia:** Camino a El Fierro, Aguadita, 1/21/1974, A. L. Cabrera et al. 24511 (LP). **Dpto. Jáchal:** Quebrada de Huachi, 11/1/1941, A. P. Rodrigo 2988 (LP); Jacimiento mauí fuo de los Barreales (Pampa de Panacán), 12/12/1957, F. Roig & A. Ruiz Leal 2293 (MERL). **Dpto. Zonda:** Estancía Maradona, Agua Pinto, 2/7/1986, R. Kiesling et al. (K); Cno. a Estancia Maradna, 11/12/1982, R. Kiesling & A. A. Sanchez 4086 (MERL).

TUCUMAN: Dpto. Tafi del Valle: Sierra de Cafore [?], 2/7/1928, S. Venturi 10065 (US); Colalao del Valle, 2/14/1928, S. Venturi 9534 (A, US).

6. *Menodora linoides* Phil.

Anales Univ. Chile 23(2): 378, 1863. Holotype: CHILE: REGION V: Petorca: Inter Chincolco et Concumen, prov. Aconcagua, 1/1863, *Landbeck s.n.* (SGO 053888).

Common name: *linacillo*

Illustration: Chile: Plantas en Extincion, p. 151, fig. 27 (Muñoz 1973).

Plants fastigiate, or somewhat spreading ***suffrutescent perennials***, 5—20 (40) cm tall, with no roots seen, and a caudex with many branches. ***Stems*** erect, branching throughout, opposite below, alternate in inflorescence; older wood tan, glabrous, rugose, rimose, younger stems green, often tinged red, moderately to deeply fluted, angled in cross section, glabrous or glabrate, often puberulent, trichomes short, white or hyaline; internode length at midbranch (2) 3—8 (12) mm. ***Leaves*** opposite becoming subopposite or alternate bracts in inflorescence, sessile, subcoriaceous, elliptic to oblong-elliptic or oblanceolate, becoming quite reduced in inflorescence, (2) 3.9—10 (19) by (0.6) 1—2.4 (4), length to width ratio (2.3) 2.6—5.9 (10) mm, glabrous or minutely puberulent, apices acute, apiculate, mucronate or obtuse, margins entire, thickened, base attenuate, decurrent, uninervate, nerve prominent abaxially, usually slightly swollen at node. ***Inflorescence*** frequently appearing solitary or a simple dichasium of 1—3 flowers usually with opposite branching. ***Pedicels*** (1.5) 1.6—3.5 (5) mm long, 0.4—0.5 mm in diameter, glabrous, holding fruit erect, subtended by a leaf-like bract, bracts occurring in opposite pairs. ***Calyx*** often tinged red; tube turbinate, prominently nerved, glabrous or hispidulous mostly at base and along nerves, (1.8) 1.9—2.2 (2.5) by (1.6) 1.8—2.3 (2.5) mm, broadening in fruit to 3 mm; lobes 5 (rarely trifid, appearing to be 15), 2—4.3 (7) by0.4—0.6 (0.7) mm, thin, prominently nerved, broadly subulate, sparsely hispidulous and punctate, apices acute or acuminate, margins entire or rarely bifid or trifid. ***Corolla*** infundibuliform, yellow, outer petals often red or purplish-tinged in bud, tube 3—5.2 (6) mm, 1—1.2 mm in diameter at base, opening to (2.5) 2.6—3.1 (3) mm in diameter at throat, pilose within; limbs (4) 5, acute, (6) 7.2—13.5 (15) by (2.5) 2.6—5.3 (6) mm, glabrous. ***Stamens*** filantherous; filaments adnate ca 2 mm below throat, 4—8 (10) mm long, glabrous; anthers exserted ca 2—3 mm above throat, (2) 2.4—4.6 (5) by 0.6—0.8 mm, dorsifixed, latrorse. ***Pollen*** not observed. ***Ovary*** bicarpellate, bilobed, each carpel with a single locule and 4 ovules. ***Style*** 8—10.9 (11) mm, glabrous. ***Stigma*** capitate, equalling or just exceeding the anthers. ***Fruit*** with cocci globose, circumscissile, glabrous, 6—7 by 6—7 mm in diameter; pericarp thin, membranaceous, more or less translucent, often rubescent; each coccus containing 1—2 seeds. ***Seeds*** obovoid or plano-convex to lenticular, 4.5 by 2.5—3.5 mm, regularly faveolate-alvelolate, castaneous or atratous in color.

Known in Chile only from the type collection and two recently collected localities in northern and central Región V (Valparaíso), the more northerly population probably representing the type locality (Faúndez, Larraín, and Girón 2005; Muñoz, Moreira, and León 2006) at 1240—1800 m elevation. Flowering Dec to Mar, with fruit by Mar.

The recent rediscovery of *Menodora linoides* in Chile (Faúndez, Larraín, and Girón 2005; Muñoz, Moreira, and León 2006) some 140 years after its first and only collection is very exciting. It is the sole member of the family known from Chile, and represents a peripheral outlier in the geography of the genus. As such, it will be very interesting to investigate its place in the phylogeny of the group. Morphologically, it has the general habit and characters of a *M. integrifolia* with entire leaves, or a small *M. decemfida*. The latter is its closest neighbor, occurring on the east slope of the Andes in Argentina, and I believe it to be probably its closest relative as well.

The herbarium at SGO has two specimens that until recently were the only vouchers known for this species. Both were collected by Landbeck in January 1863, thus both are probably of the type material. However, the specimen that is noted as being part of Philippi's personal herbarium, SGO 038535, gives the locality as simply "Concumen," rather than "Inter Chincolco et Concumen" as found in the protologue and the other specimen (SGO 053888), and further carries a tag with the number 1585. Without a doubt Philippi had both of these in hand when he described the species. Nonetheless, it is not clear that Landbeck 1585 (SGO 038535) represents the same specimen mentioned in the protologue, and so I restrict the holotype to being SGO 053888.

SPECIMENS EXAMINED:

CHILE: REGION V: Petorca: Concumen, 1/1863, *Landbeck 1585* (SGO).

7. *Menodora pulchella* Markgr.

Notizbl. 8:219, 1922. Holotype: BOLIVIA: TARIJA: Condorhuassu bei Tarija, 3200 m, 2/6/1904, Fiebrig 2984 (B) destroyed; photo (F!). Isotypes: F, NY!

Illustrations: Lilloa 28:239, fig. 7 (Meyer, 1957); Fl. Prov. Jujuy 8:38, fig. 16 (Zuloaga, 1983).

Plants small, densely mound-forming suffrutescent perennials, (3) 3.4—9.6 (10) cm tall, with a woody taproot and caudex with many branches. ***Stems*** spreading, branching throughout, opposite; older wood tan to grey or black, glabrous, rugose, younger stems green, usually tinged red, obscurely fluted, more prominent above, terete below, often flattenedand slightly angled above in cross section, sparsely hispid, especially at nodes and axils and along decurrent groove, trichomes short, white or hyaline, 0.05—0.11 (0.13) mm; internode length at midbranch 2—8 (10) mm. ***Leaves*** opposite, rarely subopposite to alternate, sessile to subpetiolate, subcoriaceous, trifid, with broad, obtuse lobes, largest near ends of branches, below infloresecence, (3) 4.6—8.7 (10) by (3) 4—7.2 (8) mm, length to width ratio (0.8) 0.9—1.5 (1.8), ultimate segment (1.5) 1.7—2 mm wide, glabrate to hispidulous, apices obtuse, rarely acute, margins thickened, base attenutate, decurrent, often puncate below, trinervate, nerves prominent abaxially, swollen at node. ***Inflorescence*** appearing solitary, rarely a simple to compound dichasum of 1—6 flowers with opposite branching. ***Pedicels*** (2) 2.3—5.5 (8) mm long, 0.35—0.56 mm in diameter, glabrate to densely hispid, holding fruit pendant, subtended by a leaf-like trifid (rarely linear) bract, bracts usually in opposite pairs. ***Calyx*** gamosepalous, persistent, often tinged red; tube turbinate, glabrous to hispid, rarely prominently nerved, 2—2.6 (3) by (1.5) 1.7—2.7 (3) mm, lobes 5—6 (7), (2.5) 3.1—4.8 (5) by0.4—0.7 (0.9) mm, thin, nerved, linear, rarely linear-oblanceolate or spatulate, apices acute, margins entire, rarely bifid. ***Corolla*** infundibuliform, yellow, outer petals often red in bud, tube 6—7 mm, 1—1.5 mm at base, opening to (3) 4 mm at throat, pilose within; limbs (4) 5 (6), obtuse or rarely mucronate, (5) 6—10 by (3) 3.5—6 (7) mm, glabrous. ***Stamens*** filantherous; filaments adnate 1.6—2.4 (2.6) mm below throat, (4) 4.1—6.2 (7) mm long, glabrous; anthers exserted 1.9—3.4 (4) above throat, (2) 2.1—3.7 (4) by 0.5—1 mm, dorsifixed, latrorse. ***Pollen*** 50 (60) µm. ***Ovary*** bicarpellate, each carpel with a single locule and 4 ovules. ***Style*** (13) 13.2—15.8 (16) mm, glabrous. ***Stigma*** capitate, bilobed, just exceeding the anthers. No definitively mature fruit seen.

Distributed sparsely at high elevations on the Argentina-Bolivia border and southern Bolivia at (2875) 3200—4000 m elevation. With flower or fruit Jan to early Feb.

This high elevation species is poorly known and rarely collected. In the molecular phylogeny, it is closely related to *Menodora integrifolia* but does have unique indels and other molecular characters that make it distinct. Morphologically, it is very similar to the *trifida* forms of *M. integrifolia*, and in larger individuals may in fact be indistinguishable; *Centurión 559* (NY) cited below has the woodier habit of *pulchella*, and similarly obtuse leaf and calyx lobe apices, but is a considerably larger individual than most specimens reviewed, and was collected at a lower elevation; it may represent an intermediate form of *M. integrifolia.*

SPECIMENS EXAMINED:

ARGENTINA: JUJUY: Dpto. Santa Catalina: Quebrada Toquero, 1 km from Bolivian border, Jose Panero 8503 (TEX). **Dpto. Yavi:** Cuesta de Toquero, camino a Santa Catalina., 1/31/1940, A. L. Cabrera 7796 (LP); Quebrada de Toquero, camino a Santa Catalina., 1/25/1948, A. L. Cabrera 9457 (BAB); Cerro Pumahuara.[Cerro Pumahuasi?], 1/28/1948, A. L. Cabrera 9461 (LP); Alrededores de La Quiaca, camino a Sta. Catalina, 1/20/1966, A. L. Cabrera et al. 17631 (CTES); Escaya a La Quiaca., 2/8/1937, Alberto Castellanos s.n. (BA); 17 km W of La Quiaca, on Rt 5, 12 km E of Cienaguillas, 2/1/2000, B. B. Simpson 1-II-00-7 (TEX); Canyon W of La Quiaca on road to Cienegila, 1/3/1979, Barry Hammel 5998 (MO); Cerro Condor, 3/27/1940, T. Meyer & M. Bianchi

34152 (GH); **BOLIVIA: COCHABAMBA**: **Punata:** 6 km al NE de Punata - o 1 km al NE de La Villa, 3/5/1988, Centurión 559 (NY). **TARIJA**: Condorhuássu bei Tarija, 2/6/1904, K. Fiebrig 2984 (NY).

8. *Menodora integrifolia* (Cham. & Schltdl.) Steud.

Nom. Bot. 2nd ed., 2:124, 1841. Basionym: *Bolivaria integrifolia* Cham. & Schltdl., Linnaea 1:208, 1826. Holotype: Cisplatinae Brasilia, *Sellow s.n.* (B), destroyed 1943; Lectotype (designated here): *Brasilia meridionalis*, *Sellow s.n.* (UC!). Isolectotypes: G!, G-DC!, HAL, K! [sheets at G, K give locality as "Brasilia;" HAL gives locality as "Brasilien, prov. Montevideo,"(http://cluster.urz.uni-halle.de:8080/herbarium/jsp/index.jsp, accessed 12/13/2006)]

Bolivaria trifida Cham. & Schltdl., Linnaea 1:209, 1826. Holotype: *Brasiliae provincia Cisplatina, Sellow s.n.* (B), destroyed 1943. Lectotype (designated here): *Brasilia*, *Sellow s.n.* (K!). *Bolivaria chlorargantha* J. Rémy, Ann. Sci. Nat. Bot. III. 8:225, 1842. Holotype: circa Chuquisaca, [December], *D'Orbigny s.n.* (P). *Bolivaria pinnatifida* Schltdl., Linnaea 26:474, 1853. Without type, raised from seed sent from Bolivia, but otherwise lacking provenance. *Calyptrospermum integrifolium* (Cham. & Schltdl.) A. Dietr., Sp. Pl., 6 ed., 1:227, 1831. *Calyptrospermum trifidum* (Cham. & Schltdl.) A. Dietr. Sp. Pl., 6 ed., 1:227, 1831. *Menodora trifida* (Cham. & Schltdl.) Steud., Nom. Bot. 2nd ed., 2:124, 1841. *Menodora integrifolia* var. *trifida* (Cham. & Schltdl.) Kuntze, Rev. Gen. Pl. 3.2: 197, 1898. *Menodora integrifolia* var. *trifida* (Cham. & Schltdl.) Steyerm., Ann. Missouri Bot. Gard. 19:131, 1932, *nom. superfl. Menodora integrifolia* f. *erecta* Arechav., Anales Mus. Nac. Montevideo 7: 61. 1909. Without type. *Menodora integrifolia* f.

subprostrata Arechav., Anales Mus. Nac. Montevideo 7: 61. 1909. Without type. *Menodora hassleriana* Chod. ex Chod. & Hassl., Bull. Herb. Boissier II. 3:915, 1903. Holotype: PARAGUAY: CONCEPCIÓN: In campo humido in regione cursus superioris fluminis Apa, 12/1901, *E. Hassler 8278* (G!). *Menodora pinnatisecta* Steyerm., Ann. Missouri Bot. Gard. 19:133, 1932. Holotype: ARGENTINA: CHACO: Bermejo: Las Palmas, 11/1917, *Pedro Jorgenson 2643* (GH!). Isotypes: A!, LIL! [Label at LIL includes "semi-arbustos, baja, flores amarillas, común en el campo."] *Menodora chlorargantha* (J. Rémy) Steyerm. Ann. Missouri Bot. Gard. 19:156, 1932. *Menodora integrifolia* (Cham. & Schltdl.) Steud. var. *odonelliana* T. Meyer, Lilloa 28:231, 1957. Holotype: ARGENTINA: LA PAMPA: Caleu-Caleu: Río Colorado, 11/21/1944, *C. A. O'Donell 1642* (LIL!). Isotypes: A!, US! *Menodora pinnatisecta* Steyerm. var. *missionum* T. Meyer, Lilloa 28:238, 1957. Holotype: ARGENTINA: MISIONES: San Ignacio: Arroyo Bucre Grande, 2/12/1946, *J. Schwarz 2060* (LIL!). Paratypes: ARGENTINA:MISIONES: San Ignacio: La Plantadora, 2/2/1948, *J. Schwarz 5494* (LIL!); Arroyo Macaco, 4/9/1949, *J. Schwarz 5701* (LIL!). *Menodora integrifolia* (Cham. & Schltdl.) Steud. var. *pinnatisecta* (Steyerm.) Burk., Fl. Ill. Entre Rios 6:56, 1979.

Illustrations: Fl. Bras., 6:1 pl. 85 (Martius, 1868); Lilloa 28:221, 225, 232, 234, figs. 3-6 (Meyer, 1957); Fl. Prov. Buenos Aires 5:19 fig. 9 (Fabris, 1965); Fl. Ill. Prov. Tucuman , 89 (Meyer, 1977); Fl. Ill. Entre Ríos 5:52, 54, figs. 21-22 (Burkart, 1979); Aportes Bot. Salta 2:15: 6, Lám. 1 (Novara, 1994).

Plants fastigiate, occasionally somewhat spreading or twining ***subherbaceous perennials***, (9) 15.2—43.4 (68) cm tall, with a woody taproot, caudex 4—27 mm diameter with few branches. ***Stems*** spreading, more or less erect, branching throughout, rarely remotely, opposite or alternate, the latter generally above midbranch and in the inflorescence; older wood tan to gray to black, atratous, often hispid becoming glabrate with age, rugose, rimose, younger stems green, often tinged red, shallowly to deeply fluted, usually more so on younger stems, canaliculate decurrent groove occasionally well-defined, terete to strongly angled, upper nodes occasionally flattened in cross section, glabrate to hirtellous or hispid, often hispdulous in leaf axils, trichomes rudimentary (often reduced to minute papillae) or very short, white or hyaline, somewhat spreading or ascending, rarely retrorse, (0.02) 0.03—0.05 (0.08) mm; internodes longest near midbranch, (1) 6—17 (26) mm, but quite variable, usually surpassed by the subtending leaves. ***Leaves*** opposite to midstem becoming subopposite or alternate bracts in the inflorescence, rarely opposite nearly throughout or irregularly opposite or alternate, sessile to subpetiolate, submembranaceous, linear to lanceolate or oblanceolate, often variously bifid, trifid, pinnatifid or pinnatisect, these usually below midbranch rarely above or often predominant throughout, entire leaves (3) 8.4—27.5 (60) by (0.5) 1.1—5.3 (12), length to width ratio (2.6) 3.6—9.4 (16.9), lobed leaves (2) 8.4—23.4 (45) by (1.5) 5.5—18 (30.86) mm, length to width ratio (0.7) 1—2 (3), width at departure of lowest lobes (0.63) 0.9—3.4 (6.85) mm, usually punctate, especially below, rarely hispidulous above or at base, rarely pilose along nerve below, apices acute, acuminate, obtuse, mucronate or apiculate, margins thickened, entire or if lobed, often with a few smaller dentiform lobes, base attenuate or cuneate, decurrent, uninervate or pinnanervate, nerves prominent abaxially, laterals less so, swollen at node. ***Inflorescence*** a compound dichasium of 1—30 flowers, lowest branches often opposite but becoming alternate, rarely opposite throughout or appearing solitary. ***Pedicels*** 1—9.7 (25) mm long, 0.4—0.6 (0.7) mm in diameter, glabrous to hirtellous, holding fruit erect, subtended by a linear to linear-lanceolate or linear-oblanceolate, rarely broader or trifid, glabrous to sparsely hispidulous, punctate bracteiform leaf. ***Calyx*** tube turbinate, prominently nerved, glabrous to hispidulous; lobes hispidulous, often punctate, at least on internal faces, (1) 1.7—2.3 (2.9) by (1) 1.4—2.4 (4) mm, broadening in fruit to (1.7) 2.8—3.8 (4.8) mm; lobes (4) 5—6 (9), (2) 2.8—5.2 (8) by (0.3) 0.4—0.8 (1.2) mm, thin, prominently nerved, linear or subulate-deltoid, rarely oblanceolate, adjacent lobes rarely fused, apices acute, margins entire. ***Corolla*** infundibuliform, yellow, outer petals occasionally red in bud, tube (2) 3.2—5.6 (7) mm, (0.5) 0.7—1.1 (1.5) mm at base, opening to (1.5) 2.2—3.4 (4.4) mm at throat, glabrous or pilose within; limbs (4) 5 (7), obtuse, acute or mucronate, (2.9) 4.4—7.6 (10) by (1.5) 2—3.4 (5) mm, glabrous. ***Stamens*** 2, rarely 3, filantherous, epipetalous, rarely as 2—3 petaloid appendages; filaments adnate inserted 1—2.1 mm, (1.7) 2—4.2 (5.5) mm long, glabrous; anthers exserted ca 0.8—3 (4) mm, (0.9) 1.3—2.1 (3) by (0.3) 0.4—0.6 (0.9) mm, occasionally with a conical or linear process extending above the connective, dorsifixed, latrorse. ***Pollen*** (0.04) 0.05—0.07 (0.09) mm. ***Ovary*** bicarpellate, bilobed, each carpel with a single locule and 4 ovules. ***Style*** (4.5) 5.8—10.1 (16) mm, glabrous. **Stigma** capitate, bifid, equalling or just exceeding the anthers. **Fruit** with cocci globose or obovoid, rarely ellipsoidal, circumscissile, glabrous, (4) 4.9—6.1 (7) by (2.6) 4.1—5.7 (7) mm in diameter; pericarp thin, membranaceous, more or less translucent; each coccus containing 2—4 seeds, fewer by abortion. ***Seeds*** elliptic to obovate, trigonal, rarely lenticular or plano-convex, (3.3) 4—4.9 (5.4) by (2) 2.5—3.4 (5) by (0.8) 1—1.6 (2) mm, testa finely to coarsely and regularly reticulate, with a prominent adaxial rib.

Widespread in South America east of the Andes from central Bolivia south to northern Patagonia (Río Negro and Chubut) in Argentina, southwestern Brazil, Uruguay, and

Paraguay, from (20) 70—2600 (3300) m elevation. Flowering (Sep) Oct to Mar (through May), in fruit (Sep to Oct) Nov to Apr (through Jul).

Menodora integrifolia is the most widespread species of the genus in South America. It is also one of the most plastic and variable species in the genus, with a wide range of variation found in a number of characters, including the basic habit of the plants, the shape of the leaves, and flower size; evidence for this can be seen in the long list of synonyms given above. Variation in the leaf shape has been the major character upon which species or varieties have been formally recognized. This variation falls into three morphological varieties: *integrifolia* (unlobed, entire leaves), *trifida* (trifid leaves; most recently restored by Correa (1999) to species, but including var. *odonelliana*) and *pinnatisecta* (pinnatisect leaves; including the larger ones of variety *missionum*). In a molecular phylogeny of the genus (see previous chapter), all of these types fell into a single, poorly resolved clade, with neither a morphological nor geographic pattern to groupings within the clade.

While there is a more or less geographic pattern associated with the varietal variation, there is also quite a bit of intergradation, making determinations to variety often problematic. This is particularly true of the region between and adjoining the Ríos Uruguay and Parana where the *integrifolia*, *pinnatisecta*, and *trifida* “varieties” can all be found, occasionally even on the same individual. It is not uncommon to find a pinnatisect form that gives way to large, *integrifolia*-type leaves or bracts above, or a *pinnatisecta* or *integrifolia* that sports a single branch of *trifida*-type leaves. West of the Paraná in Argentina, the dominant varietal form is *trifida*, but it is not uncommon to find individuals of only unlobed, entire leaves of the *integrifolia* type, particularly from Tucuman north into Bolivia.

The problem of recognizing the varieties is complicated by consideration of some of the types as well. Both *integrifolia* and *trifida* were collected by Friedrich Sellow prior to 1826, and though without exact locality or date, were probably collected in modern Uruguay (Burkart, 1979). Both types were presumably at Berlin, and were destroyed by fire in 1943. Isotypes of *integrifolia* were fairly widely distributed (G, K, UC, HAL) but for *trifida*, the only Sellow collection I've seen is at Kew. This bears little resemblance to the common trifida form, however, and is referable in my opinion to the var. *missionum* form described by Meyer.

After much deliberation over the nature and range of morphological variation in this species group, and consideration of the complete lack of varietal or geographic clustering in the molecular phylogeny, I have decided to dispense with varieties in favor of a single variable, polymorphic species without distinct infraspecific entities.

SPECIMENS EXAMINED:

ARGENTINA: BUENOS AIRES: Baradero, alto de la barranca, 11/19/1937, Burkart 8494 (MO); La Pantanosa-Rio Negro, Carmen de Patagones, 2/1/1898, C. S. s.n. (LP); Cerro de la Peregrina, 20 km N of Mar del Plata, road to Balcarce, 12/11/1938, Eyerdam et al. 23653 (G); Olgarrobo, 12/1/1964, Fasus 5663 (CTES); Pampas a Buenos Ayres, 10/30/1829, Gillies s.n. (GH). **Partido de Coronel Suárez:** Estancia El Lolén, 12/12/1979, Pertosi 88 (CTES); Villa Arcadia, en cerros próximos al arroyo Sauce Corto. Balneario Los Angelitos, 1/13/1999, Seijo 1402 (CTES, GH); **Partido de Villarino**: Cerca de Cardenal Cagliero, 11/20/1962, Cabrera & Fabris 14862 (LP); Estancia Los Guanacos, 12/1/1964, Fabris 5642 (LP); Oljarroso, 12/1/1964, Fabris 5663 (LP). **Partido de Zárate:** Lima, barrancas del rio Paraná de las Palmas, 3/14/1976, Cabrera & Troncoso 27627 (SI); Zaráte. En la barranca del rio Paraná, 2/10/1947, Krapovickas 2855 (MO);

Lima, 12/8/1982, Múlgara et al. 328 (US). **CATAMARCA: Ambato:** Los Vorela. Area de clausura 0.5 km N de entrada de Los Varela, frente a entrada de Chuchucaruana, 3/21/1995, Toledo et al. 12768 (CTES); La Rinconada, 9 km S de Los Vorela. Sierra de Graciana, 3/27/1995, Toledo et al. 12849 (CTES). **Ancasti:** El Cajón, 4/18/1950, Brizuela 1278 (LIL); La Higuerita. [Ayajasco?], 3/28/1950, Brizuela 1069 (NY, UC); La Brea, 4/20/1950, Brizuela 1333 (LIL). **Andalgala:** Choya y Lomas, 1/7/1907, Castillón 553 (LIL). **Capayán:** Miraflores, 1/14/1947, Brizuela 111 (LIL); Quebrada de la Cebile, 3/2/1985, Kiesling et al. 5908 (SI). **Capital:** El Jumeal, 2/7/1975, Ulibari 898 (CTES, SI). **La Paz:** El Portillo Chico, 3/8/1947, Brizuela 1000 (LL); Ramblones, 12/23/1946, Brizuela 466 (LIL); La Paz: Alta, 1/15/1947, Brizuela 683 (NY); El Lindero, 2/28/1947, Brizuela 876 (TEX, UC); Puerto Pilimón, 1/26/1947, Brizuela 185 (LIL); Portillo Chico, 2/5/1950, Brizuela 685 (LL); El Aropaco, 4/5/1950, Brizuela 1020 (LIL); La Huerta, 4/24/1947, Brizuela 1157 (LIL); Mil Ocho, 4/24/1947, Brizuela 1231 (LIL); San Nicolás, 12/2/1949, Brizuela 142 (LIL); Quebracho Colorado, 1/12/1950, Brizuela 376 (LIL); El Aibal, 2/6/1950, Brizuela 740 (LIL); Icaño, 5/8/1950, Sopaga 18 (LIL). **CORDOBA:** Monte (flat) NE of Dean Fumes, 6/18/1943, Bartlett 20488 (MICH); 20 km al E de Taninga, 12/6/1957, Boelcke 7749 (CTES); Embalse Rio Tercero, 1/12/1940, Burkart 10381 (MO, SI); Taninga a los Túneles, 12/6/1958, Burkart 20867 (SI); Sierra Chica: Gastancia: La Reducción, 1/1/1936, Burkart 7422 (K); Sierra de Olta, Rodeo Grande, 2/7/1940, Castellanos 33816 (LIL); Cosquín, 2/10/1950, Cuezzo & Balegno 2098 (LIL); Rio Leballos, Sierra chica de Córdoba, 2/1/1878, Galander s.n. (K); Ascochinga, 10/20/1936, Giardelli 495 (SI); Alta Gracia, 1/12/1940, Hunziker 586 (LIL); La Falda: alredodores, 1/15/1936, Job 521 (LP, NY); Córdoba, 11/4/1891, Kuntze s.n. (NY); Lossen 305 (GH); San Esteban, Nicora 1570 (SI); Charbonier, 1/22/1941, Nicora s.n. (SI); San Marcos, 1/23/1941, Nicora s.n. (SI); San Marcos, 2/16/1941, Nicora s.n. (SI);

Santa María, 11/20/1947, Ragonese-Picinini 6139 (LIL); Capilla del Monte, camino al Zapato, 7/20/1935, Rodrigo 223 (LP); Qosquin, loma sobre "la Foma.", 2/1/1936, Rodrigo 334 (LP, NY); Valle de la Punilla: La Falda, 2/22/1947, Rossi 947 (LIL); Bella Vista, 3/28/1944, Ruiz de Huidobro 258 (UC); Pueblo Güemes, 4/7/1944, Ruiz de Huidobro 410 (NY, UC); Río IV, 12/9/1905, Stuckert 15235 (LIL); Alta Córdoba, 11/8/1896, Stuckert 609 (LIL). **Calamuchita:** La Cruz, 2/21/1947, Gutierrez 110 (TEX); Dolores, 1/8/1938, Nicora 1663 (SI); Villa Dolores, 3/25/1947, Terribile 691 (LIL). **Capital:** Barrio San Martin, 3/17/1944, O'Donell & Rodriguez 337 (A); Cerro de las Rosas, 6/7/1946, Pierotti 5129 (LIL); Barrio Perezoni, 3/24/1944, Ruiz de Huidobro 289 (LIL); Parque Sarmiento, 3/19/1947, Terribile 650 (LIL). **Colón:** Between Ascochinga and La Cumbre, Sierra Chica, 12/13/1938, Goodspeed 23236 (GH, UC); La Reducción, 12/15/1946, Gutierrez 28 (LIL). **Córdoba:** Mendiolaza, 3/16/1944, Ruiz de Huidobro s.n. (A). **Cruz del Eje:** Serrezuela, Punta de Sierra, 11/7/1945, Cuezzo 908 (MO, NY). Cruz del Eje, 12/20/1947, Meyer 12890 (LIL). **Ischilín:** Desvío km 832, 2/3/1951, de la Sota 3796 (LIL); Quilino, 12/16/1947, Meyer 12987 (GH); Avellaneda a km 827, 12/27/1947, Meyer 13181 (CTES); Quilino km 685, 12/17/1947, Meyer 13563 (CTES); Quilino, 4/3/1944, O'Donell & Rodriguez 385 (A); Los Tártagos, 3/31/1944, O'Donell & Rodriguez 649 (LIL); Ojo de Agua, 11/15/1971, Pederson 9917 (K); Villa Quilino, 11/14/1950, Ragonese & Caso 7437 (CTES); Quilino, 12/17/1946, Villafañe 80 (US). **Pocho:** Entre Taninga y Alta del Tala, 12/6/1958, Leal & Roig 19965 (MERL). **Punilla:** On gravel road 0.9 rd km NE of jct with Ruta Nacional 38 (km 47-48) near Arroyo Vacqueria, ca 1.2 km S of Valle Hermosa, 12/23/2001, Chumley et al. 7381 (TEX); Charbonier, 11/26/1948, de la Solta 445 (LIL); San Salvador, 1/24/1951, de la Sota 4094 (LIL); Between Cosquín and Bialet Massé, 11 km N of turning to Tanti, 1/24/1966, Hawkes et al. 3307 (MO); Valle Hermoso, 3/20/1944, Ruiz de Huidobro 140 (LIL); Los

Coces, 1/24/1947, Villafañe 526 (LIL); **Río 1e:** Río 1e, 12/9/1946, Balegno 990 (MO). **Río Seco:** Villa de Maria, 12/18/1947, Balegno 1424 (LIL). **San Alberto:** [Villa] Cura Brochero, 2/2/1948, Meyer 13519 (LIL). **San Francisco de Chañar:** San Fco. de Chañar, 12/6/1944, Balegno 322 (NY). **San Justo:** Balnearia, 12/18/1946, Balegno 1094 (LIL). **Tercero Abajo:** Tio Pujio, 4/8/1950, Krapovickas 6650 (LIL, SI). **Totoral:** Las Peñas, 2/6/1951, de la Sota 3726 (LIL). **Tulumba:** Tulumba, 11/3/1945, Cuezzo 778 (LIL); Tulumba, 2/4/1951, de la Sota 4199 (LIL); Dean Funes a Sauce Punco, 12/15/1947, Meyer 13476 (LIL). **CHACO:** Colonía J. Larrea, 9/25/1972, Bordón 61-E10 (CTES); Ruta 94 de Las Breñas a R. Saenz Peña, a +/-2 km de ruta 16, 11/12/1980, Legname et al. 7575 (MO); San Lorenzo. En depto. Guemes, Impenetrable, puesto Albornoz. Clausura Tocta, 4/12/1972, Schulz 18093 (CTES); Enrique Urien, 11/1/1945, Schulz 806 (NY). **12 de Octubre:** 14 km W de General Pinedo, Ruta 94, 12/29/1970, Krapovickas & Cristóbal 17329 (CTES); **Bermejo:** Dpto. Bermejo. Ca 2 air km SE of Las Palmas, 12/16/2002, Chumley et al. 7414 (TEX); Las Palmas, 2/1/1917, Jorgensen 2643 (A); Las Palmas, 2/1/1917, Jorgensen 2643 (GH); Las Palmas, 11/1/1917, Jorgensen 2643 (LIL); **Campo del Cielo:** [General] Capdevila, 12/15/1946, Schulz 977 (LIL); **General Pinedo:** Estancia San José, 8/8/1960, Schulz 11267 (CTES); General Pinedo, 3/15/1955, Schulz 8934 (CTES); General Pinedo, 8/27/1968, Schulz 16371 (CTES). **Nafralju:** Napalpi: Corzuela, 1/19/1947, Buratovich 935 (NY). **Primero de Mayo:** Margarita Belén, 10/11/1945, Aguilar 415 (MO); On paved road to Colonia Benítez ca 0.5 km E of Ruta Nacional 11, 12/16/2002, Chumley et al. 7411 (TEX); In Margarita Belén, on road to Isla Cerrito, 12/16/2002, Chumley et al. 7412 (TEX); On road to Colonia Benítez ca 7 air km E of Margarita Belén, ca 3 rd km NE of jct with road to Riacho Iné, 12/16/2002, Chumley et al. 7413 (TEX). **Resistencia:** Resistencia, 12/17/1916, Arribalzaga 45 (LIL); Colonia Benitez: Reserva Biológica E.E. Agrop, 3/25/1969, Carnevali 1335 (CTES); Cacuí, 12/5/1950, Meyer 16403 (LIL); Fontana, 4/1/1937, Meyer 3063 (LIL); Rio Arazá (FCSF), 5/17/1945, Meyer 8591 (K); Tirol, 5/21/1945, Meyer 8609 (LIL); Colonia Benitez, 1/4/1942, Schulz 1867 (CTES); Colonia Benitez: Paraje: Est. Exper. INTA portion tracc. Sangre, 1/22/1960, Schulz 10942 (CTES); Colonia Benitez, 10/1/1931, Schulz 214 (SI); Colonia Benitez, 12/1/1952, Schulz 8382 (CTES); Colonia Benitez, 11/1/1933, Schulz 860 (CTES, NY). **Tapenagá:** Cote-Lai, 12/30/1942, Meyer 5515 (LIL). **CHUBUT:** Sierra de la Ventana, Spegazzini 1881 (SI). **CORRIENTES:** Arroyo Yuquerí (Aguirre) centro de la prov. Corrientes, 10/5/1886, Niederlein 1024 (BA). **Capital:** 12 km al SE de Corrientes, camino a S. Luis, Ruta 5, 4/3/1974, Arbo & Schinini 536 (CTES); Corrientes, Bonpland s.n. (NY); Ca 19 km E of Corrientes on road to Santa Ana, ca 1 km S of jct with Ruta Nacional 12, 12/14/2002, Chumley & Thien 7409 (TEX); Perichón, 12/1/1975, Crovetto 10173 (CTES); Ciudad de Corrientes, 3/1/1902, Hicken 26 (SI); Molina [Molino] Punta, 12/26/1965, Krapovickas & Cristóbal 11767 (CTES, UC, US); Ciudad de Corrientes, 1/26/1944, Meyer 5897 (LIL); 15 km al E de Corrientes, camino a S. L. del Palmar, Ruta 5, 12/6/1975, Quarín 3228 (CTES). **Cosme:** Sta. Ana, Corpus, Bonpland s.n. (P). **Curuzú Cuatiá:** 5 km SE de Curuzú Cuatiá , 3/10/1985, Cáceres & Zamudio 301 (CTES); Arroyo Mocoretá, 11/29/1940, Castellanos s.n. (BA); 10 km N de Curuzú Cuatiá, 10/10/1977, Cristóbal et al. 1655 (CTES, MO); Curuzú Cuatiá, 11/29/1944, Ibarrola 1521 (LIL); Curuzú Cuatiá (cercanias), 3/2/1945, Ibarrola 2539 (NY); Ruta 14 km Ca. 685, 12/12/1957, Pederson 4694 (G, NY, P, UC, US); Near Perrugoria, 3/23/1967, Pederson 8111 (A); Ruta 24, 6 km NE de Perrugoria. Ea. La Eugenia, 3/9/1995, Schinini et al. 29211 (CTES); Ruta 119, 47 km S del acceso a Mercedes, 2/20/1974, Tressens et al. 2225 (CTES, MCNS); Ruta 12, 17 km E de Paso López, 10/30/1974, Tressens et al. 546 (CTES, GB). **Empredado:** Along Ruta Provincial 9 ca 1 km S of Arroyo Empredado, ca 33 air km NE of Empredado, 12/15/2002, Chumley & Thien 7410 (TEX). **Esquina:** 26 km SE de Libertador, Estancia La Blanca, 3/12/1975, Krapovickas 27412 (CTES); 4 km S de Ruta 126, camino de Tres Bocas a Paso Yunque, 3/13/1975, Krapovickas 27655 (CTES); 47 km W de Sauce, Ruta 126, 10/23/1977, O. Ahumada et al. 1471 (CTES). **General Paz:** Lomas de Vallejos: Rincón de Vences, 10/21/1945, Ibarrola 3582 (LIL). **Goya:** Paraje Invernada, 11/13/1969, Carnevali 3324 (CTES). **Ituzaingó:** Puerto Luján, 1/1/1990, Heinonen 266 (CTES); 15 km E de RN 12, camino a San Carlos, 2/12/1971, Krapovickas et al. 18143 (CTES); 11 km N de San Carlos, 4/11/1974, Krapovickas et al. 25004 (CTES); Ea. Santa Rita, Ayo. próximo al casco, 3/2/1987, Krapovickas et al. 41010 (A, CTES). **Mburucuyá:** Estancia Sta. Teresa, 2/12/1958, Cristóbal et al. 224 (CTES); Campo "Dios Gracia.", 1/19/1951, Pederson 956 (US). **Mercedes:** Felipe Yofre. Ca 0.5 km N of Yofre, 12/17/2002, Chumley et al. 7415 (TEX); Ea. Cuenca, Yofre, 11/16/1989, Fernandez 1075 (CTES); Pueblo Mercedes al Norte, 3/16/1945, Ibarrola 2670 (UC); Yofré, 3/22/1945, Ibarrola 2701 (A, NY); Ayo. Medina desde Ruta 23 y San Roquito, 1/5/1975, Irigoyen & Schinini 186 (CTES); Mercedes, 2/7/1925, Millán 343 (BA); Mercedes, 2/7/1925, Parodi 6236 (GH); Mercedes: Alrededores, hacia el Norte, 11/1/1936, Rodrigo 820 (LP, NY); Ruta 23, 20 km E de Mercedes, 10/29/1973, Schinini 7561 (CTES); Ayo. Pay Ubre Grande y camino a Itá Corá, 2/21/1984, Tressens et al. 2292 (CTES, MICH). **Monte Caseros:** Mocoretá, 4 km al sud, 2/13/1945, Ibarrola 2395 (NY). **San Cosme:** Vivero Forestal Paso de la Patria, 3/3/1972, Carnevali 2901 (CTES). **Santo Tomé:** Dos leguas norte de Santo Tomé, 11/20/1944, Ibarrola 1521 (LIL); Estancia Garruchos, cachuera, ayo. Chimeray, 2/6/1972, Krapovickas et al. 21140 (CTES); Ea. Timbó, Portrero Luna, 12/5/1981, Tressens et al. 1653 (CTES); Garruchos, costa río Paraguay, 2/11/1993, Tressens et al. 4392 (CTES, TEX). **Sauce:** Arroyo Sauce, 12/22/1976, Ferraro 1009 (CTES, SI); Chacra el Timbó, 3 km N de Sauce, 10/22/1977, O. Ahumada et al. 1315 (CTES). **ENTRE RIOS:** Concepción del Uruguay, cerca parque Unzue, 4/19/1965, Burkart 25770 (MICH); Concepcion del Uruguay, 4/15/1880, Lorentz s.n. (P). **Colón:** Parque Nacional El Palmar, 2/18/2000, Batista et al. 2327 (CTES); Palmar, a 13 km E de R14, barrancas del rio Uruguay hasta el arenal, 1/17/1976, Romanczuk 32 (SI). **Diamante:** Diamante, 12/15/1960, Burkart 22262 (CTES, NY, US); Diamante, sobre las barrancas, 12/20/1963, Gamerro 1334 (LP). **Federación:** Arroyo Tunas, 4/14/1960, Burkart & Gamerro 21858 (CTES); Route 14, 2 km S de la limite avec la prov. Corrientes et Le Rio Mocoreta. Champ sec, 11/6/1973, Goodall & Tirel 284 (P); Estancia "Buena Esperanza.", 10/21/1961, Pederson 6222 (A, US); Ruta 14 al N Chajari Pelador, 1/21/1977, Troncoso et al. 1691 (SI). **La Paz:** La Paz, 11/16/1989, Burkart & Bacigalupo 21332 (CTES). **Paraná:** Paraná, cerca camino La Toma, 11/2/1962, Burkart 23774 (K); Paracao, 10/31/1962, Burkart et al. 23773 (NY, SI); Hernandarias, Pto. Vibora, 12/5/1986, Guaglianone et al. 227 (NY, SI); San Benito, 12/1/1946, Huidobro 3577 (MO); Paraná, 10/25/1946, Meyer 10014 (LIL). **Uruguay:** Río Gualeguaychú, 12/27/1941, Nicora 3247 (SI, LIL). **Villaguay:** Alrededores de la ciudad de Villaguay, costa del Ao. Villaguay, 2/16/1985, Bottino 270 (MERL). **JUJUY:** Estes Hacienda, 40 km S of Jujuy, 10/5/1938, Eyerdam & Beetle 22428 (UC, GH). **Capital:** Camino al Cadillal, 11/17/1978, Cabrera et al. 29944 (SI). **El Carmen:** Pampa Blanca, 3/1/1963, Cabrera et al. 15553 (LP); Ruta 66 camino a San Salvador de Jujuy, a 500 m empalme ruta 34, 3/12/1986, Guaglianone et al. 1795 (SI). **Perico del Carmen:** Perico del Carmen, 11/18/1975, Sciavone et al. 11749 (CTES). **San Pedro:** San Pedro, 5/10/1948, Krapovickas 4771 (CTES); San Pedro de Jujuy, 10/20/1930, Venturi 10574 (US). **LA PAMPA:** A 86 km de San Martin, Leal 26281 (MERL). **Caleu-Caleu:** Comisaría de Rio Colorado, Caleu-Caleu, Gobernación de La Pampa, 4/15/1943, Bartlett 19945 (MICH, US); Rio Colorado, 11/21/1944, O'Donell

1642 (A, LIL, US); Anzoáteguy, 11/24/1944, O'Donell 1702 (LIL). **Lihuel Calel:** Sierra de Lihuel Calel, 11/6/1972, Krapovickas et al. 22583 (MO). **Loventue:** Victoria: Ea. "Las Vertientes," próximo a Cerro Quemado, 2/1/1960, Legaspi s.n. (CTES). **Utracan:** Entre General Acho y Gamay, 12/1/1959, Bacigalupo s.n. (SI). **LA RIOJA: General Belgrano:** Dique de Olta (5 km a W de Olta). Aledaños de espejo de agua, 6/16/1977, Biurrun 865 (CTES); Dique de Olta. Aledános del lugar de ingreso de río Olta, 11/19/1998, Biurrun & Molina 5435 (CTES); RN 38, entre Chamical y Chañar, a 20 km de la primera. Campo Experimental Las Vizcacheras (INTA). Potrero El Quebrachal sector sur, 6/4/1999, Biurrun et al. 6112 (CTES); Olta, 4/16/1955, Leal 17236 (MERL); Ruta Nacional 38 entre Chamical y Chañar, km 267. Paraje llamado "la Llanura" Campo Exp. del INTA, 11/25/1989, Leguiza & Andrada 34 (CTES). **General Ocampo:** Milagro, 12/11/1944, Varela 771 (A); Milagro, 12/11/1944, Varela 773 (A, US). **Gobernador Gordillo:** Chamical, immediaciones del Tira Federal, 2/16/1977, Biurrun 639 (CTES); A 5 km de E ciudad. "Bajito Honda" a 500 m de la entrada, cerca de aguada, 6/6/1999, Brizuela et al. 12 (CTES); Gobernador Gordillo [Chamical], 3/13/1942, Nicora s.n. (SI); Chamical, camino a San Javier, 4/9/1975, Roig & Méndez 8645 (MERL). **Rosario Vera:** General Roca: Chepes, 10/10/1945, Cuezzo 1012 (LIL). **MENDOZA: La Paz:** Desaguadero, immediaciones del Paso de los Tropas, 2/17/1944, Leal 8777 (HRL); Immediaciones del Rancho de Totora, 4/9/1944, Leal 9040 (HRL); Camino a La Paz, 1/26/1939, Troncoso 6042 (SI). **MISIONES: Apóstoles:** Apóstoles, 11/30/1943, Burkart 14458 (SI); Apóstoles, Ruta 14, 2/13/1978, Cabrera & Saenz 29169 (SI); At km 31 on Ruta Nacional 105, ca 4 km N of San Jose, 12/18/2002, Chumley et al. 7420 (TEX); 4 km N de San Jose, 3/20/1983, Cristóbal et al. 1903 (CTES). **Cainguás:** Campo Grande, 5/11/1950, Schwindt 4414 (LIL). **Candelaria:** Cerro Corá, 1/7/1946, Bertoni 2592 (LIL); Loreto, 12/19/1981, Cabral et al. 318 (CTES); Posadas, Bonpland, in lapidosis, 12/26/1907, Ekman 1949 (NY, US); Bonpland, 12/12/1909, Jorgensen & Hansen s.n. (CTES); Loreto, 1/20/1972, Krapovickas & Mroginski 20760 (CTES); Cerro Corá, 3/8/1969, Krapovickas et al. 14952 (CTES); Santa Ana, 10/30/1945, Montes 1242 (GH); Loreto, 11/21/1950, Montes 15222 (SI); Loreto, 11/12/1944, Montes 357 (NY, SI); [Colonia] Yabebiry, 4/19/1945, Montes 772 (NY); Loreto, 7/5/1944, Montes 88 (LIL); Santa Ana, 12/2/1946, Schwarz 3526 (GH, UC); Alma Fuerte, 3/8/1945, Schwarz 784 (NY), UC). **Capital:** San José, Arroyo Pindapoy, 12/28/1944, Sesmero 265 (LIL). **Concepción de la Sierra:** Ruta 2, camino de Concepción de la Sierra a Sta. María, 2/9/1996, Morrone et al. 570 (SI). **Guarani:** Bana Pepiréguazu, 12/12/1949, Montes 7240 (SI); Ruta 14, km 252 (próximo arroyo Chafariz), 1/25/1950, Schwindt 3120 (LIL); Ruta 14, km 304 (próximo arroyo Chafariz), 3/1/1950, Schwindt 3313 (LIL). **Iguazú:** Puerto Esperanza, km 12, 10/18/1950, Montes 9457 (LIL); Eldorado (Zona Schwelm), 10/5/1949, Schwindt 2248 (LIL). **San Ignacio:** Sto. Pipó, 9/6/1950, Diem 1572 (SI); 15 km E de Ruta 12. Próximo a arroyo Las Dunas, 11/19/2000, Keller 394-B (CTES); Teyucuaré, 3/18/1952, Montes 15569 (LIL); Gobernador Roca, 11/15/1947, Schwartz 5187 (LIL); Estero Leiva, 4/8/1946, Schwartz 2212 (LIL); Arroyo Bucre Grande, 2/12/1946, Schwarz 2060 (LIL); La Plantadora, 2/2/1948, Schwarz 5191 (LIL); Colonia Ñacanguazú, 1/26/1948, Schwarz 5458 (GH); Arroyo Macaco, 4/9/1948, Schwarz 5701 (LIL). **San Pedro:** Monte Carlo, 2/18/1949, Schwindt 1060 (LIL); San Pedro a Tobuna (Ruta 14), 4/24/1950, Schwindt 4045 (LIL). **NEUQUEN: Confluencia:** Neuquén, 12/4/1944, O'Donell 1887 (LIL). **RIO NEGRO:** Umgelung von Leones am Rio Larice chico, 5/4/1879, Lorentz s.n. (K); Rio Negro, 2/1/1946, Scala s.n. (LP); Rio Negro, Rio Negro, 2/1/1916, Scala s.n. (NY). **Avellaneda:** Choele-Choel, San Blás, 2/1/1912, Garbers s.n. (LIL); 50 km al SE de Choele-Choel sobre ruta 250 a Conesa, 12/18/1967, Leal 25522 (MERL). **General Conesa:** Region Conesa y Rincón de Palo, 1/1/1916, Scala 56 (SI). **General Roca:** Vicinity of General Roca, Rio Negro, 9/1/1914, Fischer 221 (GH, MO, NY); Rio Negro F.C.S, 12/29/1914, Fischer 221 (SI, US). **Pichi Mahuida:** Cnel. E. Bustos, ruta 22 km 879, 2/11/1948, Boelcke & Serrano 3061 (SI); 10 km S of town of Rio Colorado, 12/18/1938, Eyerdam et al. 23553 (GH, MO, SI, UC). 80 km al W de Rio Colorado, 12/18/1967, Leal 25509 (MERL); Rio Colorado, 11/20/1944, O'Donell 1609 (LIL). **San Antonio:** Sierra Grande. On open ground at western edge of Sierra Grande, ca 0.5 km W of old mine, 12/26/2002, Chumley 7424 (TEX); 6 km al N del camino a 15 km al NE de a Geotécnica, en direc. a Sa. Pailemán, 12/12/1994, Fortunado et al. 4745 (NY, US). **SALTA:** Camino Cuesta del Arca - Trancas, C. S. s.n. (LP). **Anta:** Tacui, 45 km ak sur de Macapillo limite con Santiago del Estero, 5/6/1991, Novara & Tercuel 10290 (MCNS); Finca San Javier, 6/21/1974, Parada 164 (MCNS). **C. Pellegrini:** Cerro del Remate, 12/8/1927, Venturi 5659 (US). **Caldera:** Estes Hacienda, 40 km S of Jujuy, 10/5/1938, Eyerdam & Beetle 22428 (G); [La] Calderilla (camino de Salta a Jujuy), O'Donell 4936 (LIL). **Candelaria:** El Datíl, 2/7/1949, Montenegro 370 (LIL); Ruiz de los Llanos, 1/28/1947, O'Donell 4334 (GH, TEX, UC, US); Ruiz de los Llanos, 1/1933, Schreiter s.n. (A), 68614 (UC); **Capital:** Cerros General Velez. On gravel road ca 1.4 km E of Universidad Catolica, ca 15 km N of Salta, 12/27/2001, Chumley et al. 7382 (TEX); Cerro de 20 Febrero, 3/16/1982, de Varela 148 (MCNS); La Merced, 2/26/1949, Legname 461 (LIL); Salta, 2/3/1949, Montenegro 231 (LIL); Los Tres Cerritos, 2/4/1949, Montenegro 280 (LIL); La Lagunilla, 5-6 km al E del Cerro San Bernardo, 10/23/1988, Novara 8134 (MCNS); Finca La Candelaria. Paso Los Lapaches, 3 km al este de Chachapoyas, 1/12/1990, Novara & Bruno 9353 (MCNS); Sierras de Vélez: cerros 3-4 km al E de Universidad de Católica de Salta, 500 m ak S dek camino que conduce a La Lagunilla, 1/25/1997, Tolaba 78I (CTES, MCNS). **Chicoana:** Los Los, 2/16/1948, Filipovich 422 (LIL). **General Güemes:** Campo Santo. Güemes, 4/3/1945, O'Donell 2638 (NY); Campo Santo. Antes de Cabeza de Buey, 1/29/1947, O'Donell 4368 (LIL). **La Viña:** On Ruta Nacional 68 ca km 136, south side of roadcut between Arroyo Osma and town of Osma, 12/30/2001, Chumley et al. 7383 (TEX); Talapampa, 4/16/1908, Lillo 8083 (LIL); Las Moras. Ruta 68 km 144. Fin de cultivos sobre de Lineamiento El Toro, 11/3/1988, Novara 5615 (MCNS); Adyacencias del Dique Puerta de Diaz, 4-6 km al oeste de Coronel Moldes, 12/6/1987, Novara 7244 (MCNS); Castañares, ferrocarril abandonado entre La Viña y Guachipas, 2/22/1990, Novara & Bruno 9569 (MCNS); Osma: Ruta Nac. 68 km 136, entre El Carril y Coronel Moldes. Lomadas al E del camino, 10/7/2000, Tolaba 2693 (MCNS). **Metán:** Joaquín V. González, 1/19/1945, Aguilar 246 (LIL); Joaquín V. González, 1/30/1945, Aguilar 310 (NY, UC); 14 km WNW de El Tunal. Orilla del río Juramento, 4/4/1980, Krapovickas & Schinini 35728 (CTES); El Rincón, 5/19/1949, Luna 1495 (LIL). **Rosario de la Frontera:** Rosario de la Frontera, 2/20/1947, de la Solta 1252 (LIL); Rosario de la Frontera, al sur. Paraje: Ruta 55 hacia Ruiz de las Llanos, 1/28/1947, Schulz 6553 (CTES); Los Baños, 11/7/1927, Venturi 9190 (US). **SANTIAGO DEL ESTERO:** Between Forres and Robles, Ferrocarril Central de Argentina, 3/23/1943, Bartlett 19729 (MICH), US); Sol de Julio, Ferrocarril Central del Argentina, 3/24/1943, Bartlett 19789 (MICH); Bandera, 8/1/1973, Insfrán 873 (CTES); La Banda, 4/14/1907, Lillo 6077 (NY). La Banda, 3/27/1907, Lillo 6078 (GH); Los Herreros, 4/4/1913, Monetti s.n. (MO, NY). **28 de Marzo:** Anatuya, 11/8/1946, Huidobro 31112 (TEX); Coronel Barros, 11/11/1946, Huidobro 3133 (UC, NY). **Alberdi:** Campo Gallo, 4/4/1945, Farhat 54 (LIL). **Avellaneda:** Colonia Dora, 11/12/1945, Farhat 109 (LIL). **Capital:** La Dársena, 11/19/1947, Meyer 12745 (UC). **Guayasán:** Campo Verde, 6/9/1943, Bartlett 20420 (GH, MICH, NY, UC, US); San Pedro, 1/26/1949, Montenegro 193 (LIL); Villa La Calera, 4/6/1944, Pierotti s.n. (LIL); El Cevilar, 3/13/1944, Pierotti 26 (LIL). **Leales:**

Chañar Pozo, 10/1/1919, Venturi 585 (A, US). **Moreno:** Weisburd, 4/26/1947, Castellanos s.n. (LIL). **Ojo de Agua:** Las Horquetas, 11/30/1944, Balegno 206 (LIL). **Pellegrini:** Quebracho Coto, 3/2/1947, Luna 18 (LIL). **Quebrachos:** Sumampa, 11/23/1944, Balegno s.n. (LIL); Quenti-Zaco, Sumampa [?], 11/25/1944, Bruzzone 1600 (LP). **Río Hondo:** Termas de río Hondo, Aeropuerto, Ruta Nac. 9, 1/1/1971, Krapovickas & Cristóbal 17386 (CTES); Mansupa, 1/24/1949, Legname 153 (LIL). **Robles:** Espada, 12/24/1941, Argañaraz 366 (LIL); Fernandes [Fernández], 1/10/1945, Garcia 651 (A, NY). **SANTA FE:** Camino entre Bandera y F. Inca, 10/29/1964, Alonso et al. 574 (SI). **General Oligado:** Reconquista: Cuneta de la Ruta Nacional 11, altura 776-777, 11/10/1986, Blanchou 2203 (CTES). **Iriondo:** Lucio V. Lopez, sobre barrancas rio Carcareña, 12/9/1982, Rosario & 4191 (SI). **Vera:** Distr. Santa Lucia km 70-800, lote 115 (de la Forestal) camino a Fortin Olmos, 11/10/1965, Tedone 4940 (LP). **SAN LUIS:** Las Cañitas, 2/1/1938, Pastore 2063 (SI). **Belgrano:** Socoscora, Ea. Lomas Blancas, 1/20/1979, del Vitto-Belgrano 27666 (MERL). **Coronel Pringles:** Camino a la Finca "Carolina.", 4/28/1986, de Volpoui 940 (SI); El Durazno, 1/1/1934, Vignati 216 (LP). **General Pedernera:** El Morro, 1/1/1913, Pastore 43 (SI). **Junin:** Sierra de San Luis: Quebrada del Tigre, ruta 5, entre Santa Rosa [del Conlara?] y Bañado de Cautana, 2/19/1960, Hunziker & Cocucci 14866 (MO); Sierra de San Luis: Bajo de Velis, 1/22/1895, Kurtz 8456 (LP, NY). **TUCUMAN: Burroyacú:** Burroyacú, 4/4/1944, Varela 24 (A); El Puestito, 11/14/1928, Venturi 7534 (GH, MO, US). **Chicligastá:** Chicligastá, 10/15/1913, Monetti 1266 (GH, NY). **Cruz Alta:** Estación Aráoz, 11/21/1925, Schreiter 4024 (LIL). **Leales:** Las Salinas, 6/4/1913, Monetti 145 (LIL); Chañar Pojo, 10/1/1919, Venturi 585 (SI). **Montero:** Alurralde, 12/8/1907, Lillo 7210 (NY); Alurralde, 1/1/1889, Schickendanz s.n. (LIL). **Río Chico:** La Cocha, 2/1/1919, Bailetti 390 (LIL); Río Chico, 2/1/1919, Bailetti 390 (MO). **Santa Bárbara:** Sierra de

Santa Bárbara, abra de los Morteros, 12/18/1962, de la Sota 2979 (LP). **Trancas:** Vipos, 12/22/1907, Lillo 7265 (NY, US); Trancas, 11/15/1930, Schreiter 7766 (GH); De Tapia de Vipos, 11/15/1930, Schreiter 7766 (NY); Vipos, 1/6/1922, Schreiter 1866 (TEX); Trancas, 12/30/1925, Schreiter 56530 (NY); Vipos, 12/1/1921, Venturi 1541 (A, GH, US).

BOLIVIA: Bolivian plateau [rarely as Yungas or Zongo, date usu. only 1891], 11/1891, Bang 942 (GH, MO, NY, US); Padcaya, 12/12/1903, Fiebrig 2531 (GH, MO, NY, US); Sierra de la Cruz, 5/1/1892, Kuntze s.n. (NY). **CHUQUISACA:** El Salvador - Cimboc - La Pista, 1/24/1992, Toledo & Joaquin 10371 (CTES). **Luis Calvo:** Comunidad El Viñal, S de El Salvador-Cimboc-Puesto de Ovando, 4/14/1993, Toledo et al. 11795 (CTES). **Nor Cinti:** Sucre. Cinti, Palcoyo, 3/29/1934, Hammarlund 410 (NY). **Oropeza:** Chuquisaca, 1/1/1850, D'Orbigny 1220 (G); 1 km N of Yotala, 10/30/1993, Wood 7602 (K); ca 2 km from Sucre towards Tarabuco, 12/5/1993, Wood 7696 (K). **Tomina:** Corso, ca 8 km de Tomina. Cañon Higueras clausura 5, 3/6/2001, Teran 188 (TEX). **COCHABAMBA:** About 5 km SE of Cochabamba, 3/20/1939, Eyerdam 24924 (MO). **Ayopaya:** Al rededor de Independencia, 5/11/1988, Beck & Seidel 14596 (LPB). **Campero:** Totora: Cerro del Higuierto, 3/27/1920, Steinbach 3888 (GH); Mizque, 2/12/1967, Steinbach 670 (GH, MO, UC, US). **Capinota:** Capinota, 1/16/1985, Pedrotti et al. 48 (LPB). **Cercado:** Tupuraya a 4 km de ciudad, 3/7/1965, Adolfo 316 (US); Past transito checkpoint on old Cochabamba-Santa Cruz road, ca km 13-15 E of Cochabamba, 1/13/1990, Dorr & Barnett 6990 (CTES, NY). **Cochabamba:** Campero, 2/15/1999, Antezana 1015 (BOLV); Cerro San Pedro, 2/1/1947, Cárdenas 3909 (US); Cerro San Pedro, near Cochabamba, 2/8/1947, Cutler & Cardenas 10008 (GH); Cercada, Serrania San Pedro, 11/18/1996, de la Barra 155 (BOLV); About 5 km SE of Cochabamba, 3/20/1939, Eyerdam 24924 (GH, UC); Cerrito, ciudad Cochabamba, 12/13/1928, Steinbach 8761 (GH, MO, NY, UC, US); Valle del Cercado de Cochabamba [Faldas de la colina de San Pedro], 5/1/1966, Steinbach 142 (GH, MICH, MO, NY, TEX, UC, US). **Mizque:** Canton Molinero, 11/29/1986, Sigle 172 (TEX). **Quillacollo:** Quillacollo 22 km hacia Oruro en camino asfaltado, 3/31/1979, Beck 906 (LPB); Parotaní, 3/1/1951, Cárdenas 4791 (US). **LA PLATA:** Bolivian Plateau [Yungas], 11/1/1891, Bang 942 (US). **Murillo:** Bolivian Plateau. Songo. [Zongo], 11/1891, Bang 942 (NY). **POTOSI: Cornelio Saavedra:** Potosí 80 km hacia Sucre, Alto Retiro, 3/30/1993, Torrico et al. 265 (LPB). **SANTA CRUZ:** Samaipata, Steinbach s.n. (LIL). **Caballero:** On road to Puquina Arriba, 2.5 km from the turnoff from the highway from Comarapa to Samaipata, 7/11/1998, Nee & Atha 50027 (NY). **Florida:** 1.5 km S of La Tuna, on road from Mairana to Postrervalle, 6 km by air SSE of Mairana. Bottom of Mairana valley, 12/30/1997, Nee 47632 (NY). **Valle Grande:** Clausura Cochabambita, 1/27/1993, Joaquín & Martínez 11302 (CTES). **TARIJA:** Acueducto 5 km W de Tarija, 5/18/1971, Krapovickas et al. 18842 (CTES). **Cercado:** Camino a Junacas, ca 5 km despues St. Ana area quemada, W-exp. 15°, suelo pedgroso, 5/14/1986, Bastión 1279 (TEX); Camino a Erquis, 2/25/1986, Bastión 821 (TEX); Colón, arriba de La Angostura, 11/30/1984, Beck 11003 (TEX); Camino a Yesera, 6 km, 3/12/1988, Ehrich 467 (TEX); Prov. Cercado, Depto. Tarija, 8 km NNW an der Hauptstrasse von Tarija, 1/1/1980, Feuerer 7536 (LPB, NY); De Tarija a Narvaez, Kiesling et al. 3705 (SI); Yesera, 1/28/1953, Meyer 17983 (LIL). **José Maria Aviléz:** Ca Uriondo, area del Proj. San Jacinto, 12/9/1985, Bastión 88 (TEX); Quebrada de Barbascuyo, 4/21/2000, Beck & Paniagua 27208A (TEX). **Tarija:** Alrededores de Tarija, 2/13/1929, Zelada 9 (LIL).

BRAZIL: RIO GRANDE DO SUL: ca 50 km S de Bajé, BR-153, camino a Aceguá, 12/19/1981, Arbo & Schinini 2488 (CTES); Gaudichaud 1015 (P); Gaudichaud 3294 (P); Gaudichaud 650 (P); Gaudichaud 689 (P); Gaudichaud 691 (P); Gaudichaud 693 (P); Alegrete a Capavarí, Estado Rio Grande del Sul, 3/16/1948, Palacios & Cuezzo 1901 (LIL); Tupanciretan, 1/31/1941, Rambo 10088 (LIL); San Gabriel, 1/6/1943, Rambo 25816 (LIL); Quaraí, Estancia do Jaran (Dr. Aldo Pareira Giudice), 12/26/1944, Rambo 26305 (LIL); Saint-Hilaire 2588 (P).

PARAGUAY: Hassler 1281 (NY, P); Hassler 7493 (NY); Mburica, 12/1930, Jorgensen 4045 (US); 11/25/1943, Rojas 9430 (MO); Campo Grande, Aviación, 2/14/1946, Rojas 13246 (LIL). **AMAMBAY:** Isla de montes húmedos, 9/15/1933, Rojas 6292 (MO). **CONCEPCIÓN:** Est. Sta. Maria, 1/18/1897, Anisits 2612 (P); N. Paraguay: Zwischen Rio Apa und Rio Aquidaban. Estrella, 12/3/1908, Fiebrig 4368 (GH); In campo humido in regione cursus superioris fluminis Apa. Iter ad Paraguarium septentrionalem, 12/1901, Hassler 8278 (G-DC); In regione [calcarea] cursus superiorus fluminis Apa, 1913, E. Hassler 11073 (MICH, MO, NY, P, SI, CU, US). **GUAIRA:** En el campo al pie de la Cordillera de Villa Rica, Jorgensen 4045 (LP, MO); Cerro-hú, 11/25/1950, Sparre & Vervoots 565 (LIL). **MISIONES:** San Ignacio, 1/1/1914, Chodat s.n. (G). **PARAGUARÍ:** Paraguarí, 1875, Balansa 2365 (G, P); Espinitles, Paraguarí, Chodat s.n. (G); Paraguarý, 2/23/1903, Fiebrig 908 (A, GH, US); Paraguari, 2/1/1894, Grosse 3729 (GH, NY); Florula Cordillera Centralis, In regione collium: Cerros de Paraguay, [Bull. Herb. Boiss. Ser. 2e, 3:915, 1903: Paraguarý], 12/1900, Hassler 6475 (GH, MICH, MO, NY, P, UC); Quiindy, 2/1932, Jorgensen 4045 (A); Quiindy, 11/1931, Jorgensen 4045 (NY); de Spacarai a Pirayú, 3/1/1971, Schinini 3902 (CTES).

URUGUAY: Banda Oriental de Uruguay, Saint-Hilaire 2410 (P); Brasilia, 1826, Sellow s.n. (G); Brasilia meridionalis, 1826, Sellow s.n. (G-DC, UC). **ARTIGAS:** Ruta 30, al margen del Arroyo Catalan Grande, 12/11/1995, Neffa et al. 259 (CTES); Ruta 30, al margen del Arroyo Catalan Grande, 12/11/1995, Neffa et al. 259 (GH); Ruta 30. Al margin del Arroyo Catalan Grande, 12/11/1995, Neffa et al. 259 (NY). **CANELONES:** Repressa Arroyo Canelón Grande, 3/5/1964, del Puerto 3266 (US); Montevideo [hand-written label Bois De Ste Lucia], 10/25/1876, Fruchard s.n. (P, US); Montevideo [hand-written Ste Lucia], 1/25/1874, Fruchard s.n. (P). **CERRO LARGO:** Ao. Palleros, 1/1/1936, Rosengurtt B1563 (US); Bañado de Medina, 2/19/1938, Rosengurtt B-2517 (NY). **FLORIDA:** Estancia Rincón de Santa Elena. Picada Castro. Arroyo Mansalvillagra, 1/1/1947, Gallinal 5853 (MO). **PAYSANDÚ:** Rio Queguay off route 3 where old road crossed the river, 12/13/2004, Simpson 13-XII-04-2 (TEX); **RIVERA:** Near Rivera, 12/7/1943, Bartlett 21081 (GH, MICH, NY, TEX, US). **SALTO:** Near Termas de Arapey, 1/15/1995, Pederson 16188 (CTES). **TACUAREMBÓ:** 10 km al SW de Tacuarembó, 2/7/1981, Cabrera & Zuloaga 32340 (SI); Tacuarembó, 3/19/1913, Osten 6625b (GH,US); High road ROU 31, by bridge on the Ao. Las Peñas, 3/5/1991, Pederson 15673 (CTES, NY).

9. *Menodora heterophylla* Moric. ex DC.

Prodr. 8:316, 1844. Holotype: USA: TEXAS: Entre Laredo and Bejar [San Antonio], 2/1828, *Berlandier 1499* (G-DC!). Isotypes: G!

Bolivaria grisebachii Scheele, Linnaea 25:254, 1852. Holotype: 15 mi W of New Braunfels, 10/1846, Lindheimer s.n. (BONN - destroyed?).

Menodora pinnatifida Mart., Ann. Sci. Nat. Bot. III. 19:365, 1853. Holotype: without locality or date, *Lindheimer s.n.* (M?).

Common name: redbud, low menodora

Plants spreading, decumbent ***subherbaceous perennials***, (7) 8.9—14.2 (15) cm tall, with a slender taproot, caudex 3—5 mm at ground with many branches. ***Stems*** decumbent, branching throughout, opposite, alternate in inflorescence; older wood tan, glabrate, rugose or rimose, younger stems green, moderately to deeply fluted, with a more or less obvious decurrent groove, angled in cross section, glabrate to hirsute especially younger stems, trichomes short, white or hyaline, occasionally deltoid, 0.01—0.04 (0.06) mm; internode length at midbranch (5) 8—19 (35) mm. ***Leaves*** opposite, occasionally subopposite or alternate above, sessile to subpetiolate, submembranaceous, trifid to pinnatfid, also commonly linear to lanceolate or rarely oblanceolate, (3) 10.7—22 (26) by (2) 4.9—12.5 (15), length to width ratio 1—3 (5), ultimate segment (1) 1.2—1.8 (2) mm wide, glabrate or very obscurely hirsute, most notably along margins, occasional short trichomes along nerve below, punctate below, apices acute, margins somewhat revolute or thickened, major lobes often with a few smaller dentiform lobes, base attenuate, decurrent, pinnanervate, laterals sometimes obscure, midvein prominent, often swollen at node. ***Inflorescence*** with flowers appearing solitary or a variable dichasium of 1—5 flowers, terminal. ***Pedicels*** (2) 3—7.4 (12) mm long, (0.2) 0.2—0.7 (0.9) mm in diameter, glabrous, occasionally hirsute, holding fruit pendant, subtended by a linear-lanceolate, rarely bifid or trifid, as the leaves bracteiform leaf. ***Calyx*** tube turbinate, glabrate or hispidulous particularly along nerves, lobes sparesly, (1.5) 1.7—2.4 (3) by 1.5—2.4 (3) mm, broadening in fruit to (2.9) 3.1—4.3 (5) mm; lobes (9) 10—12 (16), (1.7) 3.8—6.9 (9) by (0.4) 0.3—0.7 (1) mm, thin to thick, prominently nerved, linear, apices acute, margins entire. ***Corolla*** infundibuliform, yellow, outer petals often red in bud, tube (2.7) 3.9—6.1 (7) mm, (0.9) 1—1.3 (1.4) mm at base, opening to (2) 2.5—3.9 (4) mm at throat, pilose within; limbs (4) 5 (6), obtuse or mucronate, (5.4) 6.6—9 (9.9) by (2.5) 3.3—5 (5.4) mm, glabrous. ***Stamens*** filantherous; filaments adnate (1.1) 1.6—2.9 (3) mm below throat, (2.5) 3.2—5.1 (5) mm long, glabrous; anthers exserted ca (0.5) 1—2.5 (3.1) mm above throat, (1) 1.2—2.2 (2.5) by (0.4) 0.5—0.7 (0.7) mm, dorsifixed, latrorse. ***Pollen*** 50—60 (70) µm. ***Ovary*** bicarpellate, bilobed, each carpel with a single locule and 4 ovules. ***Style*** (7) 7.9—12.3 (13.4) mm, glabrous. ***Stigma*** capitate, occasionally broadly so, bilobed, stigma equalling or exceeding the anthers, to ca 2—4 mm beyond. ***Fruit*** with cocci globose or elliptic, circumscissile, glabrous, 5—6.4 (7) by (3) 4—6 mm in diameter; pericarp thin, membranaceous, more or less translucent; each coccus containing 4 seeds, fewer by abortion. ***Seeds*** obovate, trigonal or rarely plano-convex or meniscoid, (5.5) 5.6—6.4 (6.5) by (4) 4.3—5.1 (5.5) by (2) 1.9—2.8 (3) mm, testa irregulary reticulate, light or golden tan in color.

Distributed in grasslands from central Texas south to central Tamaulipas and west to eastern Coahuila at (0) 80—400 (564) m elevation. With flower or fruit in every month of the year, but principally Mar to Apr, Jan and Jun.

This species is probably the most herb-like in the genus. In hot dry summers, it often dies back completely. With its subherbaceous, usually decumbent habit, lobed leaves, pendant fruit, and generic *Menodora* flowers, it makes quite a contrast with its woodier, erect, entire-leaved sister species *M. longiflora*. These two sister species capture much of the breadth of variation found in the group.

I have not found types for either of the two species cited in synonymy, but as Turner (1991) noted for *M. pinnatifida*, there can be little doubt as to the determination, especially given their provenance (both were received from Ferdinand Lindheimer). The latter species was described by Martius in an article describing specimens grown from seed in the botanic garden at Munich (not Monaco, as cited by Turner 1991), but curiously notes that mature seeds were not seen. The home institution for the type of *Bolivaria grisebachii* is at present undetermined, but as Ferdinand von Roemer gave Scheele access to Lindheimer's collections, it might be assumed that they might have been housed at his home institution in Bonn; unfortunately, this collection was destroyed in 1944. Although Lindheimer's exsiccatae were widely distributed, I have seen no material that matches Scheele's description, although there are a number of Texas collections of *M. heterophylla* made in 1846 that lack an exact locality and date.

Turner (1991) cited the type for the species as *Berlandier 1461*, but in the *Prodromus* (de Candolle, 1844), it is noted as *1499*, and this is the number borne by both sheets at Geneva. I have not reviewed any specimens from GH or MO bearing this number. Steyermark (1932) noted *Bolivaria pinnatifida* Schltdl. as a synonym of *M. heterophylla*, but as plants for that species were grown from seed received by Schlechtendal from Bolivia, that species is referred to *M. integrifolia*.

SPECIMENS EXAMINED:

MEXICO: without locality: Near Cienega along Federal Hwy, 6/26/1935, J. A. Drushel 9556 (US). **COAHUILA:** Allende, about 55 km SW from Eagle Pass, 5/10/1939, Ernest G. Marsh 1777 (GH, TEX). **Mpio. Muzquiz:** Hacienda La Rosita, 5/15/1936, [without collector] (MEXU); Had. La Rosita, 1936, [without collector] 6438 (MEXU); Muzquiz, 4/15/1938, E. G. Marsh 1117 (GH, TEX); Hacienda La Rosita, 6/26/1936, F. Lyle Wynd

C. H. Mueller 297 (GH, MO, NY, US). **Mpio. Progreso:** Carratera Monclova-Sabinas (57) 5 km delante del entronque a Hermanas, 10/9/1996, J. A. Villarreal & J. Zavala 8502 (MEXU). **NUEVO LEON:** MEX Hwy 85, 2.0 rd mi S of Sabinas Hidalgo, 86 air km NNE of Monterrey, 3/27/1976, Bruce Hansen et al. 3868 (LL, MEXU); El Carrizo, near Monterrey, 9/4/1904, C. G. Pringle 13456 (US); Valley, Monterrey, 7/29/1889, C. G. Pringle 2408 (GH, MEXU, MO, NY, UC, US); 12 mi N of Vallecillo, along Mexico Hwy 85, 12/21/1970, Dunn et al. 17013 (MO); 23 mi N of Sabinas Hidalgo, 3/26/1944, Grady L. Webster & Fred A. Barkley 14491b (MO, TEX, UC); Monterrey-Saltillo road, 3/24/1946, Robert L. Crockett 8101a (LL). **TAMAULIPAS:** On road to Ciudad Anahuac, 2 km SW of Nuevo Laredo, 11/26/1961, Clara de la Garza Laura de la Garza 36 (TEX); 25 mi S of Matamoros, 6/29/1919, E. O. Wooton s.n. (US); San Fernando to Jimenez, 2/26/1902, E. W. Nelson 6602 (GH, US); Vicinity of Victoria, 4/5/1907, Edward Palmer 256 (US); Vicinity of Victoria, 4/5/1907, Edward Palmer 85 (GH, MO, UC, US); Valley E of Camargo, 6/1/1847, J. Gregg 883 (MO); Carretera Riberena 22 km al S de Nuevo Laredo, 3/22/1964, Jose A. Vasquez 40 (TEX); 8 mi S of Nuevo Laredo, on international hwy, 11/16/1961, Lorenzo Escalante 25 (TEX); Jarita Road, 2 km S of Nuevo Laredo, 4/21/1962, Martha Dominguez William McCart 8291 (TEX). **Mpio. Santander:** "Big Bass Camp," a fishing camp on NE side of Lago Vicente Guerrero, an artifical lake created in 1971, at point where old MEX 101 disappears beneath the lake, 30 km SW of Santander Jiménez, 6/16/1982, M. Nee & G. Diggs 24438 (NY).

U. S. A.: TEXAS: Entre Laredo et Bejar, 2/1828, Berlandier 1499 (G, G-DC, MO); Mexican Boundary Survey: chiefly in the Valley of the Rio Grande below Doñana, C. C. Parry et al. 1101 (NY); From western Texas to El Paso, New Mexico, 6/1/1849, Charles Wright 562 (GH, US); [without locality], Charles Wright s.n. (GH, NY); [without locality], 1846, F. Lindheimer 454 (GH, NY, UC, US); [without locality], 1846, F. Lindheimer 455 (GH, MO, UC); [without locality], 1846, F. Lindheimer 463 (US); [without locality], Riddel s.n. (NY). **Andrews County:** 6 mi. E on Lamesa Hwy, 9/16/1958, James Scudday s.n. (LL, NY). **Atascosa County:** 2 mi SE of Pleasanton, 3/22/1937, A. M. McCullough 48 (NY); 5-3/4 mi E of Pleasanton, 4/1/1949, V. L. Cory 55213 (US). **Bastrop County:** Colorado, P. V. Le Roy s.n. (NY). **Bee County:** 4 mi. N of Beeville, Hwy 59, Keith Peterson 136 (TEX); along FM 623, 3.3 mi SW of Pettus (int. US 181), at side rd to NW to Dirks Oil Field, Tuleta quad, 28-35-21 N, 97-50-30 W. 380-400 ft., 3/21/1988, Steve L. Orzell & Edwin L. Bridges 6056 (TEX). **Bexar County:** San Antonio to SW, 6/18/1925, B. C. Tharp s.n. (NY); San Antonio, 3/24/1902, B. F. Bush 1181 (GH, US); circa Bexar [San Antonio], 11/1828, Berlandier 516 (GH); Ft. Sam Houston, 3/5/1944, C. C. Albers 44058 (TEX); San Antonio, near Salado Creek at I-410 N, along Ira Lee Road, 3/12/1984, C. S. Lieb 448 (NY); San Antonio, 8/23/1906, Carleton R. Hall 955 (US); San Antonio, 1/1/1897, E. H. Wilkinson 7 (MO); San Antonio, 9/23/1879, Edward Palmer 790 (GH, NY, US); SA Experimental Farm. [USDA?], 3/14/1907, Frank B. Headley s.n. (US); San Antonio, G. Jermy 164 (GH); San Antonio, G. Jermy 262 (GH); 1904, G. Jermy 35 (NY); 1903, G. Jermy s.n. (MO, NY); San Antonio, G. Jermy s.n. (US); Gust. Jermy s.n. (MO, NY); NW of San Antonio, 3/29/1942, H. D. Ripley & R. C. Barneby 4139 (NY); San Antonio, 4/27/1940, Hermann von Schrenk s.n. (MO); San Antonio, 4/17/1911, J. Clemens and Mrs. s.n. (UC); San Antonio, 4/19/1911, J. Clemens s.n. (TEX); Julius Jermy 55 (US); Julius Jermy 9 (US); 8 mi SW of San Antonio, Bandera Rd., 10/23/1943, Mary C. Metz 65 (TEX); San Antonio to Laredo, 3/26/1885, Nathaniel Thayer Kidder s.n. (GH); 10 mi. S of San Antonio on Maverick Ranch, R. C. Burr Sr. M. C. Metz 446 (TEX); San Antonio, 5/17/1932, Sister Mary Clare Metz 121 (NY, UC). **Blanco County:** 3/13/1938, Eunice Brackett s.n. (GH, TEX); Pedernales Falls State Park, M. C. Johnston L. A. Johnston 7411 (TEX). **Brewster County:** 50 mi.S of Marathon, Maravillos Cr., B. H. Warnock 209790 (TEX). **Brooks County:** Falfurrias, 11/30/1951, B. C. Tharp 52-562 (TEX); Baurite Cr. where it crosses Hwy 281 at the Jim Wells county line marker, B. L. Turner et al. 93-168 (TEX); US Hwy 281, 2 mi N of Falfurrias, 3/22/1964, Fernando G. Llaguno 70 (LL); Falfurrias. In vacant block E of courthouse, 3/31/1949, V. L. Cory 55213 (US). **Burnet County:** Marble Falls, 5/29/1922, B. C. Tharp s.n. (GH); E side of Lake Buchanan W of Burnet, Rt. 2341 at South Fork Morgan Creek crossing, just N of Council Creek Village, 6/17/1984, Barbara Ertter & Linda Vorobik 5464 (NY); Marble Falls, Carsuer Studhalter 4348 (TEX); Marble Falls, 8/10/1892, E. N. Plank s.n. (NY). **Calhoun County:** along bay near Long Mott, M. C. Johnston 53243.2 (TEX). **Cameron County:** Near Olmito, 3/16/1942, C. L. Lundell & Amelia A. Lundell 10762 (GH, LL, MEXU, NY, UC, US); Reynoldsville, 4/13/1905, F. L. Lewton 176 (US); Vicinity of Brownsville, Ivan Shiller 142 (US); Vicinity of Brownsville, Ivan Shiller 275 (US); Bahia Grande country E of Brownsville, 4/14/1925, John K. Small & Edgar T. Wherry 11856 (NY); Loma de [la] Estrella, 4/9/1952, Marshall C. Johnston 243-1 (TEX); Horse Island, 6/1/1952, Marshall C. Johnston 243-2 (TEX); Resaca levee, 6/1/1952, Marshall C. Johnston 243-3 (TEX); Loma Alta, 6/1/1923, R. Runyon 548 (GH); near Riverside, Brownsville, R. Runyon 5993 (TEX); Laguna Atascosa National Wildlife Refuge, 2/24/1961, Raymond J. Fleetwood 3453 (TEX); Berrada Station, 11/1/1936, Robert Runyon 3137 (TEX); Barreda Station. [now Russeltown.], 3/17/1937, Robert Runyon 5116 (TEX); Bank of Arroyo Colorado, Harlingen, 3/5/1956, Robert Runyon 5117 (TEX); Loma Alta, 6/1/1923, Robert Runyon 548 (TEX, US); W. 8th & Railroad, Brownsville, 4/28/1966, Robert Runyon 6061 (GH, TEX); Loma Alto, 8 air mi NE of Brownsville, 11/30/1945, V. L. Cory 51375 (NY); Bahia Grande country E of Brownsville, 4/14/1925, John K.

Small & Edgar T. Wherry 11856 (NY). **Colorado County:** Colorado, S. M. Tracy 8087 (GH, NY, TEX, US). **Comal County:** New Braunfels. [hand written labels on some sheets offer "Victoria" or "on the Cibolo" or "Llano." Each w/diff. collection dates.], 2/1845, F. Lindheimer 454 (NY). **Dimmit County:** Asherton, 3/31/1963, Herminia Torres 82 (LL); 2 mi NW of Carrizo Springs, 5/2/1952, Marshall C. Johnston et al. 3536 (LL). **Duval County:** FM 285, 10 mi W of Falfurrias, 4/10/1965, Alonso Rios & Henry Cavazos 93 (LL); 7 mi S of San Diego toward Benavides, 6/25/1962, D. S. Correll & I. M. Johnston 25501 (LL); San Diego, Mary B. Croft 13 (NY); TX Hwy 359, 10 mi SW of Benavides, 3/22/1962, Elvira G. Garcia 114 (TEX); TX Hwy 359, 6.5 mi E of Bruni, 11/4/1962, Gilberto Vergaro et al. 8571 (TEX); US Hwy 59, 11 mi NE of Freer, 4/10/1965, Luis Botello & Rey Ayala 19 (TEX); 7 mi. W of Alice, along hwy on hill along San Diego Cr., M. Lavin 4639 (TEX); 16 mi NW of Freer on US Hwy 59, 4/10/1965, P. Malcara & F. Gutierrez, Jr. 37 (LL). **Edwards County:** ca 25 mi SW of Rock Springs along highway 674, ca 1 mi S of Two Mile Canyon. 29-47 N, 100-18 W, 5/23/1999, B. L. Turner 99-364 (TEX); Barksdale, Clifton Casey s.n. (TEX). **Fayette County:** Near La Grange, 4/30/1944, C. A. Albers 243 (NY); La Grange, C. C. Albers 44039 (TEX). **Frio County:** S of Frio State Park, F. A. Barkley 13819 (TEX); Floodplain of the Rio Frio N of Dilley, 2/27/1944, Joseph T. Painter W. D. Lucas and Fred A. Barkley 14217 (UC); 5.5 mi S of Pearsall, 5/1/1954, M. C. Johnston et al. 3471 (TEX); TX hwy 85, 4 mi W of Dilley, 4/6/1962, Santiago Alvarez Pablo Guajardo, Jorge Salazar & William L. McCart 8019 (TEX); Rio Frio N of Dilley, 2/26/1944, Willya D. Lucas Joseph T. Painter & Fred A. Barkley 14217 (TEX). **Gillespie County:** 10 mi. S of Fredericksburg, at Pedernales R., B. H. Warnock 6829 (TEX); Threadgill Valley, G. Jermy 447 (US). **Goliad County:** Rev. C. B. Williams 6 (TEX); O'Connor Fant ranch, horse pasture, S of San Antonio River, N side Rte. 239, ca 2 mi E of Rte 183. 2.3 rd mi E of Rte. 183, 7/22/1991, Steven R. Hill 22446 (GH, NY). **Hays County:** San Marcos, 4/24/1909, H. & W. s.n. (UC); San Marcos, Heald Wolf 900 (TEX); San Marcos and vicinity, 4/15/1897, S. W. Stanfield s.n. (NY). **Hidalgo County:** 6 mi E of Sullivan City, 3/8/1959, B. L. Turner 4489 (TEX); 15 mi NW of Mission, 4/4/1941, C. L. Lundell Amelia A. Lundell 9971 (LL, UC, US); Common throughout the Valley Mission (Novitiate), 5/8/1933, Elzada U. Clover 1063 (NY); Santa Ana National Wildlife Refuge, 4/14/1977, J. C. Solomon 2736 (MO); Edinburg, 4/1/1927, L. H. Hooker 6000 (US); La Joya, 2/9/1942, Mrs. E. J. Walker 40 (GH, TEX); Mercedes, R. L. Crockett 849 (LL); Santa Ana Wildlife Refuge, S of Alamo, 10/21/1959, Raymond J. Fleetwood 3142 (TEX); Sullivan City. 10-50 m, 4/13/1941, Robert Runyon 3136 (TEX); US Hwy 281, 5 mi N of Edinburg, 3/7/1964, Ruben Antonio Leal 35 (LL); Edinburg, 10/1/1927, School 6000 (LL); 50-500 ft N of old Military Hwy, 300-500 W of Sam Fordyce Rd, ca 1.7-1.8 air mi SE of jct US 83 and FM 886 at Sullivan City. Lower Rio Grande Valley National Wildlife Refuge Sam Fordyce Tract, Sullivan City quad, 26-15-24 N, 98-31-55 W, 2/1/1994, W. R. Carr 13317 (TEX). **Irion County:** near Mertzon, 4/19/1937, B. H. Warnock T538 (US). **Jim Hogg County:** FM 285, 4 mi. W of Hebbronville, A. Rios & H. Cavazos 96 (LL); **Jim Wells County:** Premont, 4/17/1958, F. W. Gould M. Hycka 8091 (UC); Premont, 6/9/1929, J. A. Drushel 6327 (NY); US 281, 8 mi. N of Falfurrias, Maria de Jesus Solis 69 (TEX); 4.5 mi S of Premont, 9/14/1954, Marshall C. Johnston 541544 (TEX). **Karnes County:** 3 mi. SE of Gillet, TX 119, Joe C. Johnson 1241 (TEX). **Kimble County:** Junction, north side, Texaco station exit along I-10, 7/29/1997, B. L. Turner 97-317 (TEX); under US 290 bridge over Llano R. in Junction, H. Mears J. Mears 1477 (TEX); [handwritten label on sheet at MO & UC:"Brown to Tom Green co., up to Callahan."], 5/15/1882, J. Reverchon 1328 (MO, NY, UC, US); East side of Junction, at exit 457 (for Spur 481) along Interstate Highway 10, 4/28/2001, Timothy W.

Chumley et al.7343 (TEX). **Kinney County:** Fort Clark, 3/22/1893, Edgar A. Mearns 1324 (US); Strickland [Stricklin] Spring, 4/1/1893, Edgar A. Mearns 1340 (US); Spofford Junction, 3/12/1893, J. Burtt Darry 30 (UC); Just N of Bracketville along Hwy 674, 6/2/1972, Larry C. Higgins 5589 (NY); Kickapoo Caverns State Park; in first major W draining draw to the S of the Lodge & barn area to its confluence with the main N-S running creek to the W of the Lodge, M. H. Mayfield & B. Westlund 1760 (TEX); Spofford, Trelease 26 (MO); Spofford Junction, 3/21/1900, William M. Canby et al. 112.5 (GH). **Kleburg County:** Kingsville, 4/1/1940, J. F. Sinclair M-22 (TEX); near Riviera, M. C. Johnston 53243.3 (TEX). **La Salle County:** TX 44, 1 mi. W of Encinal, Anita Sanchez 103 (TEX); TX Hwy 44, 1 mi W of Encinal, 4/21/1963, Anita Sanchez 103 (TEX); 11 mi. N of int. at E side of Encinal (jct TX Hwy 44) along IH-35, Guy Nesom Billy Turner & John Bain 7535 (TEX); US Hwy 81, 1 mi N of Encinal, 3/16/1963, Maria de Jesus Solis 121 (LL). **Lampasas County:** 4 mi NE of Bend, at junction FM 580 and 581, 4/18/1967, C. Morris s.n. (NY); Lampasas, 10/29/1800, J. F. Joor s.n. (MO). **Llano County:** Granite Mountain [Granite Knob], 4/13/1930, B. C. Tharp s.n. (TEX); Llano, 5/14/1899, W. L. Bray 319 (US); Llano, 5/13/1899, W. L. Bray 3319 (TEX). **Maverick County:** 1919 Olive St., Eagle Pass, 4/10/1977, D. H. Riskind 2065 (TEX); S side of Eagle Pass, 6/13/1963, D. S. Correll & D. C. Wasshausen 27773 (LL); along Hwy 277, 3.9 mi. S of jct with 1665, ca. 100 mi. N of Laredo, L. C. Barnett L. J. Dorr 45 (MO, TEX); Below Laredo, 3/26/1932, Marcus E. Jones 29400 (MO). **McMullen County:** Lively Ranch, about 20 SW of Tilden, 5/31/1949, C. M. Rogers C. C. Albers & G. L. Webster 6859 (TEX); Hwy 59, 25 mi. NE of Freer, Evangelina Saenz 70 (TEX); along US 59, 2.8 mi SW of Live Oak county line, ca 0.8 mi NE of Duval County line; 4.0 mi SW of int. FR 624, S of Lagarto Cr., Clegg quad, 28-03-52 N, 98-22-07 W. 540-550 ft., 3/22/1988, Steve L. Orzell Edwin L. Bridges 6056 (TEX). **Medina**

County: 1 mi.W of D'Hanis, off US 90, C. L. Lundell 13551 (LL); 5 mi NW of Devine, route 173, 7/10/1958, D. S. Correll & I. M. Johnston 19526 (LL); Route 90, downtown Castroville, 3/10/1984, Julia Larke 8 (NY, TEX); Route 90, downtown Castroville, 3/10/1984, Julia Larke 8 (NY); On W side of Castroville, off US Hwy 290 at Alsace Street, in field along highway next to church, 5/12/2000, Timothy W. Chumley & Micheal J. Moore 7302 (TEX); On Medina Road 511, ca 1.7 rd mi N of US Hwy 90, ca 5 air mi W of D'Hanis, 5/12/2000, Timothy W. Chumley & Micheal J. Moore 7303 (TEX). **Menard County:** 19 mi.SE of Menard, on John Royal Ranch, F. W. Gould 5715 (TEX). **Mills County:** Mullin, Mamie Egg s.n. (TEX). **Nolan County:** Sweetwater, 5/27/1918, E. J. Palmer 13726 (MO,US). **Nueces County:** Corpus Christi, 3/9/1894, A. Arthur Heller 1390 (GH, MO, NY, P, UC); Corpus Christi, 3/8/1917, E. J. Palmer 11214 (TEX, UC); Agua Dulce, 2/1845, F. Lindheimer 383a (GH); Corpus Christi, 4/10/1930, H. C. Benke 5431 (MO); RR ROW 1/2 mi S of Agua Dulce Cr crossing of Hwy 44, 11/30/1954, Marshall C. Johnston 542302 (TEX); Corpus Christi, 9/15/1860, Mrs. E. Virdon s.n. (MO); Sur la bord un creek á Port Lavaca, 8/14/1849, Trécul 1089 (P); Corpus Christi, 9/21/1936, V. L. Cory 20670 (GH). **Presidio County:** On the Cibolo, 7/1847, F. Lindheimer s.n. (GH). **Refugio County:** Steer Hill Pasture, west terrace of Melon Creek, 1.8 mi S of Hwy 774. Near Melon Creek, just N of Lake Sebastian, 5/17/1977, Steven R. Hill 5298 (NY). **Runnels County:** Ballinger, 1/1/1889, G. C. Nealley 378a (US); border of Ballinger, lake, J. C. Johnson 651 (TEX). **San Patricio County:** Sinton, 3/22/1931, B. C. Tharp s.n. (TEX); Along RR 4 mi NW of Sinton, 10/24/1948, C. M. Rogers 6644 (TEX); 3 mi. NW of Mathis, on Frels' Ranch, G. G. Williges 332 (TEX); Welder Wildlife Refuge, Section 50, 6/27/1957, George G. Willeges 6 (TEX); Li Ranch, entrance is 1.5 mi E of St.; Paul and Hwy 181. 0.2 mi N of windmill in main pasture N of sorghum fields, 3/18/1977, Steven R. Hill 4708 (NY); Near Mathis, 4/5/1931, Susan Delano McKelvey 1705 (GH, US); 2-2/3 mi NW of St. Paul, at Bee County line, 3/28/1948, V. L. Cory 54150 (LL). **Starr County:** 15 mi N of Rio Grande City, 2/15/1962, Cynthia Cabrera 59 (TEX); Roma, 1/1/1889, G. C. Nealley 262 (US); 4 mi. S of Viboras, J. R. Crutchfield 1169 (LL); US Hwy 755, 6 mi SE [SW actually] of Santa Elena, 11/9/1963, Joe May et al. 22 (TEX); 4 mi S of Viboras, 3/19/1966, John Crutchfield 1169 (NY); Along rd to Arroyo Morteras, a tributary of the Rio Grande W of Salineno, 7/26/1975, M. Butterwick & S. Strong 1363 (TEX); FM 649, 1 mi N of Viboras, 3/23/1962, Santiago Alvarez et al. 7917 (TEX). **Sutton County:** along Hwy 189 just where it crosses into Val Verde Co., bottom of Jackson Draw, Southwesternmost part of county, B. L. Turner 98-195 (TEX). **Taylor County:** 5 mi SW of Abilene, 6/30/1962, B. L. Turner T. E. Melchert s.n. (TEX); Camp Barkeley, 10/15/1942, W. L. Tolstead 5828 (UC); at Camp Barkeley, 10/15/1942, W. L. Tolstead 7689 (NY, TEX, UC); 1/4 mi N of Interstate 20 ca 1 mi from jct with Hwy 277, NW of Abilene, 4/20/1963, William F. Mahler 3294 (TEX). **Tom Green County:** NW of San Angelo, Grandview Campground (Area 1) on W side of O. C. Fisher Lake, 3/19/1983, B. Ertter & Jeffrey L. Strachan 4693 (TEX); At Concho River about 10 mi W of San Angelo, 8/31/1953, Barton H. Warnock 11521 (LL); Eden to San Angelo, 6/8/1929, Eula Whitehouse s.n. (TEX). **Travis County:** Onion Creek, 3/25/1936, B. C. Tharp s.n. (TEX); Austin, 4/27/1938, B. C. Tharp s.n. (MO, NY); University campus, Austin, 4/5/1910, Burge 2955 (TEX); Hills, Austin, 5/13/1872, Elihu Hall 293 (MO, NY, US); Shoal Creek, Austin, 4/21/1909, Heald Wolf s.n. (TEX); University campus, Austin, M. S. Young 72 (TEX, UC); University campus, Austin, 3/22/1918, M. S. Young s.n. (GH); At McKinney Falls State Park, on N side of Onion Creek on hillside near upper falls, ca 12 air mi SE of Austin, 10/10/2001, Timothy W. Chumley 7370 (TEX). **Uvalde County:** Uvalde, 4/6/1930, B. C. Tharp s.n. (TEX); Sabinal, 6/8/1918, E. J. Palmer 10118 (MO); Near Uvalde, 4/28/1928, E. J.

Palmer 33608 (NY); Uvalde to Spofford, 4/1/1933, Eula Whitehouse s.n. (TEX); 20 mi. NW of Uvalde, 1 mi. S of jct of #55 & #344, M. Butterwick & J. Smith 303 (TEX). **Val Verde County:** Painted Cave, Rio Grande River, 3/12/1893, J. Burtt Darry 41 (UC); 5-6 mi E of Del Rio, 4/16/1949, B. C. Tharp & Charles Havard 49341 (NY, TEX); Laughlin Air Force Base, ca 100 yards N of intersection of Second St. and Peace Keeping Avenue, near main terminal along drainage ditch, north side, 9/27/1998, B. L. Turner 98-499 (TEX); At Pumpville turnoff, 4/3/1953, Barton H. Warnock 14960 (LL); 35 mi N of Del Rio near Loma Alta, 6/7/1957, Barton H. Warnock & W. D. McBryde 15118 (LL); 8 mi N of Comstock along highway 163, 5/1/1949, Barton H. Warnock & B. L. Turner 727 (LL); San Felipe Springs, near Del Rio, D. S. Correll et al. 15987 (LL); Del Rio, 12/7/1891, E. N. Plank s.n. (NY); Del Rio, 8/21/1938, Forrest Shreve 8378 (GH, NY); 5 mi W of Del Rio, 6/9/1931, J. A. Moore & J. A. Steyermark 3006 (MO); Del Rio, 4/19/1930, Marcus E. Jones 26718 (UC); 8 mi NW of Del Rio (ca 4 mi NW of jct of US 90 and 277, 4/1/1947, Rogers McVaugh 7744 (GH, TEX). **Victoria County:** Along railroad in Victoria, 4/7/1900, H. Eggert s.n. (GH, MO); Along railroad in Victoria, 4/7/1900, H. Eggert s.n. (MO); SW Victoria, 7/30/1931, Ora M. Clark 3980 (MO). **Webb County:** 13 mi S of Encinal on I-35. 650 ft., 4/3/1971, B. J. Cox 2900 (TEX); 21 mi NW of Laredo, B. L. Turner s.n. (TEX); About 13 mi NW of Webb on Hwy 83, 7/16/1957, D. S. Correll & I. M. Johnston 18099 (LL); About 13 mi N of Webb, Route 83, 4/4/1957, D. S. Correll 20757 (LL); Laredo, Rio Grande river. 180 mi from San Antonio, 8/10/1879, Edward Palmer 791 (MO, US); US 83, 23 mi. S of Catarina, Esther K. Dickey 54 (TEX); US Hwy 59, 14 mi NE of Laredo, 3/9/1963, Felipe Cisneros 19 (GH, TEX); FM 1472, 14 mi. NW of Laredo, Francisca Guajardo 55 (LL); 30 mi E of Laredo, 12/25/1951, Harry Shute 51-1713 (TEX); Along hwy 83 to Carrizo Springs, 15 mi N of Laredo, 3/24/1960, Howard S. Gentry & Arthur S. Barclay 18435 (LL, US); 2016 Canada Ave, Laredo. Lot

6, Block 1799ED, 7/5/1960, Josephine Baird s.n. (TEX); 12 mi N of Laredo, 3/20/1935, K. M. Wiegand & M. C. Wiegand 1678 (GH); 12.7 mi S of Encinal on I-35, 4/3/1971, W. E. Harmon Dunn 5598 (MO); State Loop 20, 4.4 mi SE of Laredo, 11/3/1962, William L. McCart Renne Allred III 8 (LL). **Willacy County:** near hdqtrs., Sauz Ranch, M. C. Johnston 53243.1 (TEX). **Wilson County:** 5 mi. S of Nixon, on Hwy 97 [Hwy 90] at roadside park, B. Thompson A. Graham 48 (TEX); Sutherland Springs; 25 mi SE of San Antonio, 8/25/1879, Edward Palmer 791 (GH, NY); Hwy 87 4 mi E of Stockdale, at Cibolo Creek, 3/24/1955, Marshall C. Johnston William L. McCart 5080 (TEX). **Zapata County:** In vicinity of Zapata, 4/7/1957, D. S. Correll C. Schweinfurth 15716 (LL, UC); Zapata, 3/7/1964, E. Javier Gonzalez & Rurico Gutierrez 32 (LL); US Hwy 83, 22 mi S of Laredo, 4/4/1965, Olga A. Garcia et al. 621 (TEX). **Zavala County:** off US 83, 15 mi. N of Crystal City, along RR, C. L. Lundell 13596 (LL); On US Hwy 83, ca 2 rd mi S of Uvalde line, ca 12 air mi S of Uvalde, 5/12/2000, Timothy W. Chumley & Micheal J. Moore 7304 (TEX).

10. *Menodora longiflora* A. Gray

Amer. J. Sci. II 14:45, 1852. Lectotype (Steyermark, Ann. Missouri Bot. Gard. 19:146, 1932): USA: TEXAS: [Comal Co.]: Upper Guadaloupe [Guadalupe River], 6/1847, *Lindheimer 652* (MO); Isolectotypes: US!, GH!. Syntype: Wright 564 (GH!); Isosyntype: NY!, UC!, US!

Menodora pubens A. Gray, Amer. J. Sci. II 14:45, 1852. Lectotype (Turner, Phytologia 71:5:348, 1991): USA: NEW MEXICO: Grant Co.: Copper Mines, 8/19/1851, *Wright 1696* (GH). *Menodora hispida* Palmer, J. Arnold Arb. 10:43, 1929; Holotype: USA: TEXAS: Jeff Davis Co.: Limpia Canyon, near Ft. Davis, 10/8/1926, Palmer 32112 (A). *Menodoropsis longiflora* (A. Gray) Small, Fl. S. E. U.S. 917, 1903.

Common name: showy menodora

Plants fastigiate ***suffrutescent perennials***, (28) 32.7—43.6 (48) cm tall, with a woody taproot, caudex 4—12 mm diameter with many branches. ***Stems*** strict, branching remote, opposite, rarely irregularly alternate but more regularly so in the inflorescence; older wood tan to gray to black, atratous, glabrous, rugose, rimose; younger stems green, shallowly fluted, terete in cross section, glabrate to strigillose, rarely hirsute-pilose or strigillose-canescent, trichomes short, white or hyaline, retrorse, rarely much longer, 0.01—0.15 (0.51) mm; internodes fairly uniform, but longest near midbranch, (5) 11—26 (38) mm, usually exceeding the subtending leaves. ***Leaves*** opposite, often becoming alternate bracts in the inflorescence, sessile or subpetiolate, subcoriaceous, linear to elliptic, often slightly lanceolate or oblanceolate, occasionally obovate or spatulate below, fairly uniform in size but largest near midbranch, (5) 12.1—28.2 (37) by (1) 1.5—5.3 (10.2) mm, length to width ratio (2.5) 4.5—9.3 (11), glabrate to hispidulous, often punctate especially below, apices acute to apiculate, ocasionally obtuse or mucronate below, margins entire, thickened, base attenuate, decurrent, uninervate, nerve prominent abaxially, swollen at node. ***Inflorescence*** a compound dichasium of 1—12 flowers with opposite or alternate branching. ***Pedicels*** (1) 5.7—27.2 (45) mm long, (0.4) 0.5—0.8 (1.2) mm in diameter, glabrate to strigillose-canescent, rarely hirsute-pilose, holding fruit erect, subtended by a linear-lanceolate, glabrous or hispidulous bract, bracts often in opposite pairs. ***Calyx*** tube turbinate, nerved, glabrous or strigillose, occasionally densely so, rarely hispidulous, 1.9—2.9 (3.2) by (1.6) 1.8—2.8 (3) mm, broadening in fruit to (3) 4—5.8 (6.7) mm; lobes (6) 9—10 (11), (2.6) 6.9—15.2 (21) by (0.2) 0.3—0.7 (0.8) mm, thick, prominently nerved, linear to broadly subulate, hispidulous, apices acute, margins entire. ***Corolla*** hypocrateriform, yellow, tube (22.7) 29.9—45.2 (50) mm, (0.8) 1.1—1.9 (2) mm at base, opening to 2.8—4.9 (7) mm at throat, glabrous within; limbs 5—6, acute, rarely obtuse, 10—12 (13) by (3) 3.2—5.7 (6) mm, glabrous. ***Stamens*** filantherous; filaments included, adnate ca (3.6) 4.2—5.8 (6.1) mm below throat, (0.5) 0.7—1.6 (1.8) mm long, glabrous; anthers included, top of anthers at or 0.8—2.6 mm below throat, (2.8) 3.2—4.4 (4.8) by (0.5) 0.7—1 mm, with a flat, deltoid, rarely subulate or absent 0.5 mm extension of the connective, dorsifixed, latrorse. ***Pollen*** 80—110 (130) µm. ***Ovary*** bicarpellate, bilobed, each carpel with a single locule and 4 ovules. ***Style*** (13.3) 21—44.7 (54) mm, glabrous. ***Stigma*** capitate, variously inserted or exserted ranging from 4 mm below anthers or equalling or just exceeding them at throat, or exserted 2—3 mm beyond. ***Fruit*** with cocci globose or ellipsoid, circumscissile, glabrous, (5) 6.7—9.6 (11) by (4) 6.1—8.9 (10) mm in diameter; pericarp thin, membranaceous, more or less translucent; each coccus containing 4 seeds, fewer by abortion. Seeds obovate or elliptic, trigonal or lenticular, (3) 4.5—6.1 (7) by (2) 3.2—4.5 (5) by (1) 1.6—2.5 (3.5) mm, regularly reticulate.

Rare in southern New Mexico but widely spread in central and west Texas south to Nuevo Leon and Tamaulipas, west to central Chihuahua at (300) 510—1700 (2615) m elevation. Flowering (Jan and mid-Apr) mid-May to Oct., with fruit (Jan) Jun to Nov.

In flower, with its long corolla tube, this species is unmistakable. In fruit, it can be mistaken for *M. laevis*, which overlaps in the western half of the range. Usually, *M. longiflora* has distinctly longer calyx lobes, and relatively large fruit and seed, but in some specimens (such as those from Eddy County, New Mexico) the latter measurements fall squarely within the range of those for *Menodora laevis*; in those cases, leaf arrangement (predominantly opposite in *longiflora* vs. alternate in *laevis*) may be the best way to determine the species.

Turner (1991) noted an outlying collection for this species (Acatzingo, *Arséne 10* (F)) far to the south in Puebla, and believed the locality to be poosibly in error; it is distinctly out of the typical range, though without reviewing the specimen I cannot verify the determination.

Kartesz and Gandhi (1993) clarified authorship and typification for *Menodora. longifolia* and *M. scabr*a. Steyermark (1932) had attributed both names as "(Engelm.) Gray," and Turner (1991) cited authorship as "Engelm. *ex* A. Gray." In both cases, this was because Gray (1852) in his protologue cited an Engelmann manuscript in which the species were described as *Bolivaria*. Since these were never validly published as species of *Bolivaria*, they are not basionyms, and so should not be cited as such (Kartesz and Gandhi 1993). While it is clear that Gray was recognizing Engelmann for his work on the species, it is also clear that Engelmann is not the author of their names, *i.e.*, the binomials, since Gray alone was substituting *Menodora* in place of *Bolivaria*. Thus, proper authorship of the names is simply, "A. Gray." This seems to shortchange the contribution of Engelmann, but it is in accordance with the strict interpretation of the Botanical Code.

SPECIMENS EXAMINED:

MEXICO: CHIHUAHUA: Santa Eulalia Mts., 9/26/1885, C. G. Pringle 539 (GH, US); Ca 31 air mi NW of Julimes in a SW-facing canyon above Rancho El Recuerdo in Sierra de Carrasco (S of Sierra de Chorreras), 9/15/1973, James Henrickson 12951b (TEX); Ca 39 air mi NE of Ciudad Chihuahua on E side of Sierra El Morrion near Mina La

Esperanza, 9/10/1980, James Henrickson & P. Bekey 18464 (TEX); Cañon de la Madera, southeastern flank of Sierra Rica, N of Rancho de la Madera. 5 km up the canyon, 9/25/1942, Robert M. Stewart 2512 (GH); Fern Canyon, side canyon of Santa Elena Canyon of Rio Grande on S side of River, ca 3 mi W of Santa Elena Canyon Picnic Area of Big Bend National Park, Texas, 11/24/1973, Tom Wendt & Emily J. Lott 102 (LL, MEXU). **COAHUILA:** Sierra la Paila, ca 9 air km NNE of Estacion Martes at foot of Cerro Alto, 7/25/1993, B. L. Turner et al. 93-140 (MEXU); Near Parras, 10/15/1910, C. A. Purpus 5004 (GH, MO, UC, US); Puerta de San Lazaro, Sierra de San Lazaro, 8/30/1939, C. H. Muller 3041 (UC); Santa Rosa Mts., 7/13/1938, E. G. Marsh 1362 (TEX); Saltillo and vicinity, 5/15/1898, Edward Palmer 118 (GH, MO, UC, US); Mountains 24 mi NE by N from Monclova, 9/3/1880, Edward Palmer 792 (GH, US); Juraz, about 100 mi N of Monclova on the Sabinas River, 9/23/1880, Edward Palmer 794 (GH, US); Sierra de Santa Rosa, S of Muzquiz, 7/13/1938, Ernest G. Marsh 1362 (GH); 8 km SW of Rancho San Miguel in Cañon de los Burros, NE part of Serranias del Burro, 6/2/1972, F. Chiang et al. 7514 (LL, MO); 20 km N of Rio Sabinas crossing on road from Muzquiz to La Cuesta, 6/6/1972, F. Chiang et al. 7528 (LL, MO, NY); Sierra del Pino, at mouth of southern canyon, 8/19/1940, I. M. Johnston & C. H. Muller 375 (GH, LL); Sierra del Pino: vicinity of La Noria, 8/23/1940, I. M. Johnston & C. H. Muller 676 (GH, LL); Western base of Picacho del Fuste, northeasterly from Tanque Vaionetta, about lat. 27° 34' N, 8/24/1941, I. M. Johnston 8373 (GH); Sierra de la Madera: vicinity of "La Cueva" in Corte Blanco fork of Charretera Canyon, 9/15/1941, I. M. Johnston 9083 (GH); Sierra de "La Paila," parta baja, límites entre los municipios de Gral. Cepeda y Ramos Arizpe. Arriba del Campo Experimental La Sauceda, 10/18/1972, J. Marroquín 2231 (MEXU); 12 air mi E of Boquillas in Sierra del Carmen area, 10.4 road mi W of Rancho El Jardín, 7/27/1973, J. Henrickson 11532 (TEX); Ca 20 air mi ENE of

Boquillas, 3.5 mi W of Cerro Agua Chile, 7/29/1973, James Henrickson 11577 (TEX); Ca 35 air mi W of Cuatro Ciénegas, in mid-Canyon de la Hacienda of Sierra de la Madera, 8/6/1973, James Henrickson & T. Wendt 12023 (TEX); 75 air mi S of Big Bend National Park basin, mid portion of the Valle de Pinos (Vacas) of the Sierra Santa Fe del Pino, 8/5/1976, James Henrickson & Barry Prigge 15206 (TEX); Sierra de La Paila, in the Cañon de Mimbre, 7 rd mi NE of Hipolito, 5/16/1977, James Henrickson et al. 16173 (TEX); Ca 25 air mi WNW of Cuatro Ciénegas, in the lower portion of Canyon de la Hacienda of the Sierra de la Madera, N of Rancho Cerro de la Madera, 9/26/1998, James Henrickson 20538 (TEX); 3.7 rd mi S of Parras, 8/30/1971, James Henrickson 6165a (TEX); Along COA hwy 53, La Cuesta, Malena Mountains, about 3 mi E of El Puesto Tres Caminos, NW of Múzquiz, 8/3/1971, James L. Reveal et al. 2582 (US); Hwy 57, 70 mi N of Saltillo, 6/3/1966, James S. Wilson 11379 (TEX); Hwy 57, 70 mi N of Saltillo, 6/3/1966, James S. Wilson 11456 (TEX); 12 mi NNW of Palos Blancos, 20 mi N of Ocampo, 6/11/1956, Jean Graber 107 (TEX); E slope of Sierra del Carmen. 9 km N of Rancho El Jardín on road winding to Mina El Popo. Ca 7 km S of Canyon del Diablo, 7/28/1973, M. C. Johnston et al. 11846a (LL, MEXU); Cañon de San Enrique, eastern side of Sierra La Encantada, 5 km W of Rancho Buena Vista, 9/4/1941, Robert M. Stewart 1378 (GH, LL); Mesa Grande, high mesas 40 km NW of Hacienda de la Encantada, 9/14/1941, Robert M. Stewart 1609 (GH); Cañon de Ybarra, the principal canyon at NW end of the calcareous Sierra del Pino, 9/23/1941, Robert M. Stewart 1858 (GH, LL); Vicinity of Rancho El Tule, southern foothills of the igneous Sierra Hechiceros; about 24 km due N of Castillon and close to the Chihuahuan boundary. 8 km S of El Tule, 6/12/1941, Robert M. Stewart 442 (GH, LL, MO, MEXU); Arroyo in the Sierra de la Paila 6.9 mi NW Hipolito which is 8.9 mi N Hwy 40 W of Saltillo, 9/17/1978, Thomas F. Daniel 883 (MICH); Cañon del Diablo, in backside of limestone

Sierra del Carmen plateau. In main conyon just above (W of) entrance from N of canyon that drains E side of Pico de Cerda; ca 1.5 mi due SW of Mina El Popo and 2.5 mi E of Pico de Cerda, 8/10/1974, Tom Wendt 543 (TEX); Microondas hill 21 mi by rd N of Saltillo on Hwy 57, 9/29/1988, William R. Anderson 13488 (MICH, MO, NY). **Mpio. Castaños:** Puerta de San Lazaro, Sierra de San Lazaro, 8/30/1939, C. H. Muller 3041 (GH, LL); Sierra la Gavia, Rcho. La Gavia. Parte alta del cañón, 8/10/1995, M. A. Carranza & J. Encinas 2343 (MEXU). **Mpio. Cuatro Ciénegas:** Rancho Falcón, Cuesta del Dulce, about 12 mi W of Hacienda Berrendo, 8/19/1937, F. Lyle Wynd 727 (A, GH, MO, NY, US). **Mpio. G. Cepeda:** S. Paila (Valle Seco), 7/4/1944, G. B. Hinton 16550 (MEXU, US). **Mpio. M. Muzquiz:** Ca 130 rd km NW of Muzquiz on COA Hwy 25 (Muzquiz-Boquillas), mid-slope of Sierra la Encantada basin and mining areas, 6/3/1992, Guy Nesom & Mark Mayfield 7386 (TEX). **Mpio. Ocampo:** Sierra la Encantada, Rancho Puerto del Aire, 9/8/1990, M. A. Carranza et al. C744 (MEXU); Sierra la Encantada, aprox. 170 km de Muzquiz, Cuesta de Malena, brecha a Boquillas del Carmén, 9/8/1990, M. A. Carranza et al. C802 (MEXU). **Mpio. Parras de la Fuente:** Sierra de Parras, 2.4 km (1.5 mi) al S del Ej. Colorado, 8.8 km (5.5 mi) al Oe. de Parras, 8/19/1982, Clark C. Cowan & Andres Rodriguez G. 3623 (TEX). Sierra de Parras, ca 11 air km S of Parras on toward Manchaca. 1980-2000 m, 9/19/1993, Guy Nesom et al. 7641 (TEX). **Mpio. Ramos Arizpe:** El Cedral, Sierra de La Paila. 1300-1600 m, 8/20/1987, J. A. Villereal & M. A. Carranza 3880 (TEX); Sierra de La Paila, Ejido el Cedral por el cañon El Carmen, 8/26/1992, Jesús Valdés R. et al. 2215 (MEXU). **Mpio.Villa Acuña:** Serranias del Burro, Rancho El Bonito, between canyons El Bonito and La Pantera., 9/20/1977, D. H. Riskind & Neil Lathy Mueller 2291 (TEX); Rancho El Rincon, on SW margin of Serranias del Burro (part of the Sierra del Carmen) ca 80 km SE of Big Bend National Park, Texas. 1400-2100 m, 8/8/1991, Sandra Aguilar Ruiz &

Diana L. Doan-Crider 163 (TEX). **NUEVO LEON:** 11 mi W of Santa Catarina, 7/12/1946, A. Hernandez et al. 16m530 (TEX); In Cañon Bustamante, where the Sabinas River divides the Sierra Morena and the Sierra Bustamante. Along slopes of the easternmost drainage on S side of river. 1200-1500 m, 10/17/1993, Alan Prather & Tom Patterson 1464 (TEX); Monterrey, Santa Catarina. La Fama, 7/15/1911, Bro. G. Arséne & Bro. Abbon 6148 (MO, US); Ca 120 km S of Laredo [TX] along Hwy 85 to Monterrey, ca 11 km S of Sabinas Hidalgo, 10/10/1982, James Henrickson 19302 (TEX); Ranch Resendez, Lampazos, 6/22/1937, Mary Taylor Edwards 314 (MO, TEX); Along Mexico Hwy 85 S of Sabinas Hidalgo, ca 46 rd km N of Monterrey, 5/23/2001, Timothy W. Chumley et al. 7356 (TEX). **Mpio. Aramberri:** (La Escondida to Aramberri) to Dolores, 11/9/1993, Hinton et al. 23851 (TEX). **Mpio. Bustamante:** Sierra Gomas, Bustamante Canyon, 8/13/1988, T. F. Patterson 6595 (TEX). **Mpio. Galeana:** 1 mi E of Puente Dios, S side of Sierra Las Animas; ca 10 km due N of Galeana, 7/26/1993, B. L. Turner et al. 93-162 (MEXU, TEX); Ciénega del Toro to Santa Rosa, 10/3/1995, Hinton et al. 25648 (MEXU, TEX); In arroyo behind cemetary at Rayones, 6/27/2001, Timothy W. Chumley & Steve Siedo 7357 (TEX); Ca 1 rd mi W of Rayones, on road to Santa Rosa, ca 8.4 rd mi E of Santa Rosa, 5/22/2002, Timothy W. Chumley et al. 7393 (TEX);. Ca 7.5 air mi E of Santa Rosa along road to Rayones, 5/22/2002, Timothy W. Chumley et al. 7395 (TEX). **Mpio. Montemorelos:** 25 km al NE de Rayones hacia Montemorelos, 8/8/1990, R. et al. 994 (MEXU). **Mpio. Rayones:** Galeana to Rayones + 24 km, 10/17/1990, Hinton et al. 20770 (GH, TEX); Ciénega del Toro to Santa Rosa, 9/14/1996, Hinton et al. 25864 (TEX); Santa Rosa to Rayones, 9/14/1996, Hinton et al. 25870 (TEX). **TAMAULIPAS:** Vicinity of San Miguel. Cerro de la Tamaulipeca, 7/24/1930, H. H. Bartlett 10541 (GH, MO, US).

U. S. A. : NEW MEXICO: without exact locality: New Mexico, Charles Wright 1695 (GH); 1696 (MO, US). Las Vegas to Santa Fe, 9/3/1929, Eula Whitehouse s.n. (MO). **Chaves County:** On US Hwy 82 ca 21.5 rd mi E of Mayhill between mile markers 57 and 58, 8/9/2001, Timothy W. Chumley & Brian Vanden Huevel 7358 (TEX). **Eddy County:** Lincoln (Alamo) National Forest: Ridge 1 mi S of McCollum's Ranch, 10/3/1915, William R. Chapline 485 (GH). Lincoln (Alamo) National Forest: On ridge at head of Willow Seep Canyon, Guadalupe Mts., 9/14/1916, William R. Chapline 485.5 (NY); Carlsbad Caverns, 8/1/1933, Otto Degener 5013 (NY); 1-1/8 mi W of park headquarters [Carlsbad Caverns], sec. 35 T24S R24E, 6/11/1937, N. E.Dole, Jr. 4 (UC); Carlsbad Caverns, 9/27/1931, Lois B. Payson 56 (RM); Near Carlsbad Caverns, 8/12-20/1924, Paul C. Standley 40400(US); Black River, 8/12-20/1924, Paul C. Standley 40455 (US). **Lincoln County:** 15 mi E of Capitan, 7/25/1938, C. L. Hitchcock et al. (RM, UC). **TEXAS: without exact locality:** Mexican Boundary Survey: chiefly in the Valley of the Rio Grande below Doñana, C. C. Parry et al. s.n. (NY); Western Texas, C. Wright 11935 (MO); Western Texas to El Paso, NM, Charles Wright 504 (GH, NY, UC, US); 1847, F. Lindheimer 652 (US); F. Lindheimer s.n. (GH); 1887, G. C. Nealley s.n. (US). **Blanco County:** 6/20/1939, B. C. Tharp s.n. (GH, LL, MO, UC); Perdernales, F. Lindheimer s.n. (NY). **Brewster County:** Glenn Spring, Big Bend National Park, 7/10/1983, A. M. Powell & S. Powell 4064 (MO); Black Gap area ca 4 mi below Headquarters, 10/8/1983, A. M. Powell & S. Powell 4163 (TEX); Chisos Mts., 9/10/1925, B. C. Tharp 3639 (TEX); 10/9/1936, B. C. Tharp s.n. (MO, NY, UC); 1 mi S of Ernst Tinaja, Sierra de Caballo, Big Bend National Park, over-looking Ernst Valley, 8/11/1997, B. L. Turner & Matt Turner 97-353 (TEX); Lower Juniper Canyon, Chisos Mountains, 6/24/1937, Barton H. Warnock 20800 (TEX); At Chisos Pens, Chisos Mountain area, 6/10/1937, Barton H. Warnock 20801 (NY, TEX); At Chisos Pens, Chisos Mountain area, 6/10/1937, Barton H. Warnock 20801 (NY); Sul Ross College Hill, Alpine, 8/2/1936, Barton H. Warnock 20802 (TEX); Paradise Canyon along highway 4 mi W of Alpine, Davis Mountains, 6/12/1947, Barton H. Warnock 5958 (LL); Green Valley, Glass Mountains, 7/23/1941, Barton H. Warnock W319 (TEX, UC); N side of Bissett Hill, Glass Mts., 7/3/1941, Barton H. Warnock W510 (GH); Chisos Mts., 7/9/1931, C. H. Mueller 8112 (GH, NY, TEX, US); 50 mi W of Sanderson, 6/25/1940, C. L. Hitchcock & L. R. Stanford 6792 (UC); Off Hwy 90, 19 mi E of Marathon, 8/3/1945, C. L. Lundell Amelia A. Lundell 14209 (LL); Big Bend Nat'l Park. Chisos Mts., Pine Canyon, D. S. Correll & D. C. Wasshausen 27878 (LL); 17 mi E of Marathon, Rt 90, 10/31/1966, D. S. Correll 34088 (GH, LL); Up-draw W of Sul Ross State Teachers College hog barn, Alpine, 10/15/1946, George William Brown B131 (GH, TEX); Chisos Mountains, Upper Blue Creek Canyon, 6/25/1931, J. A. Moore & J. A. Steyermark 3242 (A, GH, MO, NY UC, US); A-Hill, Alpine, 8/6/1947, L. C. Hinckley 3969 (LL, NY); On Big Hill about 5 mi S of Alpine, 7/30/1952, L. C. Hinckley 4886 (US); NE side of Bullis Range, S of Bullis Gap, on Bullis Gap Ranch, 5/17/1977, M. Butterwick & E. Lott 3616 (TEX); Ca 1/2 mi S of Tres Papalotes in the Solitario, Big Bend Ranch, 6/3/1975, M. Butterwick & S. Strong 643 (TEX); Nail place, Chisos Mts., 8/13/1915, M. S. Young s.n. (TEX, UC); Elephant Mesa, 6/3/1959, Marshall C. Johnston 4054 (TEX); CCC camp area, Chisos Mountains, 7/5/1936, Omer E. Sperry s.n. (TEX); East slope area 2 mi S of Alpine, 9/10/1935, Omer E. Sperry T147 (US); Sul Ross Hill, Alpine, 6/19/1941, Reginald Rose-Innes & Brunelle Moon 1257 (GH, TEX); Chisos Mts., Juniper Canyon, 7/17/1921, Roxana S. Ferris & Carl D. Duncan 2820 (MO, NY); Oak Spring run-off, 8/23/1970, Semple 383 (MO); Northern Chisos Mts., 9/15/1933, T. L. Steiger 1206 (NY); Foothills of Chisos Mts., 7/15/1883, V. Havard s.n. (US). **Comal County:** Upper Guadalupe, 6/1847, F. Lindheimer 652a (MO); Commanche Spring: New Braunfels, 7/15/1849, F. Lindheimer 983 (GH, MO, US). **Crockett County:** 15 mi.W of Ozona, B. H. Warnock 15222 (LL); US Hwy 290, 12.9 km W of its junction with I-10, 9/25/1993, Daniel Atha 297 (NY). **Culberson County:** Mouth of McKittrick Canyon, Guadalupe Mountains, 7/2/1958, D. S. Correll & I. M. Johnston 19149 (LL); 30 mi. N of Van Horn, Sierra Diablo Mts., D. S. Correll 31616 (LL); Pine Springs, Guadalupe Mts., 1/31/1911, E. Whitehouse s.n. (TEX); Canyon N of Van Horn, 7/8/1900, H. Eggert s.n. (GH, MO); Guadalupe Mountains, flat below McKittrick Canyon, 7/23/1931, J. A. Moore & J. A. Steyermark 3598 (A, GH, MO, NY, UC, US); 6/23/1949, Janszen 67 (TEX); South McKittrick Canyon between Pratt Lodge and McKittrick Ridge, 7/20/1988, Larry C. Higgins 17908 (NY); Near Taylors Spring, Guadalupe Mountains, 8/28/1916, M. S. Young s.n. (TEX); Low hills, Guadalupe Mountains, 8/28/1916, M. S. Young s.n. (MO); Lower slopes of Guadalupe Mountains, 8/28/1916, M. S. Young s.n. (GH); Wild Rose Canyon, 6/12/1975, Sam Sikes & Jackie Smith 575 (LL); Guadalupe Mts. National Park, McKittrick Canyon trail, ca 0.6 km S, 0.6 km W of Hunter Ridge, 7/18/1973, T. L. Burgess 1176 (TEX); Guadalupe Mts. National Park, Upper Dog Canyon Ranger Station, 8/17/1973, T. L. Burgess 1504 (TEX); Southwestern slopes of Beach Mt., 6-1/2 mi NW of Van Horn, 7/14/1943, U. T. Waterfall 5093 (GH, MO, NY); NE slopes of Beach Mtn. about 9 mi N of Van Horn, 7/16/1943, U. T. Waterfall 5139 (GH); Banks and slopes along Pine Spring Canyon, Guadalupe Mountains, 7/21/1943, U. T. Waterfall 5224 (GH, TEX. **Hays County:** Wimberly, 6/19/1939, B. C. Tharp s.n. (TEX); Edwards Plateau, Joe C. Johnson 303 (TEX). **Hudspeth County:** 8 mi W of Van Horn, 9/7/1955, Barton H. Warnock 13651 (LL); Between hills in the Three Mile Mountains, 6 mi W of Van Horn, 8/19/1942, U. T. Waterfall 4044 (GH, MO); 7 mi W of Van Horn, in the Carrizo Mountains, 7/13/1943, U. T. Waterfall 5053 (GH); 6/22/1928, V. L. Cory 2172 (GH). **Irion County:** near Mertzon, 4/19/1937, B. H. Warnock T538 (GH, LL); Camp

Charlotte, 1/1/1889, G. C. Nealley 683/684 (US). **Jeff Davis County:** 10-1/2 mi N of Ft. Davis, 11/1/1935, (GH); lower Little Aguja Canyon, Davis Mts., B. H. Warnock B. L. Turner 8094 (LL); Foothills of Davis Mountains, 10/8/1926, E. J. Palmer 32115 (A); Ft. Davis, 8/26/1913, J. H. Andrews 62 (A); Davis Mountains: Deep gorge of Madera Canyon, Caldwells, about 10 mi N Mount Locke, 7/21/1940, L. C. Hinckley 1260 (NY); Davis Mts., 8/28/1914, M. S. Young s.n. (GH, TEX, UC). **Kerr County:** About Kerrville, 6/15/1894, A. Arthur Heller 1880 (GH, MO, UC, US); Kerrville, 10/2/1916, E. J. Palmer 10883 (A, MO); 9/1/1930, Eula Whitehouse s.n. (TEX); Kerrville, 7/15/1889, Munsen Hawkins s.n. (US). **Kimble County:** Telegraph, 10/8/1916, E. J. Palmer 10937 (A); E of Roosevelt, 7/10/1930, E. R. Bogusch E. Molly Bogusch 4739 (MO); Above the Llano River in Junction, off Texas Ranch Road 2169, ca 0.5 mi S of Interstate Hwy 10, at base of bluffs below hotel, margins of hotel parking lot, and road cut, 8/12/1999, Timothy W. Chumley 7301 (TEX). **Kinney County:** along stream, 2 mi. S of int. of Hwy 277 and 693, 6/14/1963, D. S. Correll & D. C. Wasshausen 27757 (LL); Along stream, 2 mi. S of intersection of Hwy 277 and 693, 6/14/1963, D. S. Correll & D. C. Wasshausen 27757 (GH); Just N of Brackettville along Hwy 674, 6/3/1972, Larry C. Higgins 5600 (NY). **Lampasas County:** 1 mi S of Lampasas, 6/14/1929, Simon E. Wolff 932 (US). **LlanoCounty:** along the Llano R., 7 mi. E of Llano, D. S. Correll & I. M. Johnston 17301 (GH, LL). **Mason County:** On US Hwy 29, 2.4 rd mi E of jct with Texas Ranch Road 1222, ca 9.8 air mi NW of Mason, 8/12/1999, Timothy W. Chumley 7299 (TEX); NE side of TX 29, 3.0-3.1 mi. SE of its jct. w/ RM 1222. Grit Quad. 30-48-18 N, 99-20-56 W, W. R. Carr 10869 (TEX). **McCulloch County:** Brady, B. C. Tharp 4367 (TEX). **Menard County:** On Texas Ranch Road 1311, 1.8 rd mi N of jct with US Hwy 29, ca 18.8 air mi NW of Mason, 8/12/1999, Timothy W. Chumley 7300 (TEX); W side of RM 1311, 1.8 mi. N of jct with TX 29. Calf Cr. Quad. 30-53-35 N, 99-29-40 W, W. R. Carr

11174 (TEX). **Pecos County:** 7/27/1943, B. C. Tharp 43-743 (TEX, UC); 7/15/1943, B. C. Tharp 43T243 (MO, TEX); ca 3 mi W of Longfellow (RR station). ca 30-10 N, 102-40 W, 5/19/1991, B. L. Turner 15972 & 15976 (TEX); Roadside park, ca 19 mi E of Ft. Stockton along I-10, 9/23/1996, B. L. Turner & G. Turner 96-116 (TEX); Sheffield exit from IH-10, ca. 6 mi. NNW of Sheffield, B. L. Turner & G. Turner 96-170 (TEX); 14 mi W of Pecos River along I. H. 10, along base of prominent mesa, S side of highway, 10/6/1997, B. L. Turner 97-447 (TEX); Sheffield cemetery, ca 3 mi W of Sheffield along old US Hwy 90, 10/20/1997, B. L. Turner 97-472 (TEX); 4-6 mi W of Longfellow; Sanderson Canyon, 7/6/1954, Barton H. Warnock 11865 (LL); 20-35 mi S of Ft. Stockton along Sanderson Hwy, 7/1/1955, Barton H. Warnock 13309 (LL). **Presidio County:** Above Capote Falls, 11/3/1966, D. S. Correll 34130 (GH, LL, UC); Chenates region, 1889, G. C. Nealley 471a (US); Twin Mts., 5/20/1903, J. Reverchon s.n. (MO); 2 mi S of Shafter, 7/11/1964, James Scudday 512 (UC); Brite Ranch near Capote Fall, 6/18/1941, L. C. Hinckley 1698 (TEX); Bluff E of Cienega ranch, Brite Ranch near Capote Fall, 6/18/1941, L. C. Hinckley 1698 (GH); Burnt Camp Canyon, a tributary of Fresno Canyon, 11/30/1931, L. C. Hinckley 2253 (GH, NY); Trans-Pecos Texas: The Solitario: Burnt Camp Canyon. Along banks of Burnt Camp Creek, about 70-75 mi S Marfa, 11/30/1941, L. C. Hinckley 2254 (NY). **Schleicher County:** SW-most part of county, 3 mi N of Sutton Co. along Hwy 2129, 10/12/1998, B. L. Turner 98-503 (TEX). **Starr County:** E of Rio Grande City, Archie D. Wood 846 (TEX). **Sterling County:** B. C. Tharp 3637 (TEX). **Sutton County:** 12 E of Sonora on US Rte 290, 7/5/1973, D. E. Boufford 10578 (MO); Between Sonora and "Sawyer Spring" at head of Llano River, 7/16/1923, W. W. Eggleston 16725 (US). **Terrell County:** 6 mi E of Sanderson, 8/23/1947, Barton H. Warnock 2700 (TEX); About 4 mi NW of Sanderson on Ft. Stockton road, 8/2/1945, C. L. Lundell 14198 (LL, NY, UC, US); In Ligan Canyon, Blackstone Ranch 20 mi S of Sheffield, 6/14/1949, G. L. Webster 263 (TEX); In Dunlap's Ranch, 15 air mi SE of Shefield, 7/3/1949, Grady L. Webster 472 (TEX); 5 mi. SE of Dryden, Matt Turner 4 (TEX). **Travis County:** Swiss Alps, 7/9/1929, N. & N. s.n. (TEX, UC). **Uvalde County:** at Blewett, D. S. Correll I. M. Johnston 18188 (LL); Montell, 10/14/1917, E. J. Palmer 12976 (A, MO, UC, US); Montell, 10/15/1917, E. J. Palmer 12992 (A, UC); 8 mi S of Uvalde, 5/17/1938, H. R. Reed s.n. (A); Sabinal, 6/15/1885, J. Reverchon 1556 (MO, US); Sabinal, 6/15/1885, J. Reverchon 1556 (US). **Val Verde County:** Along rd from US 90 to Del Rio power plant, ca 2.0 mi from Devils River. 975 feet, 5/10/1961, Alfred Traverse 2153 (LL); below roadside park, E side of Pecos River. 29-42 N, 101-21 W, 5/19/1991, B. L. Turner 15965 (TEX); 6 mi. E of Langtry, along Hwy 90, B. L. Turner G. Turner 96-30 (TEX); 35 mi N of Del Rio near Loma Alta, 6/7/1957, Barton H. Warnock & W. D. McBryde 15114 (LL); On NW side of Pecos River, 10/31/1966, D. S. Correll 34058 (LL); Amistad Reservoir Area [From map on label, several mi W of Comstock along rd to Langtry], 10/23/1965, David Flyr 773 (TEX); Del Rio, 9/4/1908, F. L. Lewton s.n. (LL); Devils River, 8/4/1931, Ora M. Clark 4133 (MO); On US Hwy 90 ca 4.5 rd mi W of the Pecos River, on road cut below rest area, ca 14 air mi WNW of Comstock, 5/13/2000, Timothy W. Chumley & Micheal J. Moore 7305 (TEX); W side of Sacatosa Cr., S of low water crossing in southern clear zone beyond SE end of runways, Laughlin Air Force Base, ca 5.2 air mi ESE of jct of US Rt. 90 and FM 2523 E of Del Rio, 5/6/1997, W. R. Carr 16298 (TEX).

11. *Menodora intricata* T. Brandegee

Univ. Calif. Publ. Bot. 4:380, 1913. Holotype: MEXICO: SAN LUIS POTOSÍ: Minas de San Rafael, 5/1911, *C. A. Purpus 5016* (UC!). Isotypes: G!, NY!, US!

Menodora intricata T. Brandegee var. *purpusii* Steyerm., Ann. Missouri Bot. Gard. 19: 150, 1932. Holotype: MEXICO: PUEBLA: Tehuacán, 6/1905, *C. A. Purpus 1318* (MO). Isotypes: F, GH, UC!, NY.

Plants mound-forming to fastigiate, occasionally somewhat spreading or twining ***subherbaceous to suffrutescent perennials***, (10) 14.5—36 (40) cm tall, with a woody taproot, caudex 8-12 mm diameter with many branches, occasionally appearing aphyllous. ***Stems*** spreading or erect, branching throughout, opposite or subopposite, rarely alternate in the inflorescence; older wood tan to gray to black, atratous, often appearing black-pitted, rugose, rimose, younger stems green, deeply fluted, with an obvious decurrent groove, angled, flattened in cross section, usually glabrate, often hispidulous in leaf axils or often below, trichomes rudimentary and minutely papillate or short, white or hyaline, 0.01—0.08 (0.09) mm; internodes at midbranch (3) 10—31 (53) mm, usually well exceeding the subtending leaves. ***Leaves*** opposite, occasionally subopposite, rarely alternate, the latter usually in the inflorescence, sessile or subpetiolate, submembranaceous, linear to linear-lanceolate or linear-oblanceolate, occasionally bifid or trifid, (1) 2.6—6.1 (8.6) by (0.1) 0.2—0.8 (1.5), length to width ratio (4.3) 5.7—13.8 (23.4), ultimate segment 0.2—0.8 (1.4) mm wide, glabrous or sparsely hispidulous, especially at base, apices acute or acuminate, rarely obtuse or mucronate, margins entire, base decurrent, if leaves relatively broad then attenuate, uninervate or trinervate, nerve(s) prominent abaxially, swollen at node, occasionally only slightly so if at all. ***Inflorescence*** a compound dichasium of 1—20 flowers with mostly opposite branching, occasionally alternate, occasionally appearing solitary. ***Pedicels*** (0) 0.6—6.9 (13) mm long, 0.4—0.6 (0.7) mm in diameter, glabrous to hispidulous, holding fruit erect, subtended by a linear or linear-oblanceolate bract, bracts mostly occurring in opposite pairs. ***Calyx*** tube turbinate, strongly nerved, glabrous, occasionally hirtellous, lobes hispidulous at least sparingly so, (1.3) 1.4—1.9 (2.1) by (1) 1.3—1.9 (2.2) mm, broadening in fruit to (1.7) 2.1—3.1 (3.3) mm; lobes (6) 8—9 (12), (2) 2.2—4.6 (5.6) by0.2—0.4 (0.5) mm, thin, usually prominently nerved, linear, apices acute or acuminate, margins entire. ***Corolla*** infundibuliform, yellow, tube (1.5) 2.1—5.1 (6) mm, (0.7) 0.8—1.3 (1.5) mm at base, opening to (1.4) 2—4.5 (6) mm at throat, sparsely pilose within; limbs 5—6 (7), mucronate, rarely acute, (2.6) 3.9—8.6 (10) by (1.3) 1.7—3.8 (4.2) mm, glabrous. ***Stamens*** filantherous; filaments adnate ca (0.6) 0.8—1.6 mm below throat, (0.8) 1.8—5 mm long, glabrous; anthers exserted ca (0) 1.3—2.5 (3) mm above throat, (1) 1.1—1.9 (2.2) by (0.3) 0.4—0.6 (0.7) mm, dorsifixed, latrorse. Pollen 0.06—0.07 mm. ***Ovary*** bicarpellate, bilobed, each carpel with a single locule and 4 ovules. ***Style*** (3.5) 5.5—11.2 (11.4) mm, glabrous. ***Stigma*** capitate, slightly bilobed, equalling or exceeding anthers to 2 mm. ***Fruit*** with cocci obovoid, rarely globose, circumscissile, glabrous, (3.5) 3.7—4.7 (4.9) by (2.5) 2.8—3.9 mm in diameter; pericarp thin, membranaceous, more or less translucent; each coccus containing 4 seeds, fewer by abortion. ***Seeds*** obovate or elliptical, commonly trigonal or plano-convex to somewhat lenticular, (3.2) 3.3—3.6 (3.7) by (1.8) 1.9—2.5 (2.6) by 0.8—1.1 (1.3) mm, testa regularly reticulate, often scalloped abaxially, raphal rib often poorly differentiated though occasionally raised and prominent.

Endemic to Mexico from southern Tamaulipas to northern Querétaro, and disjunct in the Tehuacán region of Puebla at 650—1400 (2000) m elevation. With flower or fruit (Mar.) mid-Apr to early Aug.

This species is distinctive for its deeply fluted stems and highly reduced leaves. It seems to prefer rocky limestone hillsides, but can be quite variable in habit, appearing strict and fastigiate, somewhat twining when growing up through other vegetation, or very dense and compact when browsed.

SPECIMENS EXAMINED:

MEXICO: PUEBLA: Mpio. Tehuacán: Tehuacán, 6/1905, C. A. Purpus 1318 (UC); Meseta de San Lorenzo, subiendo por camino que viene del Riego, 8/7/1981, F. Chiang, P. Davila & J. L. Villasenor F-2256 (TEX). **QUERETERO: Mpio. Pinal de Amoles.** Cerca de El Plátano, proximo a Bucareli, 4/15/1988, J. Rzedowski 46440 (TEX). **SAN LUIS POTOSI:** +/- 100 km NE of San Luis Potosí, 2.5 mi E of Hwy 57 towards El Huizache (at km 4.5), 6/19/2004, James Henrickson 23734 (TEX); Minas de San Rafael. [11 km SE Charcas], 7/1911, C. A. Purpus 5016 (G, NY, UC, US); Minas de San Rafael, 11/1910, C. A. Purpus 5044 (UC); Sierra Madre Oriental. Las Tablas, 8/9/1934, Francis W. Pennell 18026 (GH, NY, US); 1.3 mi S of Colonia Libertad on the high road 4.1 mi S of Las Tablas, 5/31/1981, Meredith Lane & Mark Leidig 2916 (TEX); 2 km al E del Huizache, 6/29/1985, P. Hiriart et al. 712 (MEXU); On hill on south side of Mexico Hwy 80 ca 1 km E of Presa de Guadalupe, 5/23/2002, Timothy W. Chumley et al. 7401 (TEX). **TAMAULIPAS:** W side of MEX Hwy 101, 1 mi S of Río Chihue bridge, 11.5 rd mi N of Jaumave, 28 air km SW of Ciudad Victoria, 3/19/1976, Bruce Hansen et al. 3774 (LL); 4 km al E del Llano entre Dr. Arroyo y Miquihuana, 5/21/1974, F. González Medrano et al. 6945 (MEXU); Jaumave Valley, 5 mi NE of Jaumave, 8/1/1976, Grady L. Webster & W. Scott Armbruster 20545 (MEXU, TEX); Near Nogales, Jaumave, Mexico, 7/15/1932, H. W. Von Rozynski 458 (G); Ejido San Antonio km 132 Carr Victoria-Jaumave, 4/25/1985, Mahinda Martinez 291 (MEXU, TEX); On Mexico Hwy 101 at km 132, ca 1 mi S of Rio Chihue bridge, ca 25 air km SW of Ciudad Victoria, 5/23/2002, Timothy W. Chumley et al. 7400 (TEX); San Lucas, Viereck 96 (US). **Mpio. Miquihuana:** 4 km al W de Tanque Eguía, hacia la Presa San Carlos, 5/23/1976, F. G. Medrano et al. 9021 (MEXU, MO). **Mpio. Tula:** 30 km al SW de Tula, cerca del límite de edo. (SLP y Tamps.), 8/9/1972, Francisco González Medrano et al. 4394 (MEXU).

12. *Menodora muellerae* Rehder

J. Arnold Arb. 16: 451, 1935. Holotype: MEXICO: NUEVO LEON: Sierra Madre Oriental, cedar savannah above Encinal wheatfields, about 15 mi SW of Galeana, 5/19/1934, *C. H. and M. T. Mueller 463* (A). Isotypes: F, MEXU, TEX!, US!

Plants small, mound-forming to upright ***suffrutescent perennials***, (5) 6-11 (12) cm tall, with a woody taproot and caudex with many branches. ***Stems*** spreading to erect, branching throughout, opposite; older wood tan or gray, glabrous, rugose, rimose; younger stems green, obscurely fluted, terete in cross section, glabrate to hispid, the latter particularly at nodes or axils and along decurrent groove, trichomes short, white or hyaline, occasionally long and spreading, (0.05) 0.07—0.13 (0.15) mm; internodes at midbranch 2—7 (12) mm. ***Leaves*** opposite, sessile to subpetiolate, subcoriaceous, narrowly oblanceolate to less commonly narrowly lanceolate, often broader below, largest often just below inflorescence branching, (5) 6—12 (18) by (1) 1.2—2 (2.5), length to width ratio (3.2) 3.9—7.6 (9.3), apices acute or acuminate, margins entire, thickened, base attenuate, decurrent, minutely hispidulous especially at base, occasionally punctate below, prominently uninervate abaxially, nerves swollen at node, often with more or less obscure lateral nerves. ***Inflorescence*** with flowers appearing solitary, rarely a few-flowered simple or compound dichasium of 1—5 flowers with opposite branching. **Pedicels** (1.5) 2.1—4.5 (5) mm long, (0.3) 0.5—0.8 (0.9) mm in diameter, hirtellous, rarely glabrous, holding fruit pendant, subtended by a leaf-like bract, bracts occurring in opposite pairs. **Calyx** tube turbinate, strongly nerved, sparsely hirtellous at least at base but often glabrous, (1.5) 2 by (1.5) 2 mm, broadening in fruit to (2.4) 2.6—3.2 (3.3) mm; lobes (5—9) 10, (3) 3.5—5 by0.2—0.4 mm, thin, prominently nerved, linear to broadly subulate, apices acuminate or acute, margins entire. **Corolla** infundibuliform-hypocrateriform, yellow, often red in bud, tube (9) 10.8—16.9 (18) mm, 1 mm at base, opening to 3—4 mm at throat, glabrous or pilose within; limbs 5 (6), obtuse or mucronate, (5) 5.8—7.9 (8) by (3) 3.1—4.5 (5) mm, glabrous. **Stamens** filantherous; filaments adnate (1.6) 2.2—2.6 (3) mm below throat, 1.2—6 mm long, glabrous; anthers exserted 1.4—4 mm, (1.5) 1.6—2 by 0.4—0.8 (1) mm, occasionally with a very short linear process extending beyond the connective, dorsifixed, latrorse. *Pollen* 0.05—0.08 (0.09) mm. **Ovary** bicarpellate, each carpel with a single locule and 4 ovules. **Style** (10) 12.9—2 (23) mm, glabrous. **Stigma** capitate, bilobed, style equalling or just exceeding the anthers, rarely included ca 3 mm below throat. No mature fruit seen.

Of limited distribution in central and southern Nuevo Leon and immediately adjacent regions of Coahuila to the west and Tamaulipas in the south from (1750) 2090—2190 (2462) m elevation. With flower or fruit (from late Mar.) May—Aug. (through Nov.).

Infrequently collected, this species is found rocky calcareous or gypseous substrates. In flower, it is quite easy to diagnose, but vegetatively (or in fruit) is quite cryptic, and can not be distinguished from *Menodora coulteri*, the truly cryptic *M. henricksonii*, or *M. gypsophila*, depending on the vestiture. It is possible that this may intergrade to some extent with the latter two species, and that they might best be regarded as varieties of this species; in general, though, all of these are poorly known as yet.

In Turner (1991), the specific epithet is misspelled and the author mis-attributed (cited as "*Menodora mullerae* I. M. Johnston") due to errors in the listing of the Gray Card Index at that time.

SPECIMENS EXAMINED:

MEXICO: COAHUILA: Mts. S of Saltillo on road to Puerto de Flores, 3/30/1967, Norman Boke & J. Massey 225 (MICH). **Mpio. Saltillo:** San Jose del Alamito to Los Angeles, 7/7/1995, Hinton et al. 25349 (MEXU, TEX). **NUEVO LEON: Mpio. Galeana:** Sierra Madre Oriental; cedar savannah above Encinal wheat fields, 5/19/1934, C. H. Mueller M. T. Mueller 463 (US, TEX); Santa Rita, 5/11/1981, G. B. Hinton 18820 (MEXU, NY, TEX); Cienega del Toro to Santa Clara, 11/19/1995, Hinton et al. 25810 (TEX); Hacienda Pablillo, 8/5/1936, Mary Taylor 87 (MO, UC, TEX); **TAMAULIPAS:** Ca 33 km E of Jaumave; 2-3 km Nof Hwy 70 on road to Bustamante, 10/6/1982, James Henrickson & W. Hess 19093 (TEX).

13. ***Menodora henricksonii* Chumley,** *sp. nov.*

Menodora coulterae *A. Gray similis sed stylus superne vel inferne pubescens.*

Holotype: MEXICO: COAHUILA: About 6 air km W of Saltillo, E extremity of Sierra de La Vega, at and below Estación Microndas La Vega. 1800-2000 m, 3/30/1973, *M. C. Johnston, T. L. Wendt & F. Chiang 10501* (LL!); Isotypes: MEXU!, MO!, NY!

Plants small, mound-forming to somewhat fastigiate suffrutescent perennials, (6) 8.4—19.3 (25) cm tall, with a woody taproot, caudex 4—8 mm diameter at ground with few to many branches. ***Stems*** spreading to erect, branching throughout, opposite; older wood tan or gray to black, glabrous, rugose, younger stems green, obscurely fluted, occasionally much more strongly so, rarely with a well-defined decurrent groove, terete in cross section, moderately strigillose to hirtellous-pilose, trichomes short, white or hyaline, retrorse-appressed, or rarely long and spreading, hyaline or purple-tinged, 0.09—0.31 (0.46) mm; internodes at midbranch (4) 6—9 (10) mm, generally not exceeding the leaves. ***Leaves*** opposite, sessile to subpetiolate, subcoriaceous, linear-lanceolate to linear-oblanceolate, or broader and oblong-elliptic to obovate, largest leaves near midbranch, (3) 6.3—15.4 (22.8) by (1) 1.4—3.4 (5.1) mm, length to width ratio (2.7) 3.3—6.3 (8.2), hispidulous or strigillose, especially along margins above, often punctate most obviously below, apices acute, thickened, occasionally apiculate or acuminate, obtuse or mucronate below, margins entire, thickened, base attenuate, decurrent, uninervate, nerves prominent or not abaxially, rarely swollen at node. ***Inflorescence*** with flowers often appearing solitary, but usually a few-flowered occasionally compound dichasium of 1—5 flowers. ***Pedicels*** (2.8) 3.3—7.8 (12) mm long, (0.3) 0.4—0.7 mm in diameter, sparsely to densely strigillose or hirtellous-pilose, holding fruit pendant, subtended by leaf-like bract, bracts occurring in opposite pairs. ***Calyx*** tube turbinate, not prominently nerved, sparsely to densely strigillose-hirtellous especially along nerves, rarely glabrate, lobes usually hispdiulous, (1.5) 1.5—2.7 (3.8) by (1.7) 1.8—2.1 (2.2) mm, broadening in fruit to 2—3 mm; lobes (5, 8, 9) 10—12, (3) 3.6—6.1 (7) by (0.1) 0.2—0.6 (0.8) mm, usually thin, occasionally thickened and prominently nerved, linear, apices acute to acuminate, margins entire. ***Corolla*** infundibuliform, yellow, outer petals often tinged red in bud, tube (4) 4.1—5.3 (5.4) mm, 1—1.2 (1.3) mm at base, opening to (1.9) 2.8—4.4 (4.6) mm at throat, pilose within; limbs 5 (6), obtuse to acute, occasionally mucronate, (6) 7.2—11 (11.4) by (3) 3.3—5.2 (5.9) mm, glabrous to sparsely hirtellous or pilose. ***Stamens*** filantherous; filaments adnate inserted ca 1.5—2.5 mm, 6.6—8 (8.8) mm long, glabrous or sparsely pilose; anthers exserted ca (4) 5—6 mm, (1.5) 1.7—2.6 (5) by (0.3) 0.4—1 (1.1) mm, dorsifixed, latrorse. ***Pollen*** 0.06—0.07 mm. ***Ovary*** bicarpellate, bilobed, each carpel with a single locule and 4 ovules. ***Style*** (10) 11—13.9 (15) mm, sparsely pubescent, usually terminally but occasionally only sparingly below. ***Stigma*** capitate, exceeding anthers ca 1—2 mm. ***Fruit*** with cocci globose, rarely elliptic, circumscissile, glabrous, (4) 4.3—6.8 (7) by (3.5) 3.7—5.7 (6) mm in diameter; pericarp thin, membranaceous, more or less translucent; each coccus containing 4 seeds, fewer by abortion. ***Seeds*** ovate to elliptic, trigonal or lenticular, (3.5) 3.8—4.3 (4.5) by (2) 2.2—3.2 (3.8) by (1) 1.1—1.6 (1.5) mm, raphal rib usually prominent, testa irregularly reticulate.

Of limited distribution in southern Coahuila from 1900—2400 (2500) m elevation. Flowering Mar to Apr. and Jul (Sep), in fruit Apr and Jul (Sep).

This species is recognized largely on the basis that it forms a monophyletic group in the molecular phylogeny. It is morphologically quite cryptic and polymorphic, and is poorly differentiated from two completely different (though related) taxa, *Menodora coulteri* and *M. helianthemoides*; I have recognized the two forms as varieties of the species. The coulteroid (typical) variety is morphologically identical to *M. coulteri* except in the vestiture of the style; in *M. coulteri* the style is glabrous, and it is sparsely pubescent terminally in *M. henricksonii.* Turner (1991), with his very perceptive eye, had segregated *M. hintoniorum* out of coulteroid specimens in the same region, and one of these (*Johnston et al. 10501* (TEX), the holotype selected for *M. henricksonii*) was sampled in the molecular analysis. Morphologically, he cited intricate branching as one of the key characters of his species, and in practice seems to have keyed in on a certain woody gestalt among specimens he annotated as *hintoniorum*. However, nearly all species of *Menodora* have intricate branching to some degree, and demonstrably some *coulteri* and *scabra* specimens were similarly woody. The specimens sampled in the molecular analysis shared a single unique character, a pubescent style, that was not present in other taxa. The type of *hintoniorum* has a glabrous style, and I believe it is more properly referred to *M. coulteri* for that reason.

I have recognized the helianthemoid form as variety *confusa*. Both of the exemplars I have identified have been annotated in past as *M. helianthemoides* var. *magniflora or M. magniflora* by either Jim Henrickson or Billie Turner, and *Hinton et al. 21048* (TEX) was cited by Turner (1991) as a new record for Coahuila; I had agreed with these determinations prior to molecular sampling. These specimens possess the typical broad ovate leaves with the pilose vestiture associated with *magniflora*, but the leaves and corollas are sized much more moderately, lacking the more ample proportions of the variety *magniflora*; and again, the styles are not glabrous as in *helianthemoides*.

Using a single character to recognize a new species, particularly one that may be subject to a great deal of variation, is, I feel, somewhat precocious. In order to gain a real understanding of this species, a greatly expanded molecular sampling of collections from this region of Mexico is required, and from that a better understanding of the morphology of this species may be possible. It is entirely possible that further analysis will restore *M. hintoniorum*, and that these varieties will need to be included under that species, but I feel it is better at this time to segregate these based on the available evidence.

The two varieties can be separated as follows:

1. Leaves linear-lanceolate to linear-oblanceolate; stems moderately strigillose to densely strigose .... 13a. *Menodora henricksonii* var. *henricksonii*
1. Leaves oblong-elliptic to oblanceolate or obovate; stems strigose to hirtellous-pilose .... 13b. *Menodora henricksonii* var. *confusa*

13a. Menodora henricksonii Chumley var. *henricksonii*

Plants small, mound-forming to somewhat fastigiate suffrutescent perennials, 10—20.4 (25) cm tall, with a woody taproot, caudex 7—8 mm diameter at ground with few to many branches. ***Stems*** moderately strigillose to densely strigose, trichomes short, white or hyaline, retrorse-appressed, hyaline or purple-tinged, (0.09) 0.10—0.22 (0.25) mm. ***Leaves*** linear-lanceolate to linear-oblanceolate, occasionally broader. ***Anthers*** 2—2.8 (3) by (0.3) 0.4—1.1 mm, occasionally with a short cylindrical extension of the connective. ***Style*** (11.8) 11.9—13 mm, sparsely pubescent terminally with flat, moderately long, brownish-tinged trichomes.

Distribution limited to southern Coahuila. 1900—2400 (2500) m elevation. Flowering Mar to Apr and Jul (Sep), in fruit Apr and Jul (through Sep).

SPECIMENS EXAMINED:

MEXICO: COAHUILA: About 6 air km W of Saltillo, E extremity of Sierra de La Vega, at and below Estación Microndas La Vega. 1800-2000 m, 3/30/1973, Johnston et al. 10501 (LL, MEXU, MO, NY); Collected at Saltillo, state of Coahuila and vicinity. Saltillo, 4/22/1898, Palmer 34 (GH, MEXU, MO, NY, UC, US); Carneros Pass, 9/8/1889, Pringle s.n. (MEXU); Near Est. Vega microwave tower, ca 11 mi W of Saltillo, 9/27/1974, Rollins & Rollins 7467 (GH, TEX); In arroyo, 3 km SW of Fraile, 7/11/1941, Stanford et al. 334 (GH, MEXU, MO, NY, UC). **Arteaga:** Sierra Zapalinamé, 5/19/1990, Hinton et al. 20240 (GH, TEX); Sierra Zapalinamé, 6/22/1992, Hinton et al. 22066 (TEX).

13b. Menodora henricksonii **Chumley var. *confusa* Chumley**, var. nov.

Menodorae helianthemoides *Bonpl. similis sed stylus inferne pubescens.*

Holotype: MEXICO: COAHUILA: 9 km S of Parras on Sierras Negras, 7/3/1941, *Stanford et al. 200* (MO!). Isotypes: (GH!, NY!).

Plants small, mound-forming suffrutescent perennials, 6—14 cm tall, with a woody taproot, caudex 4.5 mm diameter at ground with many branches. ***Stems*** moderately strigose to hirtellous-pilose, trichomes short, white or hyaline, retrorse-appressed, or rarely long and spreading, hyaline or purple-tinged, 0.13—0.46 mm. ***Leaves*** oblong-elliptic to oblanceolate or obovate, largest near midbranch, (6) 7.9—13.8 (14) by (2.2) 2.6—4.4 (5.1), length to width ratio (2.7) 2.8—3.3 (3.4). ***Anthers*** 1.5—2 by 0.4—0.7 mm, lacking a process extending from the connective. ***Style*** (10) 11—13.9 (15) mm, sparsely pubescent, usually terminally pubescent but occasionally only sparingly below above the throat of the corolla.

Distribution limited to southern Coahuila from 1900—2400 (2500) m elevation. Flowering Mar to Apr and Jul (Sep), in fruit Apr and Jul (Sep).

SPECIMENS EXAMINED:

MEXICO: COAHUILA: Ramos Arizpe: Sierra San José de los Nuncios, 7/19/1991, *Hinton et al. 21048* (TEX).

14. *Menodora gypsophila* B.L. Turner

Phytologia 79:1:8, 1995. Holotype: MEXICO: NUEVO LEON: Galeana: Arid hillside, Santa Rosa, 1610 m, 10/6/1995, *Hinton et al. 25643* (TEX).

Plants small, mound-forming ***suffrutescent perennials***, (9) 9.1—14.2 (15) cm tall, with a woody taproot, with some adventitious rooting rarely on larger woody lateral branches, caudex with many branches. ***Stems*** spreading, mound-forming, occasionally rooting at nodes, branching throughout, opposite; older wood tan or gray, glabrous, rimose, rugose, younger stems green, often tinged with red, obscurely fluted, canaliculate decurrent groove occasionally apparent, terete in cross section, hirtellous-pilose, trichomes long, spreading or hyaline, (0.2) 0.22—0.32 (0.37) mm; internodes (3) 4—9 (13) mm at midbranch. ***Leaves*** opposite, often appearing whorled with very short internodes at terminal ends of branches, subpetiolate, subcoriaceous, narrowly elliptic or lanceolate to oblanceolate, rarely obovate below, largest at midbranch, (4.6) 5.8—12.8 (17) by (1.1) 1.4—3.1 (4.9) mm length to width ratio (2.5) 3.4—4.7 (5.6), hirtellous to pilose, punctate sometimes obscurely, often tinged red, apices acute, acuminate or apiculate, margins entire, thickened, base attenuate or cuneate, decurrent, uninervate to trinervate, prominent abaxially, laterals often obscure. ***Inflorescence*** a few-flowered compound dichasium with opposite branching, occasionally appearing solitary, of 1—6 flowers. ***Pedicels*** (2) 3.4—9.8 (14) mm long, (0.3) 0.4—0.6 (0.7) mm in diameter, hirtellous, holding fruit pendant, subtended by a leaf-like bract; bracts in opposite pairs. ***Calyx*** tube turbinate, nerved, hirtellous, (1.4) 1.5—2.1 (2.5) by (1.2) 1.5—2.2 (2.5) mm, broadening in fruit to (2.7) 2.8—3.3 mm; lobes (5—8) 10 (11—12), (2.9) (3.1—4.9 (5.5) by0.2—0.6 (0.8) mm, thin, nerved, linear or linear-lanceolate, hirtellous, punctate, apices acute, margins entire. ***Corolla*** infundibuliform, yellow, tube (4.2) 4.4—5.9 (6.3) mm, (0.6) 0.7—1.2 (1.3) mm at base, opening to 3—3.6 (3.9) mm at throat, sparsely pilose within; limbs (4) 5—6, obtuse to acute, often mucronate, (6.6) 6.7—7.3 by 2.6—4.1 (4.3) mm, glabrous. ***Stamens*** filantherous; filaments adnate ca (1.1) 1.2—2.3 (2.5) mm below throat, (3.7) 4—5.5 (6) mm long, glabrous; anthers exserted ca (1.6) 1.8—2.8 (3.1) mm above throat, (1.4) 1.5— 1.9 (2.1) by 0.5—0.8 (0.9) mm, often with a conical extension of the connective, dorsifixed, latrorse. ***Pollen*** 60—70 µm. ***Ovary*** bicarpellate, each carpel with a single locule and 4 ovules. ***Style*** 9—11.1 (11.9) mm, glabrous. Stigma capitate, equalling or just exceeding anthers. ***Fruit*** with cocci obovate or globose, circumscissile, (2.9) 3.7—5.0 (5.9) by (3.1) 3.4—4.6 (5.6) mm in diameter; pericarp thin, membranaceous, more or less translucent; each coccus containing 4 seeds, fewer by abortion. ***Seeds*** obovate or elliptical, trigonal or plano-convex, (2.9) 3.1—3.6 (3.9) by (1.6) 1.8—2.1 (2.4) by (0.7) 0.9—1.4 (1.6) mm, testa reticulate.

Narrowly distributed on gypsic hillsides and outcrops in central Nuevo León from (900) 1500-1700 (2000) m elevation. With flower or fruit May to Sep (mid-Oct).

SPECIMENS EXAMINED:

MEXICO: NUEVO LEON: States of Coahuila and Nuevo Leon, 6/1/1880, Edward Palmer X (GH). **Mpio. Galeana:** 3 km N of Galeana, 7/26/1993, B. L. Turner et al. 93-158 (MEXU, TEX); Galeana to Rayones + 5 km, 6/27/1994, Hinton et al. 24474 (NY, TEX); Near Santa Rosa, 10/6/1995, Hinton et al. 25643 (TEX); S of Rancho Aguililla, 9/28/1996, Hinton et al. 25897 (TEX); San Jose del Alamito to El Coyote, 7/15/1998, Hinton et al. 27198 (TEX); Ca 1 rd mi W of Rayones, on road to Santa Rosa, ca 8.4 rd mi E of Santa Rosa, 5/22/2002, Timothy W. Chumley et al. 7394 (TEX); Ca 7 air mi E of Santa Rosa along road to Rayones, 5/22/2002, Timothy W. Chumley et al. 7396 (TEX); Ca 5 air km W of Santa Rosa along road to Cienega del Toro, 5/22/2002, Timothy W. Chumley et al. 7397 (TEX); Ca 6 air km E of Cienega del Toro along road to Santa Rosa, 5/22/2002, Timothy W. Chumley et al. 7399 (TEX). **Mpio. Rayones:** Cienga del Toro to Santa Rosa, 9/14/1996, Hinton et al. 25863 (TEX).

15. *Menodora mexicana* (A. DC. in DC.) A. Gray

Amer. J. Sci. II. 14:45. 1852. Basionym: *Bolivaria mexicana* A. DC. in DC., Prodr. 8:315, 1844. Holotype: MEXICO: OAXACA: Circa Oascam [Vicinity of Oaxacan], 7/1834, *G. Andrieux 228* (G-DC!). Isotypes: K!, P!

Menodora potosiensis Henrickson *ex* B. L. Turner, Phytologia 71:5:351, 1991. Holotype: MEXICO: SAN LUIS POTOSÍ: 5 km NW of Tierra Nueva, 1750 m, 6/9/1959, *J. Rzedowski 10787* (TEX!). Isotypes: MEXU!, MICH!

Plants erect, rarely somewhat spreading ***suffrutescent perennials***, (12) 17.8—37.8 (80) cm tall, with a woody taproot, caudex 5—11 mm diameter with many branches. ***Stems*** strict or occasionally somewhat decumbent, branching throughout, opposite, commonly becoming subopposite and alternate above particularly in inflorescence; older wood tan to gray to black, atratous, glabrous or rarely strigillose, rugose, rimose; younger stems green, deeply and strongly fluted, rarely moderately so, angled in cross section, glabrous to strigillose often becoming glabrate above and hispidulous at axils, trichomes short, white or hyaline, more or less retrorse, 0.05—0.09 (0.11) mm; internodes at midbranch (1.8) 8—27 (42) mm, often exceeding the subtending leaves. ***Leaves*** opposite below, usually becoming alternate bracts in inflorescence, subpetiolate, submembranaceous to subcoriaceous, lanceolate to elliptic, commonly slightly oblanceolate, rarely narrower and linear, (4.4) 7.1—19 (28) by (0.8) 1.1—4.6 (8), length to width ratio (1.3) 3—7.8 (10), apices acute or acuminate, occasionally obtuse, apiculate or mucronate especially below, margins entire, slightly revolute or thickened, base attenutate, decurrent, punctate especially below, glabrate but often hispidulous at least at base and along margins above and nerves below, uninervate, prominent abaxially, often with obvious but somewhat obscure laterals. ***Inflorescence*** often appears solitary, but is usually a compound dichasium of 1—24 flowers with alternate branching. ***Pedicels*** (1) 3.3—11.4 (19) mm long, 0.4—0.6 (0.8) mm in diameter, glabrous or glabrate to strigillose, holding fruit pendant or erect, subtended by a linear to linear-lanceolate bract. ***Calyx*** tube turbinate, usually prominently nerved, glabrous or hispidulousulous at least at base, lobes usually hispidulous, (1.5) 1.6—2.3 (2.6) by (1.3) 1.5—2.4 (2.8) mm, broadening in fruit to 3—3.9 (4.3) mm; lobes (7) 10 (15), (3.5) 4.1—7 (8.6) by (0.2) 0.3—0.5 (0.7) mm, thin, nerved, linear to broadly subulate, apices acute or acuminate, margins entire. ***Corolla*** infundibuliform, yellow, outer petals tinged red, tube (2.5) 2.8—5.2 (6) mm, (0.9) 1.1—1.6 (1.7) mm at base, opening to 2—4.9 (6.6) mm at throat, densely pilose within; limbs 5, acute or obtuse, often appearing mucronate, (6) 7.6—14.2 (16) by (3) 3.5—7.6 (8.1) mm, glabrous. ***Stamens*** filantherous; filaments adnate ca 1.3—2.6 mm below throat, often with a 90 degree bend near point of attachment, (4.8) 5.3—7.5 (8) mm long, glabrous though rarely with a few individual trichomes; anthers exserted 2.3—6 mm, (1.7) 2—2.8 (3) by (0.5) 0.6—0.9 (1.1) mm, dorsifixed, latrorse. ***Pollen*** 60—70 µm.

Ovary bicarpellate, bilobed, each carpel with a single locule and 4 ovules. ***Style*** (11.2) 11.4—16.6 (18) mm, glabrous. ***Stigma*** capitate, just exceeding the anthers or 2—5 mm beyond. **Fruit** with cocci globose or ellipsoid, circumscissile, glabrous, (5) 5.6—6.9 (7.3) by (3.5) 4.3—6 (6.8) mm in diameter; pericarp thin, membranaceous, more or less translucent; each coccus containing 4 seeds or fewer by abortion. ***Seeds*** obovate, trigonal, 5 by 4 by 1.5 mm, testa regularly reticulate.

Narrowly distributed on desert hillsides from central San Luis Potosí south to Guanajuato and Querétaro, and disjunct but apparently rare in Oaxaca from (1300) 1700—1800 (2150) m elevation. With flower or fruit (Jan) Jun to Aug (through Nov).

Steyermark (1932) cited "No specimens seen" for this species and presumably only examined a photograph of the type, although he did annotate a few specimens from San Luis Potosí as *Menodora. mexicana*, *e.g.*, *Schaffner 506* (MO!, NY!, US!); these differ from the description of *M. mexicana* chiefly in holding the fruit erect, rather than upright. Much later, in the late 1970's, James Henrickson, working on the flora of the Chihuahuan Desert, had begun to annotate a few collections from Potosí as a new species, *M. potosiensis*, but had not published the name when Billie Turner took an interest in the genus. Turner agreed with the Henrickson's determinations, and published the species in 1991. Neither Turner nor Henrickson had examined the type of *M. mexicana*, however, though Turner had a colleague inspect it in his stead. In my examination of the type at G-DC, I found it to agree completely with *potosiensis* in all but one character: the fruit is indeed pendant on the type, while those of *potosiensis* are held erect. Later, discussing the species with Jerzy Rzedowski, he informed me that pedicels are often **recurved or erect** on the same plant, and upon receiving exchange material and examining other specimens (*e.g.*, *Messer 127a* (MICH), *Rzedowski 53625* (TEX), *Huerta 1631* (TEX)) found this to hold true. On other specimens, the pedicels are erect but not strictly so, and appear somewhat lazy. For this reason, I place *M. potosiensis* into synonymy under *M. mexicana*.

Another initial concern was the locality of the type collection, given that it had only been collected once that region of Oaxaca since. However, Sousa (1979) had examined the itinerary of Andrieux in Mexico, and both the collection date and locality in Oaxaca were consistent with the itinerary he compiled. The collection by Messer (127a, MICH) confirms that it is (or was) present in Oaxaca, though apparently very rare.

SPECIMENS EXAMINED:

MEXICO: GUANAJUATO: Mpio. Tierra Blanca: El Peñón, 8 km al S de Tierra Blanca, 8/21/1989, E. Ventura E. López 7142 (TEX). **OAXACA:** Circa Oascam [Vicinity of Oaxacan], 7/1834, G. Andrieux 228 (G-DC, K, P); Mexique: nr. Oaxaca, 1833, G. Andrieux s.n. (G); Vicinity of Mitla, 7/8/1971, Ellen Messer 127a (MICH). **QUERETARO: Mpio. Cadereyta:** +/-1 km al W de San Juan de la Rosa, 11/3/2002, E. Pérez G. Ocampo 4295 (TEX); Cerca de Xhodé, en la bajada hacia Taxidhó, 8/26/1998, J. Rzedowski 53625 (TEX); Rancho Nuevo aprox. 200 m al NE, 10/9/1991, Victor M. Huerta B. 1285 (MEXU); 5 km al W de Mesa de León, 6/8/1992, Victor M. Huerta B. 1631 (MEXU). **SAN LUIS POTOSÍ:** 2 km S of road jct to Lourdes, on road from Queretaro to San Luis Potosí, 6/29/1972, F. Chiang et al. 8137 (LL); San Luis Potosí, 1879, J. G. Schaffner 506 (MICH, MO, NY, US); In montibus San Miguelito, 8/1876, J. G. Schaffner s.n. (NY); 5 km NNW de Tierra Nueva, 6/9/1959, J. Rzedowski 10787 (MICH, TEX).

16. *Menodora jaliscana* B. L. Turner

Phytologia 71:5:347, 1991. Holotype: MEXICO: JALISCO: Tecalitlán: Cerca de Gallardo; 10 km al NW de Tepalcatepec, Mich., 10/26/1963, *J. Rzedowski 17503* (MICH).

Plants fastigiate **frutescent perennials**, 30—70 cm tall, with no roots observed. ***Stems*** erect, branching throughout, opposite, rarely subopposite; older wood tan, glabrous, rugose, rimose; younger stems green, often tinged red, striate, not fluted, terete but somewhat angled above in cross section, densely strigillose, trichomes short, retrorse, 0.1 mm; internodes at midbranch (8) 11—12 mm. ***Leaves*** opposite, rarely subopposite, subpetiolate, submembranaceous, elliptic to obovate, (8.4) 8.8—18.82 (22) by (5.1) 5.4—9.1 (12), length to width ratio 1.6—2, often tinged red, apices mucronate or apiculate, margins entire, base cuneate, decurrent, hispidulous along nerves below, base of nerve above, and margins, uninervate, prominent abaxially. ***Inflorescence*** a simple dichasium, rarely appearing solitary with 1—3 flowers. ***Pedicels*** 3 mm long, 0.4 mm in diameter, densely hirtellous or hispidulous, holding fruit pendant, subtended by leaf-like bract, bracts occurring in opposite pairs. ***Calyx*** tube turbinate, slightly nerved, hispidulous especially along nerves, 2 [7—8] by 2.1 mm, broadening in fruit to 3.65 mm; lobes 9—10, 4.67 [8—12] by 0.93 mm, thin, slightly raised but not prominently nerved, oblanceolate, hispidulous, apices narrowly apiculate, margins entire. Seen only in bud, without flowers or mature fruit; from remnant, persistent amphorae of the circumscissile cocci, cocci generally inferred to be globose and ca 6 by 6 mm.

Of very limited distribution along the border of Michoacan and Jalisco from 400—500 m elevation. Flowering in Oct and probably from Aug.

A poorly known species, not known in full flower or mature fruit. It is well isolated and allopatric from other species. I expected from its morphology that it would be close to or possibly conspecific with *Menodora helianthemoides*, but with the molecular data it instead falls into the *mexicana-coulteri* clade.

SPECIMENS EXAMINED:

MEXICO: JALISCO: Tecalitlán: Cerca de Gallardo; 10 km al NW de Tepalcatepec, Mich., 10/26/1963, J. Rzedowski 17503 (MICH); Appox. 3 km al NW de Tepalcatepec, Michoacán, por el camino a Jilotlán, Jalisco, 10/18/1982, José Luis Villaseñor Ríos et al. 291 (MEXU).

17. *Menodora coulteri* A. Gray

Amer. J. Sci. II. 14: 44, 1852. Holotype: MEXICO: HIDALGO: Zimapan, without date, *Coulter 938* (GH). Isotype: K! (3 sheets).

Menodora coulteri A. Gray var. *minima* Steyerm., Ann. Missouri Bot. Gard. 19:121, 1932. Holotype: MEXICO: ZACATECAS: Cedros, *J. E. Kirkwood 20* (MO). Isotype: GH! *Menodora helianthemoides* Bonpl. var. *engelmannii* Steyerm., Ann. Missouri Bot. Gard. 19:119, 1932. Holotype: MEXICO: COAHUILA: near Saltillo, 5/7/1848, *Gregg 44 (MO)*. Isotype: GH! *Menodora hintoniorum* B. L. Turner, Phytologia 71: 5:346, 1991. Holotype: MEXICO: NUEVO LEÓN:

Galeana: Above La Bacerra, 9/12/1989, *Hinton et al. 19679* (TEX!). Isotype: MEXU!

Plants small, mound-forming to somewhat fastigiate ***suffrutescent perennials***, (5) 4.5—19.1 (33) cm tall, with a stout woody taproot, caudex 5—18 mm diameter at ground with many branches. ***Stems*** decumbent or somewhat erect, branching throughout, opposite or subopposite, rarely alternate; older wood tan or gray to black, atratous, glabrous, rugose, rimose, younger stems green, weakly to moderately fluted, terete, weakly if at all angled in cross section, moderately to densely strigillose or strigillose-canescent, trichomes short, retrorse-appressed, white or hyaline, (0.05) 0.06—0.13 (0.15) mm; internodes at midbranch (2) 3—11 (18) mm, very short at terminal end of branch with leaves appearing whorled. ***Leaves*** opposite, rarely becoming alternate above, sessile or subpetiolate, subcoriaceous, linear-lanceolate to linear-oblanceolate, (3) 4.8—13.8 (24) by (0.7) 1.2—2.4 (4) mm, length to width ratio (0.3) 1.2—7.8 (15), apices acute, acuminate, or apiculate, margins entire, thickened or slightly revolute, base attenuate, decurrent, hispidulous, usually punctate, more obviously so below, uninervate, prominently so abaxially sometimes attenuating toward apex and swollen at node. ***Inflorescence*** a few flowered often compound dichasium with mostly opposite branching of 1—3 (6) flowers, flowers often appearing solitary. ***Pedicels*** (1) 2.4—7 (11) mm long, (0.3) 0.4—0.5 mm in diameter, sparsely to densely hirtellous, holding fruit pendant, subtended by a linear-lanceolate to linear-oblanceolate, densely hispidulous bract. ***Calyx*** tube turbinate, densely strigillose or hirtellous, 1—1.7 (2) by (1) 1.1—2.1 (3) mm, broadening in fruit to 2—2.7 (3) mm; lobes (8) 10 (11), (2) 2.5—5.3 (10) by (0.2) 0.3—-0.5 (0.8) mm, thick, nerved, linear to broadly subulate, rarely linear-oblanceolate, apices acute, margins entire. ***Corolla*** infundibuliform, yellow, often red in bud, tube (2) 3—4.5 (5) mm, (0.6) 0.7—1.2

(1.5) mm at base, opening to 1.5—3.8 (6) mm at throat, sparsely to densely pilose within; limbs (4) 5, mucronate, (3.4) 4—9.2 (15) by (2) 2.3—4.5 (6) mm, glabrous. ***Stamens*** 2, filantherous; filaments adnate (0.7) 1—1.6 (1.8) below throat, (2.3) 2.9—5.7 (7) mm long, glabrous; anthers exserted (1.1) 1.8—4.1 (5) above throat, (1.2) 1.5—2.3 (2.5) by 0.5—1 (1.2) mm, occasionally with a minute, linear or conical process extending from the connective, dorsifixed, latrorse. ***Pollen*** 50—60 (70) µm. ***Ovary*** bicarpellate, bilobed, each carpel with a single locule and 4 ovules. ***Style*** (5) 6.4—11.7 (15) mm, glabrous. ***Stigma*** capitate, bilobed, equalling or just exceeding the anthers to ca 2 mm beyond. ***Fruit*** with cocci globose or elliptic, circumscissile, glabrous, (4) 4.3—5.5 (6) by (3) 3.4—5.8 (7) in diameter; pericarp thin, membranaceous, more or less translucent; each coccus containing 4 seeds, fewer by abortion. ***Seeds*** ovate, trigonal, rarely clavate, (3.5) 3.6—4.1 (4) by 2—2.3 (2.4) by 1—1.4 (1.8), testa deeply, more or less regularly reticulate.

Distributed in Mexico on rocky desert hillsides from western Nuevo León to eastern Durango south to northwestern Puebla from (630) 1300—2200 (2900) m elevation. With flower or fruit in almost every month of the year, but principally May to Sep.

Since Steyermark's treatment (1932)of the genus, this species has traditionally been treated as two varieties. Turner (1991) included *M. helianthemoides* var. *engelmannii* within his concept of variety *minima*, as it really seems a merely more canescent form of that variety. The varieties in general were separated by noted differences in the size and shape of leaves, to some extent by vestiture, and primarily in the size of the calyx and corolla. Analysis of the size differences suggests that these differences are artificial segregations along a continuum of variation, particularly with regard to flower size. Moreover, the two varieties for the most part overlapalmost completely in distribution. Since there is no distinct geographic component to the distribution of the two varieties, and the size variations in various chracters are more or less continuous and without discontinuity, I tend to follow Rzedowski and Rzedowski (2004) in treating this as a single, somewhat variable taxon.

SPECIMENS EXAMINED:

MEXICO: without exact locality: Coulter 938 (K). **AGUASCALIENTES:** Ca 20 km E of Rincón de Romos, road to Asientos, between Cerro Altamira and Cerro de San Juan. 1-2 km E of Asientos, 9/6/1967, Rogers McVaugh 23778 (MICH); 35 mi N of Aguascalientes, 8/24/1953, Wayne E. Manning & Margaret S. Manning 531245b (GH). **COAHUILA:**Saltillo, Sr. Adole L. 6435 (US); About 5 mi S of Saltillo, 9/13/1946, Fred A. Barkley 16063b (GH, NY, TEX); 3 km E of Presa de San Pedro, E of Sierra de Chiquihuitillo, 6/18/1972, F. Chiang T. L. Wendt & M. C. Johnston 7945 (LL, MEXU); 2-16 mi E of Carneros Pass on road to Hedionda Grande, 5/2/1959, D. S. Correll & I. M. Johnston 21329 (LL, NY); 3 mi W of Saltillo, route 60, 5/3/1959, D. S. Correll & I. M. Johnston 21385 (LL, MEXU, NY); Arroyo in NE-SW running canyon on NE side of the Sierra de Jimulco, 8.8 mi S of Tejaban de la Rosita, 8/12/1978, Thomas F. Daniel 492 (MICH). Hwy 57, 18 mi SE of Saltillo, 7/15/1979, D. B. Dunn et al. 23178 (MEXU, TEX); [In the valley near Saltillo.] Mexico, 5/1848, J. Gregg 44 (GH); Ca 10 mi E of Saltillo along Hwy 57, W of Cañon de Chorro, 9/27/1980, James Henrickson & P. Bekey 18641 (TEX); Torreón-Saltillo highway. 8 mi W of Saltillo, 9/15/1938, I. M. Johnston 7663 (GH, LP); 2 mi above Arteaga, 8/16/1948, L. A. Kenoyer & Crum 2866 (GH); Collected at Saltillo, state of Coahuila and vicinity. Saltillo, 4/22/1898, Edward Palmer 34 (GH, MEXU, MO,NY, US, UC); Saltillo, 5/15/1898, Edward Palmer 164 (GH, MO, NY, US, UC); Carneros Pass, 9/8/1889, C. G. Pringle s.n. (MEXU); Sierra de la Paila, 10/15/1910, C. A. Purpus 5020 (MEXU, UC); 8 mi W of Saltillo, 9/15/1938, Forrest Shreve 8735 (MICH, US); Entrada de la Carrtera 54 a Rancho Los Angeles, 52 km al Sur de Saltillo, 8/29/1995, Neil Snow & Jesús Valdéz-Reyna 6708 (MEXU); 11 km NE of Jimulco, 6/28/1941, L. R. Stanford et al. 46 (GH, MO, NY, UC); In arroyo, 3 km SW of Fraile, 7/11/1941, L. R. Stanford et al. 334 (GH, MEXU, MO, NY, UC); 26 mi SW of Monterrey, 12/1/1945, Barton H. Warnock & F. A. Barkley 14713m (TEX); 38 mi SW of Monterrey, 12/1/1945, Barton H. Warnock & F. A. Barkley 14756m (TEX); At the top of winding road 30 mi SW of Monterrey, 12/1/1945, Barton H. Warnock & F. A. Barkley 14819 (GH, MO, NY, TEX, UC); 2 mi W of Saltillo, road to Torreón, 7/2/1939, Stephen S. White 1653 (GH, LP); Sierra Madre Oriental, valley floor along MEX Hwy 40 E of Saltillo and 62 rd km W of Monterrey, 6.3 mi W of NL state line, 6/3/1982, R. D. Worthington 8369 (TEX). **Mpio. General Cepeda:** S. Paila (Valle Seco), 7/1/1944, Hinton et al. 16518 (NY, US); On NW side of Sierra La Paila, Cañada el Aquirreno, 4/5/1990, Lindsay Woodruff et al. 318 (TEX). **DURANGO:** N end of Sierra del Rosario about 20 km crowflight SW of Mapimi (approach from mine 3 km E of Santa Librada). 11/2/1973, T. L. Wendt et al. 10013a (LL). **GUANAJUATO: Mpio. San Luis de La Paz:** 3 km al W de Pozos, 10/31/1986, J. Rzedowski 41653 (TEX); 3 km al W de Pozos. Sobre la carretera a la autopista, 6/28/1987, J. Rzedowski 43474 (TEX); 3 km al W de Pozos, 6/28/1987, J. Rzedowski 43498 (TEX); Cerca de Pregón, 8/22/1988, J. Rzedowski 47054 (TEX); 3 km al S de Pozos, sobre la carretera a San José Iturbide, 8/10/1991, J. Rzedowski 50810 (TEX); 5 km al W de Pozos, sobre el camino a la autopista, 10/24/1994, Rzedowski 52588 (MEXU); Cerro Candelaria, 15 km al E de San Luis de la Paz, 10/24/1988, E. Ventura & E. López 6219 (MEXU); Misión Chichimeca, 6 km al S de San Luis de la Paz, 12/12/1989, E. Ventura & E. López 6837 (TEX); San Nicolás, 8 km al W de Pozos, 8/7/1989, E. Ventura & E. López 7018 (TEX); La Mina Grande, 8 km al E de Pozos, 8/10/1989, E. Ventura & E. López 7059 (TEX); Las Minas, 10 km al E de Pozos, 8/24/1989, E. Ventura & E. López 7163 (TEX); La Misión de la Cruz, 7 km al W de San Luis de la Paz, 10/11/1989, E. Ventura & E. López 7476 (TEX); La Mina Grande Pozos, 7/17/1990, E. Ventura & E. López 8296 (TEX); Cerro Prieto, 7/19/1990, E. Ventura & E. López 8341 (TEX); La Misión de Abajo, 7/23/1990, E. Ventura & E. López 8391 (TEX); San Nicolás, 7/30/1991, E. Ventura & E. López 9348 (TEX). **HIDALGO:** Vicinity of Zimapán, 6/22/1947, L. A. Kenoyer 1079 (GH); Vido, 4/15/1951, E. Matuda 21172 (MO); Ixmiquilpan, 8/15/1905, C. A. Purpus 1447 (GH, MO, NY UC); Near Tula, 7/3/1905, J. N. Rose et al. 8311 (US); 6 km al N de Tasquillo, 9/7/1965, L. González Quintero 3082 (MICH); 10 km al SE de Ixmiquilpan, 10/27/1965, L. González Quintero 3203 (MICH); Near Ixmiquilpan, 7/3/1905, J. N. Rose et al. 9007 (NY, US); Deep barranca E of highway ca 5 mi S of Tula toward Tepeji del Rio, 8/9/1957, Richard M. Straw & David P. Gregory 1160 (GH, MEXU, MICH, UC). **Mpio. Ajacuba:** "Las peñas coloradas," cerro al N del poblado Emiliano Zapata, vertiente S de la sierra de Chicavasco, ejido E. Zapata, 6/2/1989, Irene Diaz Vilchis & Abraham Valverde G. 500 (MEXU). **Mpio. Cardonal:** Cardonal, 19 km al E de Ixmiquilpan, 7/9/1980, Rafael Hernández Magaña & R. Hernández V. 4607 (MEXU, MO); Cardonal, 21 km al E de Ixmiquilpan, 9/11/1981, Rafael Hernández Magaña & I. Hernandez 6456 (MEXU). **NUEVO LEON:** About 10 mi SW of Villa Santa Catarina, 7/12/1946, A. Hernandez et al. 16m539 (TEX); On the Matehuala-Dr. Arroyo Hwy, at San Luis Potosi-Nuevo Leon border, 6/21/1972, F. Chiang et al. 8076 (LL, MEXU); 25 mi SW of Monterrey on Monterrey-Saltillo Hwy 54, 5/27/1966, James S. Wilson 10871 (TEX); About 40 km SW of Monterrey, 2/28/1946, Joe C. Johnson & Fred A. Barkley 16241m (TEX); 8.5 km SE of San Jose de la Popa, 3/17/1973, M. C. Johnston et al.10259 (LL).

Mpio. Aramberri: nr. Puentes, 5/13/1992, Hinton et al. 21959 (TEX); Sandia to Santa Gertrudis, 7/20/1993, Hinton et al. 23042 (TEX); Sandia to Santa Gertrudis, Aramberri, 9/9/1996, Hinton et al. 25823 (TEX); 4.6 mi N of La Ascensión on Hwy 61; 22.4 mi S of Pablillo, 7/5/1985, Melissa Luckow 2664 (TEX). **Mpio. Galeana:** S slope Potosí, 6/25/1983, Hinton et al. 18447 (MEXU, TEX); La Becerra, above, 9/12/1989, Hinton et al. 19679 (MEXU, TEX); Rancho Aguililla, 7/22/1995, Hinton et al. 25357 (TEX); La Trinidad, 8/3/1995, Hinton et al. 25487 (TEX); S of Rancho Aguililla, 9/28/1996, Hinton et al. 25897 (TEX); San Jose del Alamito to El Coyote, 7/15/1998, Hinton et al. 27198 (TEX); 1.5 mi E of Galeana, Dr. Arroyo Hwy, on roadway to San Antonio de Peña Nevada, 9/8/1999, James Henrickson & Brian Vanden Heuvel 22433 (MEXU, TEX); 2.3 mi NW of Ejido El Potosi, ca 12 mi N of San Roberto Junction, 10/24/1982, Scott Sundberg et al. (MEXU, NY, TEX); Ca 1 km N of El Potosí, on lone hill W of gravel road to mountain, 5/24/2002, Timothy W. Chumley et al. 7402 (TEX); In hills N of Nuevo Leon Hwy 31 ca 1 air km E of Santo Domingo, ca 6 air km NE of El Tokio, ca 10 air km NE of San Roberto Junction, 9/12/2002, Timothy W. Chumley et al. 7406 (TEX). **Mpio. Mier y Noriega:** Loc. a 4 km al E de El Fraile (en la frontera con San Luis Potosí, en el sur del estado de NL), 5/19/1982, Ruben Sánchez Silva 29 (MEXU). **PUEBLA:** 16 km al S de La Esperanza, 4/13/1987, Antonio Salinas T. & C. H. Ramos F-3778 (TEX). **QUERETARO:** 3 km al NE de Bernal, sobre el camino a Tolimán, 3/23/1968, J. Rzedowski 25565 (MEXU). **Mpio. Cadereyta:** 5 km al S de Vizarrón, sobre el camino a Cadereyta, 8/16/1989, J. Rzedowski 48714 (TEX); 15 km al N de Cadereyta, 7/31/1990, J. Rzedowski 49621 (TEX); Cerro Juárez, 8 km de Vizarrón, 5/11/1978, S. Zamudio 2810 (MEXU); 3.5 km al NE de Vizarrón, 8/12/1978, S. Zamudio 3057 (MEXU); 1 km al SE de La Tinaja, 8/19/1996, S. Zamudio E. Pérez C. 9967 (MEXU); Parador El Tapozán, 5/27/1990, S. Zamudio R. 7872 (TEX). **SAN LUIS POTOSÍ:** E of San Luis

Potosí, Hwy 86; 10 mi from Juarez Circle, 7/5/1971, M. Andreasen et al. 527 (MICH, MO); 22 km W of San Francisco on San Luis Potosí - Rioverde hwy, 7/1/1972, F. Chiang et al.8204 (LL, MO, NY); Km 8 carretera SLP Rio Verde, 7/26/1970, Antonio Gomez Gonzalez 1100 (MEXU); 15.7 rd mi E of El Huizache jct at Hwy 57 on MEX 80 to Ciudad del Maiz, 9/24/1978, James Henrickson & E. Lee 17561 (TEX); 13 mi N of Matehuala along Hwy 57, 9/25/1978, James Henrickson & E. Lee 17597 (TEX); Road, eastern San Luis Potosí, 8/24/1947, L. A. Kenoyer 2396 (GH); 12 mi N of San Luis Potosí, along Hwy 57, 7/12/1963, R. L. MacGregor et al. 550 (LL, US); 2-1/2 mi NW of Santo Domingo, 7/17/1966, Reid Moran 13389 (UC, US); Charcas, 7/31/1934, C. L. Lundell 5152 (MEXU, TEX); Charcas. [W of San Diego.], 7/21/1934, C. L. Lundell 5358 (MICH); Charcas. 7/31/1934, C. L. Lundell 5751 (MICH, US); Along road between Doctor Arroyo, state of Nuevo Leon, & Matehuala, 6/17/1898, E. W. Nelson 4535 (US); Chiefly in the region of San Luis Potosí, 22° N Lat. Altitude 6,000 — 8,000 ft, 1/1/1878, C. C. Parry & Ed. Palmer 300-1/2 (GH); Chiefly in the region of San Luis Potosí, C. C. Parry & Ed. Palmer 571 (US); 2 km al E. de Laguna Seca, km 20 carretera SLP-Tampico [SLP-Antiguo Morelos], 11/6/1954, Rzedowski 4223 (LL, MICH, US); San Luis Potosí, J. G. Schaffner 67 (GH, MEXU, NY); San Luis Potosí: 0.5 mi E of jct of Rt 57 from Huizache Jct to San Luis Potosí on rd to Guadalcazar, 7/21/1991, B. B. Simpson 91-VII-17-2 (TEX); Camino al Real de Catorce, 18 km del entronque Matehuala-San Luis Potosí, 6/5/1990, J. A. Villarreal et al. 5738 (MEXU). **Mpio. Ahualulco:** Km 13 de la carretera San Luis Potosí-Charcas, 7/27/1976, Martha Bustos et al. s.n. (MEXU). Mpio. **Guadalcazar:** 2 mi SE of jct Hwy 57 on rd to Cerritos, just W of Palo Altos, 9/11/1988, Guy Nesom & Julia Wells 6611 (TEX). **Mpio. Soledad Diaz Gutierrez**: 2 km al E. de Laguna Seca, km 20 carretera SLP-Antiguo Morelos, 11/6/1954, Rzedowski 4223 (LL); Laguna Seca, 7/7/1971, Rzedowski 28225 (MICH, TEX). **Mpio. Vanegas:** 10 km adelante del entronque San Tiburcio, de la carretera Saltillo-Zacatecas. Sitio 2, 8/12/1976, Martha Bustos & Julio Villa s.n. (MEXU). **Mpio. Villa de Guadalupe:**10 km adelante de la desviación Bonita-Charcas, 8/7/1976, Martha Bustos et al. s.n. (MEXU). **Mpio. Zaragoza:** About 9 mi E of San Luis Potosí on Hwy 86 between San Luis Potosí and Ciudad Valles; 2.9 mi W of jct with rd to Valle de Zaragoza, 7/5/1985, Melissa Luckow 2698 (TEX). **TAMAULIPAS:** Ca 46 km WNW of Jaumave; 10 rd km W of Miquihuana on rd to La Perdida, 10/8/1982, James Henrickson & W. Hess 19144 (TEX); 6 km al SE de Tula, 2/9/1984, L. Hernandez & F. G. Medrano 954 (MEXU). **Mpio. Miquihuana:** 4 km al W de Tanque de Eguia, hacia Presa de San Carlos, 5/23/1976, F. G. Medrano et al. 9048 (MEXU); Loc. 9 km al oeste de Miquihuana, 9/20/1984, P. Hiriart et al. 332 (MEXU). **Mpio. Reynosa:** 0.73 km al SW de Reynosa en el camino a China, NL, 5/14/1985, F. González Medrano FGM14615 (MEXU). **ZACATECAS:** 10 km WNW of Tecolotes, on rd to Coapa, 6/17/1972, F. Chiang et al. 7896 (LL, MEXU, NY); Near arroyos, nothern Zacatecas, 6/1908, J. E. Kirkwood 20 (GH); Arroyos in hills. Cedras, 7/1/1908, Francis E. Lloyd 140 (US); Campo experimental Noria de Guadalupe. CNIZA. 35 km al S Concepción del Oro, 7/12/1975, F. G. Medrano 8077 (MEXU); [Near Rancho] Sabanillo. 20 mi SE of Conc. del Oro, 9/9/1939, Forrest Shreve 9364 (GH, MICH, UC); Pico Teyran, 9/12/1939, Forrest Shreve 9394 (GH, MICH, UC).

18. *Menodora tehuacana* B.L. Turner

Phytologia 71:5:355, 1991. Holotype: MEXICO: PUEBLA: 1.5 km al E de Tehuacán, rumbo a Coxcatlán, 8/6/1981, *Fernando Chiang C. 2239* (TEX!). Isotype: MEXU.

Plants mound-forming to upright suffrutescent perennials, (9) 12.2—25.3 (30) [75] cm tall, with a woody taproot, caudex to 12 mm diameter with many branches. ***Stems*** decumbent to erect, branching throughout, opposite becoming alternate in inflorescence; older wood red to tan, oldest waxy white gray to gray to black, atratous, pilose becoming glabrate, rugose, +/- rimose; younger stems green, often tinged red, shallowly to moderately fluted, occasionally more so above, canaliculate decurrent groove obscure if present, terete, often slightly more angled above with nodes rarely appearing somewhat flattened in cross section, hirsute-pilose usually more densely so above, trichomes long, spreading, white or hyaline, 0.3—0.6 (0.8) mm; internodes at midbranch (4) 6—17 (27) mm. ***Leaves*** opposite below becoming alternate bracts in inflorescence, subpetiolate, submembranaceous, elliptic to oblanceolate, often obovate or ovate below, (4.6) 9—21.6 (32) by (1.5) 3—7.5 (10.5), length to width ratio (2) 2.4—3.5 (4.6), pilose, especially along nerve below and margins above, and punctate, most obviously below though sometimes obscure, apices obtuse and mucronate/ apiculate, rarely subcordate, margins entire, thickened, base cuneate, decurrent, uninervate, nerve prominent abaxially but usually attenuating to apex, swollen or not at node, lateral nerves often quite apparent. ***Inflorescence*** often appearing solitary, but usually a simple to compound dichasium of 1—8 flowers, lowest branches usually opposite but otherwise alternate. ***Pedicels*** 2—8.2 (12) mm long, (0.3) 0.4—0.6 mm in diameter, hirsute-pilose, often densely so, holding fruit pendant, subtended by an elliptic to oblanceolate bract. ***Calyx*** gamosepalous, persistent, often tinged red; tube turbinate, nerved but not prominently, pilose, (1.3) 1.4—2 (2.2) by (1.4) 1.5—2.2 (2.5) mm, broadening in fruit to (2.3) 2.7—3.5 (3.6) mm; lobes 9—10 (12), (3.8) 4.6—8.2 (9.9) by (0.3) 0.4—0.7 mm, thin, nerved, occasionally prominently so, linear to oblanceolate, pilose and often obscurely punctate, apices acute, margins entire. ***Corolla*** infundibuliform, yellow, outer petals tinged red, tube (2.5) 3.3—

5.9 (7.2) mm, (0.6) 0.7—1.2 (1.4) mm at base, opening to (2.1) 2.5—4 (4.6) mm at throat, pilose within; limbs 5, obtuse, rarely acute, (5.4) 6.4—10.2 (10.8) by (3) 3.2—4.9 (5.4) mm, pilose, rarely glabrous. ***Stamens*** filantherous; filaments adnate 1.4—3 mm, (5) 5.6—9.4 (10.8) mm long, glabrous; anthers exserted 3—6.4 mm, (1.6) 1.9—2.6 (2.7) by 0.5—0.8 (0.9) mm, rarely with a linear process extending from the connective above, dorsifixed, latrorse. ***Pollen*** 60—70 (90) mm. ***Ovary*** bicarpellate, each carpel with a single locule and 4 ovules. ***Style*** (6.5) 7.5—12 (13.5) mm, glabrous. ***Stigma*** capitate, equalling or just below anthers. ***Fruit*** with cocci globose or obovoid, circumscissile, glabrous, (4.9) 5.4—6.7 (7.3) by (3.2) 4.5—6.5 (7.9) mm in diameter; pericarp thin, membranaceous, more or less translucent; each coccus containing 4 seeds, fewer by abortion. ***Seeds*** elliptic to obovate, plano-convex, rarely trigonal or somewhat lenticular, (4.8) 4.9—5.4 (5.5) by (2) 2.4—3.2 (3.5) by (0.5) 0.7—1.2 (1.4) mm, light tan, alveolae poorly developed, irregularly reticulate, often scalloped, raphal rib differentiated and usually prominent.

Of limited distribution on limestone in the region of Tehuacán, Puebla from 1500—1850 m elevation. Flowering early to mid-Jun (through Aug), with fruit (Jun) Jul to Sep.

My initial impression of this taxon based on its morphology was that this was a segregate that belonged within the scope of *Menodora helianthemoides*. In the molecular phylogeny, however, it is the sister taxon to *M. helianthemoides.* Morphologically, however, it is indistinct, with the plants tending to be larger vegetatively than *M. helianthemoides*, with slightly larger leaves, often with evident (though not prominent) lateral veins, and more is densely pilose than *M. helianthemoides* with longer trichomes. While I maintain this taxon as a species, it might be better placed as a variety of *M. helianthemoides*.

SPECIMENS EXAMINED:

MEXICO: PUEBLA: Mpio. Caltepec: In the vicinity of San Luis Tultitlanapa [San Luis Atolotitlán], near Oaxaca, 6/15/1908, C. A. Purpus 3392 (GH, MO, NY, UC, US). **Mpio.Tehuacán:** 6 km al SW de Tehuacán, Puebla, por la carretera a Huajuapan de León, 9/2/1979, F. Chiang et al. F-330 (MEXU); 1.5 km al E de Tehuacán, rumbo a Coxcatlán, 8/6/1981, Fernando Chiang C. 2239 (TEX); 3-4 km al NW de El Riego, Meseta de San Lorenzo, Tehuacán, Puebla, 9/6/1981, F. Chiang et al. F-2279 (MEXU); Meseta de San Lorenzo, 7/28/1983, F. Chiang et al. F-2332 (MEXU, TEX); 11 km al ESE de Tehuacán (Meseta del Riego), 6/9/1985, F. Chiang C. et al. F-2603 (LL); Tehuacan (Meseta del Riego), 8/7/1938, E. Lyonnet 2254 (US); El Riego, 6/1/1905, C. A. Purpus 1319 (MO, NY, UC); San Antonio Cañada, a 4.5 km al E del poblado, 7/19/1990, Antonio Salinas T.et al. 5487 (MEXU); W of Tehuacan on La Mesa above El Riego, 7/15/1961, C. E. Smith, Jr. et al. 4123 (G, GH, MEXU, NY, TEX). **Mpio. Zapotitlán de las Salinas:** Tehuacán, 6/1/1912, C. A. Purpus 1319 (G, P); Near Tehuacán, 8/1/1901, J. N. Rose & Robert Hay 5931 (US); "El Tablón." 2-3 km al SSE de Zapotitlán de las Salinas, 7/22/1992, Antonio Salinas T. & Verónica Juárez-Jaimes 6957 (MO); Cerro localizado 700 m al N del poblado de Zapotitlán Salinas, 8/1/1990, Alfonso Valiente B. et al. 741 (MEXU).

19. *Menodora helianthemoides* Bonpl. in Humb. & Bonpl.

Pl. Aequin. 2: 98, tab. 110. 1812. Holotype: MEXICO: HIDALGO: [from protologue: *Inter Actopan et vicum Magdalenae*], *Bonpland 4114* (P!); Isotype: (P!, G!)

*Menodora helianthemoide*s Bonpl. var. *parviflora* Greenm., Proc. Amer. Acad. Arts 34:569, 1899. Holotype: MEXICO: HIDALGO: Bare hills above Pachuca, 2591 m, 7/30/1898, *C. G. Pringle 6918* (MO!) Isotypes: F, GH, MEXU, P!, US!, UC! *Menodora helianthemoide*s Bonpl. var. *humilis* Steyerm., Ann. Missouri Bot. Gard. 19: 118, 1932. Holotype: MEXICO: SAN LUIS POTOSÍ: region of San Luis Potosí, 22° N. Lat., 1829—2439 m, 1878, *Parry & Palmer 571* p.p. (MO!); Isotypes, in part: (F, GH!, NY!). *Menodora helianthemoide*s Bonpl. var. *magniflora* Steyerm., Ann. Missouri Bot. Gard. 19: 118, 1932. Holotype: MEXICO: region of San Luis Potosí, 22° N. Lat., 1829—2439 m, 1878, *Parry & Palmer 570* p.p. (MO!); Isotypes, in part: (F, GH!, NY!, P!). *Menodora magniflora* (Steyerm.) B. L. Turner, Phytologia 71:5:348, 1991.

Illustrations: Pl. Aequin. tab. 110.

Plants small, mound-forming, occasionally twining suffrutescent perennials, (4) 8—16 (20) cm, reported to 40 cm tall, with a woody taproot, caudex to 2 cm at ground with many woody branches. ***Stems*** spreading to erect, occasionally twining, branching throughout, opposite below, becoming subopposite to more frequently alternate in inflorescence; older wood tan to gray to black, atratous, glabrate, rarely densely hispid, rugose or rimose; younger stems green, often tinged red, obscurely to moderately fluted, occasionally more so above, terete but often flattened at nodes above in cross section, strigillose to strigose-pilose, trichomes short and retrorse-appressed to long and spreading, hyaline or white, often longer above, (0.05) 0.9—0.25 (0.35) mm; internodes at midbranch (3) 5—16 (32), rarely exceeding 20 mm. ***Leaves*** opposite, frequently becoming alternate bracts in inflorescence, often appearing whorled with short internodes at terminal ends of branches, subpetiolate, occasionally sessile, submembranaceous or occasionally more subcoriaceous, elliptic tending towards slightly ovate-lanceolate or oblanceolate, often obovate below, rarely bifid, largest near midbranch, (3.9) 8—16.5 (25.2) by (1.4) 2.5—6 (10.8) mm, length to width ratio (2) 2.3—3.5 (4.4), often tinged red, strigillose to pilose, especially above and along nerve below, rarely glabrate above, and punctate, usually more notably so below, apices acute, apiculate, or mucronate, occasionally obtuse especially below, rarely cordate below, margins entire, somehat thickened, base cuneate, decurrent, prominently univervate abaxially but attenuating toward apex, usually slightly swollen at node. ***Inflorescence*** often appearing solitary, but usually a few-flowered, occasionally compound dichasium of 1-5 flowers. ***Pedicels*** (1) 2.4—7.2 (12) mm long, (0.15) 0.4—0.7 (0.8) mm in diameter, often tinged red, densely strigillous-hirtellous to pilose, holding fruit pendant, subtended by a elliptic to elliptic-lanceolate, rarely broader, strigillose to pilose bract. ***Calyx*** gamosepalous, persistent, often tinged red; tube turbinate, usually prominently nerved, hirsute or pilose especially along nerves, rarely glabrate, (1.4) 1.6—2.1 (2.4) by (1.5) 1.7—2.3 (2.6) mm, broadening in fruit to (2.3) 2.7—3.8 (4.5) mm; lobes (9) 10 (11—18), (2.4) 3.7—7 (8) by (0.3) 0.4—0.8 (0.9) mm, thin to thick, prominently nerved, linear to broadly subulate, ocasionally oblanceolate, adjacent lobes occasionally fused, hirtellous or pilose and usually punctate, apices acute or acuminate, margins entire. ***Corolla*** infundibuliform, yellow, outer petals often red or red-tinged in bud , tube (2.6) 3—5 (5.5) mm, (0.6) 0.7—1.1 (1.2) mm at base, opening to (2) 2.3—3.6 (4.2) mm at throat, densely pilose within; limbs (4) 5 (6), obtuse to broadly acute, occasionally appearing mucronate, (5.6) 7—12.6 (15.8) by (3) 3.7—6.3 (7.2) mm, glabrate to sparsely pilose. ***Stamens*** filantherous; filaments adnate (1.3) 2—2.5 mm below throat, (3.6) 5—8.2 (9.5) mm long, glabrous; anthers exserted ca (2) 4—6 mm abovce throat, (1.7) 1.8—2.6 (2.9) by (0.4) 0.5—0.8 (0.9) mm, rarely with a linear process extending from the connective, dorsifixed, latrorse. ***Pollen*** (50) 60—70 (80) µm. ***Ovary*** bicarpellate, bilobed, each carpel with a single locule and 4 ovules. ***Style*** (8.6) 9.5—13 (15) mm, glabrous. ***Stigma*** capitate, occasionally very broadly so, often bilobed. ***Fruit*** with cocci globose to obovoid, circumscissile, glabrous, (4.7) 5.2—6.8 (7.1) by (3.4) 4.4—6.1 (6.9) mm in diameter; pericarp thin, membranaceous, more or less translucent; each coccus containing 4 seeds, fewer by abortion. ***Seeds*** obovate or elliptic, rarely crescent-shaped or clavate, trigonal or slightly flattened and plano-convex, (3.8) 4.2—5 (5.3) by (1.9) 2.2—3.1 (3.4) by (1) 1.1—1.6 (1.9) mm, testa light tan, regularly reticulate, often scalloped, raphal rib usually prominent.

Distributed from southern San Luis Potosí, Querétaro, and Guanajuato to Hidalgo, and slightly disjunct in the Tehuacán region of Puebla, from (1800) 2000—2700 (2800) m elevation. Flowering (Jan, late Mar to Apr) May—Aug, with fruit May to Aug (through Oct).

As with *Menodora coulteri*, varieties of *M. helianthemoides* have been segregated mostly by vestiture and floral size differences, and as with *M. coulteri*, these represent segments of a continuous range of variation. Turner (1991) had dispensed with most of the varieties as treated by Steyermark (1932), but believed var. *magniflora* to be distinct and raised it to specific status. The generally larger flowers and longer trichomes of *magniflora* are striking, but taken in the context of *helianthemoides* as a whole, these only represent the larger extremes in the continuum of character measurements. For this reason, I follow the treatment of Rzedowski and Rzedowski (2004) in reducing the varieties to synonymy in favor of a single, slightly polymorphic species.

SPECIMENS EXAMINED:

MEXICO: GUANAJUATO: Dentro de la propriedad de Los Ricos, otro lado del camino del donde está la casa, 6/18/1978, Elizabeth Arguelles 1067 (MEXU); Guanajuato. des collines de la Presa - août, 1/1/1902, A. Dugés 18 (GH, NY). **San Felipe:** Alrededores de El Coecillo, 8 km al SSW de San Felipe, 8/7/1987, R. Galvan J. D. Galvan 2745 (MEXU, NY, TEX). **Mpio. San Luis de la Paz:** Santa Brígida, camino a Pozos, 7/18/1991, E. Ventura & E. López 9291 (TEX); Paso del Colorado por Pozos, 10/14/1991, E. Ventura & E. López 9679 (TEX). **Mpio. Victoria:** Los Sauces de Higueras, 8/9/1990, E. Ventura & E. López 8505 (TEX); Cañada de Trancas, 8/13/1990, E. Ventura & E. López 8525 (TEX); Alrededores de Milpillas del Pito, J. Rzedowski 50957 (TEX); Cerro del Xoconoshtle, frente al Nogal, 6/28/1986, S. Zamudio Cols. 4021 (MEXU). **HIDALGO:** Above Pachuca, 7/30/1898, C. G. Pringle 6918 (MO, P, US, UC); Xihuingo, Tepeapulco, 6/28/1964, I. Martínez M. s.n. (MEXU); Km 218, N of Zimapán, 7/10/1948, Irma Schnooberger 7859 (MICH); Between Pachuca and Real del Monte, 7/19/1905, J. N. Rose et al.8712 (US); 20 km al E de Actopan, 5/14/1966, L. González Quintero 3572 (MICH); +/- 1 km al NNW de Real del Monte, 6/5/1976, Miguel Medina 1356 (MEXU); Faldas del cerro de Xihuingo, 6/28/1964, Olga Cota G. 18 (TEX); 6 km NE de Tepeapulco, sobre las laderas del Cerro Xihuingo, 6/28/1964, Rzedowski 18316 (MICH, TEX, US); Cerro de Santa Ana, 4 km al ESE de Tepeapulco, 7/19/1963, Rzedowski 18316 (MEXU, US). **Mpio. Ajacuba:** "las penas coloradas," cerro al N del poblado Emiliano Zapata, vertiente S de la sierra de Chicavasco, ejido E. Zapata, 6/2/1989, Irene Diaz Vilchis & Abraham Valverde G. 500 (TEX); "Rincon del gato," barranca al N del poblado Emiliano Zapata. sierra de Chicavasco, ejido Emiliano Zapata, 5/28/1989, Irene Diaz Vilchis & Abraham Valverde G. 439 (MEXU); "La barranca" localidad al N del poblado Emiliano Zapata vertiente S de la sierra de Chicavasco, ejido

Emiliano Zapata, 5/28/1989, Irene Diaz Vilchis & Abraham Valverde G. 439 (MEXU). **Mpio. Metzquititlan:** El Banco, 10 km al E de Metzquititlan, 3/28/1981, R. Hernández Magaña & David Rodríguez 5714 (MEXU, MO). **Mpio. Pachuca:** Pachuca, [without date], C. A. Purpus 434 (UC); Pachuca, 7/1903, C. A. Purpus 437 (MO, UC, US); 4 km al NE de Pachuca, por la carretera Pachuca-Zacualtipán (1 km antes del entronque El Chico-Real del Monte), 5/6/1978, Isidoro Sánchez V. 2161 (MEXU, MO); 4 km al NE de Pachuca, por la carretera Pachuca-Zacualtipan (1 km antres del entronque El Chico-Real del Monte), 5/6/1978, José García P. 641 (MO); 4 km al norte de Pachuca, 5/4/1980, Rafael Hernández Magaña & R. Hernández V. 4339 (MEXU). **Mpio. Tepeapulco:** Cerro de Santa Ana, 4/2/1976, A. Ventura A. 1504 (CTES, US, MEXU); Cerro Santa Ana, 6/23/1976, A. Ventura A. 1652 (MEXU, MO). **Mpio. Zimapan:** 10 km al N de Zimapan, hacia a la Mina San Miguel, 6/28/1981, R. Hernández M. et al. 6289 (MEXU, MO). **MEXICO:** Cerros al norte de Huehuetoca, Edo. de México, límite con el Edo. de Hidalgo, 8/12/1951, D. B. Gold & Eheberle 21729 (NY); C. de San Cristobal, Valle de México, 5/25/1951, E. Matuda 21081 (MEXU); Ca 2 km al SSE de Coacalco, 4/23/1967, R. Cruz Cisneros 1674 (LL, MICH); Laderas orientales del Cerro Gordo, cerca de San Juan Teotihuacán, 4/24/1966, Rzedowski 22204 (MICH). **Mpio. Coyotepec:** Sierra de Alcaparrosa, 5/1/1982, Judith E. N. Reynos 103 (MEXU). **Mpio. Huehuetoca:** Cerro Mesa la Ahumada, 5/6/1980, Romero-Rojas 353 (MEXU). **PUEBLA:** Mória, 6/15/1909, Nicolas Aresene s.n. (G). **Mpio. Caltepec:** Base of Cerro El Gavilán. vicinity of San Luis Tultitlanopan, Jose Panero 3441 (TEX); Cerro El Gavilán, al SE de Caltepec, 8/3/1984, P. Tenorio L. & C. Romero de T. 6768 (MEXU, TEX). **QUERETARO:** Los Cues, 7/20/1981, Elizabeth Arguelles 1671 (MEXU). **Mpio. Amealco:** Camino Queretaro-Amealco, 5 km aprox. pasando entronque para Huimilpan, 5/26/1985, Elizabeth Arguelles 2278 (MEXU); Km 4.5 camino de Huimilpan a Amealco, 7/12/1987, Elizabeth

Arguelles 2992 (MEXU). **Mpio. Cadereyta:** Jardín Botánico Regional de Cadereyta "Ing. Manuel Gonzalez de Cosio.", 9/14/1993, C. Orozco L. et al. 10291 (MEXU); Jardín Botánico Regional de Cadereyta "Ing. Manuel Gonzalez de Cosio.", 6/8/1992, Javier Orozco H. et al. 9917 (MEXU); Jardín Botánico Regional de Cadereyta "Ing. Manuel González de Cosío", 4/3/1992, Rafael Hernández M. et al. 9741 (MEXU); Jardín Botánico Regional de Cadereyta "Ing. Manuel Gonzalez de Cosio.", 10/5/1993, R. Hernández M. et al. 10349 (MEXU). **Mpio. Ezeqiel Montes:** Alrededores de Bernal, 6/5/1992, Rafael Hernández M. et al. 9907 (MEXU). **SAN LUIS POTOSÍ:** San Luis Potosí, 1877, J. G. Schaffner 503 (NY); San Luis Potosí, 1877, J. G. Schaffner 68 (MEXU, GH).

20. *Menodora scoparia* Engelm. ex A. Gray

Bot. Calif. 1:471, 1876. Lectotype (Steyermark, Ann. Missouri Bot. Gard. 19:148, 1932): MEXICO: COAHUILA: About Saltillo, 9/1848, *J. Gregg 527* (MO!). Isolectotypes: GH!, K!

Plants fastigiate subherbaceous to ***suffrutescent perennials***, (17) 24—57.2 (70) cm tall, with a woody taproot, caudex 3-20 mm diameter with many branches; rarely appearing almost aphyllous. ***Stems*** strict, branching remote, rarely throughout, opposite or alternate, often opposite below becoming alternate in inflorescence; older wood tan to gray to black, atratous, strigillose, rugose, rimose; younger stems green, shallowly to moderately fluted, occasionally more deeply so, canaliculate decurrent groove obscure, terete, occasionally strongly angled in cross section, glabrate (minutely papillate under magnification) to strigillose, often more densely so below, often hispidulous in axils, trichomes rudimentary and minutely papillate under magnification or very short, white or hyaline, retrorse, 0.03—0.07 (0.09) mm; internodes increasing dramatically in length to midbranch, (6) 13—33 (58) mm, usually well exceeding the subtending leaves. ***Leaves*** opposite below, becoming alternate just before inflorescence, rarely opposite throughout, often irregularly alternate or opposite, sessile or subpetiolate, submembranaceous, linear to linear-lanceolate or linear-oblanceolate, largest usually near midbranch, (2) 5.7—16.3 (22) by (0.3) 0.5—1.4 (2.9), length to width ratio (6.3) 7.8—18.7 (28), glabrate to hispidulous, apices acute, occasionally acuminate or apiculate, margins entire, thickened, base attenuate, decurrent, uninervate, nerves prominent abaxially basally attenuating to apex or commonly obscure throughout, swollen or not at node. ***Inflorescence*** a compound dichasium of 1—10 flowers with alternate branches. ***Pedicels*** (2) 2.3—20.9 (45) mm long, (0.3) 0.4—0.5 (0.6) mm in diameter, glabrate (usually minutely papillate under magnification) to sparsely strigillose, holding fruit erect, subtended by a linear, glabrous to sparsely hispidulous bract. ***Calyx*** tube turbinate, glabrous to sparsely hirtellous, (1) 1.4—2.3 (3.2) by (1.4) 1.6—2.4 (3) mm, broadening in fruit to (2) 2.5—3.9 (4) mm; lobes (5) 6—10 (11), (2) 3.1—5.3 (7) by (0.2) 0.3—0.5 (0.7) mm, thin, not nerved, linear to more broadly subulate, glabrous or hispidulous, apices acute, margins entire. ***Corolla*** infundibuliform, yellow, tube (2.7) 3.5—4.9 (5.4) mm, 1—1.9 (2.5) mm at base, opening to (2) 2.7—4 (5) mm at throat, glabrous within; limbs 4—5, acute, obtuse or mucronate, (4) 6.6—11.1 (13) by (2.5) 3.1—5 (6) mm, glabrous, occasionally apically hirtellous in bud. ***Stamens*** filantherous; filaments adnate ca 0.5—2 mm below throat, (2) 2.9—5.6 (6) mm long, glabrous; anthers exserted 2—6 mm above throat, (2.1) 2.3—3.4 (3.8) by (0.5) 0.6—1 (1.1) mm, often with a short linear or conical process extending from the connective apically, dorsifixed, latrorse. ***Pollen*** 50—90 µm. ***Ovary*** bicarpellate, bilobed, each carpel with a single locule and 4 ovules. ***Style*** (6) 7.6—11.7

(14) mm, glabrous. ***Stigma*** capitate or bilobed, equalling or exceeding anthers to 3 mm. ***Fruit*** with cocci globose or obovoid, circumscissile, glabrous, (4.3) 5—6.6 (7.1) by (3) 3.9—5.8 (8) mm in diameter; pericarp thin, membranaceous, more or less translucent; each coccus containing 2—4 seeds, fewer by abortion. ***Seeds*** obovate, lenticular or plano-convex, rarely trigonal, (3.5) 4.1—5 (5.5) by (2) 2.5—3.2 (3.9) by (0.7) 0.9—1.4 (1.5) mm, light tan, irregularly or more rarely regularly reticulate, raphal rib well differentiated and usually prominent, occasionally scalloped especially abaxially.

Discontinuously distributed on desert slopes from southern New Mexico south to Chihuahua and Coahuila, and rarely in western Nuevo León from (400) 891—1551 (1907) m elevation. Flowering (May) Jun—Aug (Oct), with fruit mid-Jun—Aug (Oct).

Gray's concept of *Menodora scoparia* made it a wide ranging desert species with two disjunct ranges, one in the Chihuahuan Desert of Coahuila and the other limited to southeastern California and northwestern Arizona. Curiously, Gray sank a taxon (*M. scabra* var. *glabrescens*) that he had previously named into synonymy under this newer taxon despite its priority. Although the known ranges of the species in each of its two desert systems have expanded as more collections were made over time, the basic concept the species and the duality of its distribution did not change until Turner (1991) included *M. scoparia* in his greatly broadened concept of a highly polymorphic *M. scabra*. *Menodora scabra sensu* Turner (1991) includes *M. scabra* and its varieties*, M. scoparia,* and *M. decemfida* var. *longifolia*.

The molecular phylogeny confirms Turner's perception that these taxa form a related group, with the addition of *Menodora yecorana*. It also suggests how these can be segregated into more useful taxonomic units (Fig. 2). In the phylogeny, the eastern

(Chihuahuan Desert) scopariods form a clade that is sister to all other scabroids; thus *scoparia* sensu Gray is polyphyletic with the western scoparioids being more closely related to some of the western scabroids than the eastern scoparioids. Since the type of *M. scoparia* belongs to the Chihuahuan Desert group, I restrict the application of the name to the eastern scoparioids. Fortunately, the name abandoned by Gray in favor of *scoparia* can be applied to the western group (see below).

Henrickson, in the draft of the Chihuahuan Desert flora, recognizes two scoparioid forms, *Menodora scoparia* and the unpublished *M. chihuahuaensis* (specimens annotated by Henrickson were usually determined previously as *M. decimfida* var. *longifolia*), and distinguishes these largely by the amount of reduction of the upper leaves, these being quite reduced and bracteate in the former and larger and usually linear in the latter. I include both of these in my concept of *scoparia*. However, I have passed some scoparioid forms with broader leaves to *M. laevis*, and I believe it was these specimens that Turner (1991) had in mind when he placed *M. scoparia* in the scabroid group. The scattered distribution of this species within the Chihuahuan Desert is worthy of more study.

SPECIMENS EXAMINED:

MEXICO: CHIHUAHUA: Sierra San Carlos; road to San Carlos Mines, 8/9/1940, I. M. Johnston & C. H. Muller 57 (GH); Near Cañon del Rayo, a large canyon on the northeastern side towards the northern end of the Sierra del Diablo, about lat. 27° 20' N. 3 km E of canyon mouth, 7/27/1941, Robert M. Stewart 939 (GH, LL). **COAHUILA:** +/- 2 mi SW of town of Las Delicias above and around the spring (Agua Grande) that flows from the Sierra de Delicias above the town, 10/16/2002, James Henrickson & D. Riskind 23108 (TEX); Ca 40 mi SW of Cuatro Ciénegas on NW side of the Sierra de los

Alamitos, along a road that leaves the hwy near km 149 and passes to the SW and into a canyon of that range. This site 7.9 mi along road, 7/21/2004, James Henrickson 23750a (TEX); Sierra de los Alamitos, 15.1 rd mi up roadway from Hwy 30 (km 149) at an abandoned Stontium mine area, 8/30/2004, James Henrickson 23956b (TEX); Sierra de los Alamitos, 20.3 rd mi up roadway from Hwy 30 (km 149) at an abandoned Strontium mine area, 8/31/2004, James Henrickson 23977 (TEX); Sierra de las Cruces, eastern foothills 7 mi N of Santa Elena Mines, 8/15/1940, I. M. Johnston & C. H. Muller 326 (GH); 6 mi N of Hipolito. Road from Monclova south to Saltillo, 8/29/1938, I. M. Johnston 7231 (GH); Western base of Picacho del Fueste, northeasterly from Tanque Vaionetta, about latitude 27° 34' N, 8/24/1941, I. M. Johnston 8375 (GH); Vicinity of Aguaje del Pajarito, canyon at W end of Sierra de la Fragua, 2-3 km N of Puerto Colorado, 9/2/1941, I. M. Johnston 8794 (GH); 13 km N of Rancho El Jardín on winding road to Mina El Popo. E. slope of Sierra del Carmen, ca 6 km S of Canyon del Diablo, 7/28/1973, M. C. Johnston et al. 11847a (LL, MEXU); Mina El Popo ca 2 km S of Cañon del Diablo on dissected E slope of Sierra del Carmen, ca 19 km by winding road N of Rancho El Jardín, 7/29/1973, M. C. Johnston et al. 11911 (MEXU); [San Lorenzo de Laguna and vicinity, 22-27 leagues SW from Parras], 5/6/1880, Edward Palmer 795 (GH, MO, NY, US); Peña, 2/1905, C. A. Purpus s.n. (UC); Cerro de Zapatero, 7/1910, C. A. Purpus 4497 (MO, UC, US); Along MEX Hwy 40, E of Torreón, 3.5 mi E of the junction of COA C-1 at Entr. La Cuchilla, 9/21/1973, James L. Reveal & Duane Atwood 3314 (US); Along MEX Hwy 40, E of Torreón, 3.5 mi E of the junction of COA C-1 at Entr. La Cuchilla, 9/21/1973, James L. Reveal 3315 (MO); Semi-arid region few mi E of Torreón, 7/7/1941, R. W. Schery 47 (MO); Eastern foothills of the Sierra de las Cruces, vicinity of Santa Elena Mines (2 km NW), 10/10/1940, Robert M. Stewart 256 (GH); Cañon del Gringo, northern slope of the Sierra Planchada, about 6 km due N of the town of Sierra Mojada. At mouth of canyon, 8/4/1941, Robert M. Stewart 1044 (GH). **Mpio. Parras:** Parras, S of, 10/9/1993, Hinton et al. 23539 (MEXU, TEX). **Mpio. Villa Ocampo:** Ca 32 air km WSW of Ocampo, at Cuesta Zozaya [Cuesta Muralla] overlook, 9/9/2002, Timothy W. Chumley et al. 7404 (TEX). **NUEVO LEON:** Monterrey, 1924, C. R. Orcutt 1318 (US).

USA: NEW MEXICO: Eddy Co.: Near Sitting Bull Falls, Guadalupe Mts., 8/16/1924, Paul C. Standley 40729 (US). **TEXAS: Brewster Co.:**NE flank of the Rosillos Mts., 7/22/1947, R. R. Bloomer 50-307 (TEX); S. Marathon, 8/5/1931, Ora M. Clark 4195 (G, MO); Terlingua Beds, on rd to Agua Frio Ranch from Hwy 118. 60 mi S of Alpine, 6/16/1963, D. S. Correll & D. C. Wasshausen 27829 (GH, LL, UC); Foothills of Chisos Mts., 7/15/1883, V. Havard s.n. (US); Bofecillos Mts., 9/15/1883, V. Havard s.n. (US); Along Rio Grande near Reagan Canyon, 12/24/1946, L. C. Hinckley 3733 (NY); 10 mi N of Terlingua Creek, 5/28/1928, E. J. Palmer 34232 (A); Sparse on Eagleford limestone hill in the Basin, Chisos, Mountains, 8/25/1936, Omer E. Sperry 264 (US); 2 mi SE Packsaddle Mt., 6/18/1949, Billie L. Turner 1116 (GH); 5 mi W Terlingua, 6/19/1949, Billie L. Turner 1165 (GH); At Lone Mt., Chisos Mts. area, 6/30/1937, Barton H. Warnock 673 (GH, TEX); Chisos Mountains: On ridges near top of Baldy, 7/30/1037, B. H. Warnock 675 (US); At Altuda Pass, Glass Mts., 6/30/1940, Barton H. Warnock W114 (GH, TEX). **Maverick Co.:** Along state farm road 1021 near El Indio, 5/24/1990, James S. Miller M. Merello & R.D. Noyes 5109 (MO). **Pecos Co.:** 7/23/1943, B. C. Tharp 43-747 (TEX, UC); 16-3/4 mi SE of Ft. Stockton, 8/10/1940, V. L. Cory 35193 (GH). **Terrell Co.:** ca. 9 mi. W of Sanderson, 6/25/1964, D. S. Correll & Craig Hanson 29889 (GH, LL).

21. *Menodora laevis* Wooton & Standl.

Contr. U. S. Natl. Herb. 16:158, 1913. Holotype: USA: NEW MEXICO: Organ Mts., 8/1881, *G. R. Vasey s.n.* (US!). Isotype: NY!

Menodora scabra A. Gray var. *laevis* (Wooton & Standl.) Steyerm., Ann, Missouri Bot. Gard. 19:137, 1932. *Menodora scabra* A. Gray var. *ramosissima* Steyerm., Ann, Missouri Bot. Gard. 19:139, 1932. Holotype: USA: TEXAS: El Paso Co.: Near El Paso, 6/19/1926, *E. J. Palmer 31083* (MO!). Isotype: A!

Plants fastigiate subherbaceous to ***suffrutescent perennials***, (11) 14.8—29.7 (39) cm tall, with a woody taproot, caudex 4.6—15 mm diameter with many branches. ***Stems*** more or less erect, branching throughout, alternate or opposite, the latter often only below midstem or at lowest nodes; older wood tan,or gray to black, atratous, glabrous, rugose, rimose; younger stems green, shallowly to deeply fluted, often more prominently so above, terete to slightly angled in cross section, glabrous to densely strigillose rarely glabrate, trichomes short, white or hyaline, retrorse, rarely rudimentary and minutely papillose, (0.03) 0.07—0.15 (0.2) mm; internodes at midbranch (4) 6—23 (55) mm, usually shorter than subtending leaves but occasionally exceeding them. ***Leaves*** alternate, usually opposite basally but quickly becoming subopposite and alternate, sessile or subpetiolate, submembranaceous, linear-lanceolate to linear-oblanceolate to broader and elliptic, rarely obovate, leaves fairly uniform in size, lower often broader, largest just below midbranch or just below inflorescence branching, (3) 6.9—16 (25.9) by (1) 1.8—4.1 (6), length to width ratio (2) 2.7—5.4 (7.2), glabrate to hispidulous, rarely punctate below, apices acute or apiculate, rarely mucronate, margins entire, thickened, base attenuate or cuneate, decurrent, uninervate, nerves prominent abaxially usually attenuating toward apex, rarely with obscure laterals, usually swollen at node. ***Inflorescence*** a compound dichasium of 1—25 flowers with alternate branching. ***Pedicels*** (0.3) 1—11.5 (28) mm long, 0.3—0.5 (0.8) mm in diameter, glabrous to densely strigillose, holding fruit erect, subtended by a linear to linear-lanceolate, glabrous to densely hispidulous bract. ***Calyx*** tube turbinate, glabrous to strigillose, (1) 1.3—2 by (1) 1.5—2 mm, broadening in fruit to (2) 2.6—3.8 (4) mm; lobes (7) 9—10 (12), (2) 3.3—6 (9.5) by (0.2) 0.3—0.5 (0.6) mm, thin and occasionally nerved, linear to broadly subulate, very rarely adjacent lobes fused and appearing bifid, hispidulous, apices acute, margins entire. ***Corolla*** infundibuliform, yellow, tube (2) 2.7—4.3 (5) mm, 0.8—1.7 (2) mm at base, opening to (2) 2.4—3.8 (4) mm at throat, glabrous to sparsely pilose within; limbs (4) 5, acute or apiculate, rarely obtuse or mucronate, (5.3) 6.1—8.4 (10) by (2.5) 2.9—4.3 (5.) mm, glabrate often hirtellous in bud. ***Stamens*** filantherous; filaments adnate ca 1—2 mm below throat, (3) 3.3—5.5 (6) mm long, glabrous; anthers exserted ca 1—3 mm, (1.5) 1.9—2.3 (2.5) by (0.4) 0.5—1 (1.3) mm, rarely with short, linear or conical process extending from the connective apically, dorsifixed, latrorse. ***Pollen*** 50—90 µm. ***Ovary*** bicarpellate, bilobed, each carpel with a single locule and 4 ovules. ***Style*** (6) 7.1—9.7 (11) mm, glabrous. ***Stigma*** capitate, bilobed, equalling or just exceeding anthers, rarely to 1 mm beyond. ***Fruit*** with cocci globose or rarely ellipsoidal or obovoid, circumscissile, glabrous, (4) 4.8—6.2 (8) by (3) 4—5.6 (7) mm in diameter; pericarp thin, membranaceous, more or less translucent; each coccus containing 4 seeds, fewer by abortion. ***Seeds*** ovate to obovate, trigonal or commonly plano-convex to lenticular, (3) 3.7—4.8 (5.5) by (1.5) 2.3—3.1 (3.5) by (1) 1.2—1.9 (2.5) mm, surface continuous, chartaceous, slightly rugose, with or occasionally without small more or less circular foveolae, an underlying reticulate pattern occasionally visible.

A species of mostly of the Chihuahuan Desert, ranging from central New Mexico south to Durango, Zacatecas, and Nuevo Leon, from (323) 800-1600 (2369) m elevation. Flowering (Jan and Apr) May to Sep (Oct), with fruit (May) Jul to Sep (through Jan).

In the molecular phylogeny of the genus, the eastern scabroids cluster as a group. Morphologically, they are somewhat diverse as well as indistinct from some of the western forms, but they are united by a single character of the seed: a continuous, light-colored, somewhat chartaceous and foveolate seed coat. This character is not found among specimens I have reviewed from populations in northern New Mexico, nor west of the Continental Divide. Generally, the plants I recognize as *Menodora laevis* have broader, more lanceolate leaves than the typically narrower and more linear leaves of *M. scabra* (although variety *sonorensis* is notable for its even broader leaves).

Steyermark applied this name (as *M. scabra* var. *laevis*) to widely distributed subherbaceous specimens from Texas to California, and applied var. *ramosissima* to a more heterogeneous group of larger, generally woodier specimens. The types for both taxa are found in the mountains of southern New Mexico and adjacent Texas, and this falls exclusively within the range of collections with seed matching the eastern, Chihuahuan Desert type. Although the types themselves lack seed, I apply the earlier name, *M. laevis*, to this group and restrict its use to the diverse scabroids of the Chihuahuan Desert.

Since it can be difficult to make determinations in this group without seed, more work is needed, particularly in terms of sampling seed and populations for molecular markers, in order to determine the actual species boundaries and the degree to which it may intergrade with other forms.

SPECIMENS EXAMINED:

MEXICO: CHIHUAHUA: 6.5 mi SE of Nuevo Casas Grandes, 7/8/1997, Atwood & Spencer 22800 (NY); Just S and SE of Mina La Nueva Esperanza on eastern slope of Sierra del Morrion. 1400-1700 m, Chiang et al. (LL); 13.5 km by winding road W of Guadalupe Victoria on road to Rancho Santa Maria de Guadalupe, 8/18/1972, Chiang et al. 8681 (LL, MEXU); Sierra de Moscos (Sierra de Palomas in geological reports), southern part, 8/19/1972, Chiang et al. 8703 (LL); 28 mi E of Parral, Route 45, 5/6/1959, Correll & Johnston 21550 (LL, NY); SE of Sierra Mula, about 5 mi S of Juarez, 10/24/1959, Correll 23310 (LL); 24 mi N of Camargo, 6/21/1950, Dressler 1124 (GH, MO); 10-12 mi SE Ciudad Chihuahua, 11/7/1959, Gentry 18122 (LL, US); Ca 24 air mi NE of Julimes, ca 5 mi S of Rancho El Recuerdo, 9/16/1973, Henrickson 13023a (TEX); Ca 36 mi NE of Escalon, 8.1 rd mi NE of Carillo railroad crossing on new road to Guimbalete, 9/17/1974, Henrickson 14138 (TEX); Ca 85 mi SSE of Ciudad Juarez, 26 air mi ENE of Villa Ahumada, E of Sierra de la Mosqueteros ca 1 mi, 8/21/1971, Henrickson 5834d (TEX); 15 mi NW of Escalon along MEX Hwy 49, 30 mi S of Ciudad Jiminez, 8/24/1971, Henrickson 5949 (TEX); 6 mi NE of Cuchillo Parado, 9/17/1971, Henrickson 6783 (TEX); Ca 15 rd mi S of Ojinaga, on road to La Perla, Ciudad Carmago, 9/17/1971, Henrickson 6825a (TEX); 26.6 road mi NE of Aldama along Hwy 16 ca 0.5 mi N of El Morrion, 9/15/1972, Henrickson 7573 (TEX); Ca 43 air mi NE of Ciudad Chihuahua in plains E of Sierra El Morrion, 9/11/1980, Henrickson & Bekey 18477 (TEX); Sierra Peguis, ca 22 air mi W of Ojinaga, 25 rd mi W of Hwy 9 on Hwy 16 towards Ciudad Chihuahua, 4/27/1977, Henrickson & Lee 15838 (TEX); 14 km al N del Cd. de Chihuahua, 9/15/1955, Hernández & Mathus N-1772 (MEXU); 3-1/2 mi S of Trincheras; along road from Ojinaga to Castillon, via La Mula, Trincheras, Pirámide and San Salvador, 8/11/1941, Johnston 8059 (GH); Near Rio Grande, NE of Sierra Mulato, above a narrow side canyon +/- 1 km below narrow box canyon in upper part of Colorado Canyon. We traversed canyon about 1 km inland and on rim and lower drainage basin behind rim, 10/5/1985, Johnston 12872 (TEX); 6 mi S of Trincheras; road from Castillón to Mula, via San Salvador and Pirámide, 9/21/1940, Johnston & Muller 1433 (GH, LL); Sierra San Carlos: road to San Carlos mines, 8/9/1940, Johnston & Muller 57 (LL); 5 km SW of Rancho El Murcielago, W and S of Sierra Grande, 6/12/1973, Johnston et al. 11281 (LL, MEXU); 2.5 km S of Rancho Las Vacas on road to Rancho Los Sauces, E of Sierra San Martin de Boracho, 6/15/1973, Johnston et al. 11332a (LL); Chihuahua, 8/20/1935, LeSueur 121 (GH, MEXU, US); N of El Carmen, 10/15/1935, LeSueur MEX 121 (TEX); Chihuahua, 8/20/1935, LeSueur MEX121 (TEX); Chihuahua, 8/20/1935, LeSueur s.n. (MO, UC); Llano de las Nogales near Santa Eulalia, 8/15/1948, Lopez 26 (GH); Collected between Casas Grandes and Sabinal. Elev. 5000-5500 ft, 9/4/1899, Nelson 6362 (GH); 11.1 mi SE of Chihuahua on rd to Meoqui, 9/18/1953, Ownbey & Ownbey 1840 (UC, US); Santo Domingo, Sierra de Santa Eulalia, 9/11/1934, Pennell 18704 (GH, NY, US); Hills near Chihuahua, 8/9/1885, Pringle 549 (GH); 10/15/1911, Stearns 66 (GH); 31 mi W of jct Rt. 45 and road to Casas Grandes, 8/22/1967, Steussy 1105 (LL, NY, TEX); 8 km S of Progreso; along road through Rancho San Jose del Progreso northward along the Sierra Seca, just W of Coahuilan boundary, 9/21/1942, Stewart 2300 (GH); 4 km N of El Pino; vicinity of El Pino, ca 10 km SE of Sierra Rica, 9/24/1942, Stewart 2416 (GH); 6 km N of El Pino; Vicinity of Rancho El Pino, ca 10 km SE of Sierra Rica, 9/24/1942, Stewart 2428 (GH); Broad valley 2 km S of Rancho de Encinillas, 7/7/1941, Stewart 724 (GH, LL); Road from Jaco, through broad valleys and skirting grassy hills, to Mesteñas (via Honorato, Victoria, and San Francisco). 1 km N of Victoria, 10/5/1941, Stewart & Johnston 2005 (GH); 25 mi S of Samalayuca on Hwy 45, 7/14/1959, Straw 1611 (MEXU, UC); Ojo de Vaca, 6/15/1857, Thurber 318 (GH);

10/23/1974, Valdes VR-731 (UMO); 16 mi S of jct Hwy 45 & Truck Rt. 45 in Ciudad along Hwy 45, 7/20/1975, Watkins et al. 581 (LL); 7/20/1975, Watkins et al. 581 (UMO); 37 mi N of Cd. Jiménez, road to Cd. Camargo, 8/1/1939, White 2186 (GH, MEXU); 12 mi S Camargo, 8/3/1939, White 2222 (LP, US); 3 mi N San Lucas, road to Chihuahua, 8/8/1939, White 2308 (GH); 10 mi W of El Pozo, road to Sta. Eulalia, 8/18/1939, White 2443 (GH, LL); Sta. Eulalia Hills, 8/8/1885, Wilkinson 8 (US); Santa Eulalia Hills, 8/8/1885, Wilkinson s.n. (UC); Santa Eulalia Mountains, 5/29/1885, Wilkinson s.n. (US); Sta. Eulalia Mountains, 5/29/1881, Williamson s.n. (US); Along New Mexico-Chihuahua border, 0.9 mi W of Monument No. 3 at edge of La Mesa escarpment; just across border from T29S R3E S13 SW1/4, 7/27/1986, Worthington 14403 (NY). **Mpio. Ciudad Juarez:** Sierra Juarez, S side, 8/2/1986, Worthington 14497 (NY). **Mpio. Praxedis G.:** Sierra San Ignacio (including and in the Sierra Esperanza), canyon 6.4 km SSW of Esperanza, 8/26/1984, Worthington & Corral 12499 (NY). **COAHUILA:** Paila, km 750 de la carretera, cerca Parras, 4/21/1946, Aguirre & Reko 35 (NY); Bolsón de Cuatro Ciénegas. Low hill ca 2 mi W of San Marcos. S. P. A. El Papalote de Santa Teresa de Sofia, 8/23/1987, Bogler & Atkins 77 (TEX); 4 mi W of Hermanas, 8/20/1984, CDRI I002 (TEX); 3 km N of Ahuichila, Cañon de Ahuichila, 6/16/1972, Chiang et al. 7832 (LL, MEXU, NY); Along railroad 13 km E of Esmeralda on road to Cuatro Ciénegas, 9/2/1972, Chiang et al. 9104 (LL, MEXU, TEX, US); 4 km E of Magueyal and 13 km W of Hacienda Zacatosa on road paralleling railroad from Esmeralda to Cuatro Ciénegas. 1250-1300 m, 9/2/1972, Chiang et al. 9138 (LL, MEXU, NY); Cuatrociénegas. At west side of statue of V. Carranza, off Coahuila Hwy 30 ca 1 km E of Cuatrociénegas, 5/18/2002, Chumley et al. 7391 (TEX); Villa Ocampo. Ca 12 rd km WSW of Ocampo, 9/9/2002, Chumley et al. 7405 (TEX); 4 mi W of Paila on Route 60, 7/22/1958, Correll & Johnston 19973 (LL, NY); Cañon de Fora in the Sierra de La

Fragua ca 25 mi W of Cuatro Ciénegas along road to La Vibora, 9.6 mi E Estación los Belloc, 8/15/1978, Daniel 543 (MICH); Mountains about Saltillo, 9/1848, Gregg 527 (GH); Ca 22 air mi E of Boquillas, NE of Pico de Sentinela of the Sierra del Carmen, 2 mi N of Piedra Azul, 7/27/1973, Henrickson 11390 (TEX); Ca 12 air mi E of Boquillas, in Sierra del Carmen area, in canyon E of Mina Popo, 7/29/1973, Henrickson 11549 (TEX); Ca 43 air mi W of Cuatro Ciénegas, 4 mi SW of Hacienda Zacatosa on slopes just E of the pass through Sierra Zacatosa, 8/7/1973, Henrickson 12074 (TEX); Ca 39 air mi NE of Tlahualilo, on E side of Sierra de los Remedios, 8/9/1973, Henrickson 12185 (TEX); Ca 35 air mi SSW of Cuatro Ciénegas, in northern slope of Sierra de Los Alamitos, ca 9.2 road mi S of El Hundido, in Izotal, 9/29/1973, Henrickson 13678 (TEX); Ca 23 air mi Nwof Las Delicias, in a valley N of Sierra de las Delicias near old mine, 8/29/1974, Henrickson 6104 (TEX); 3.7 road mi S of Parras, 8/30/1971, Henrickson 6165 (TEX); Ca 14 air mi E of Jaco, 45 air mi N of Esmeralda, on SW side of Sierra de Cruces, 9/19/1971, Henrickson 6928b (TEX); 7.6 road mi N of Esmeralda, 9/19/1971, Henrickson 6944 (TEX); 52 mi WNW of Cuatro Ciénegas, 12 mi E of La Vibora in Bolson de Mapimi region of Chihuahuan Desert, 9/20/1972, Henrickson 7900 (TEX); Ca 74 air mi SW of Cuatro Ciénegas, at N end of Puerto de Ventanilla, at S end of Valle de Sobaco, along Torreón-Cuatro Ciengas hwy, 5/3/1977, Henrickson & Lee 15886 (TEX); Ca 15 air km S of Cuatro Ciénegas, on W slope of the N end of Sierra San Marcos, about 1-2 km S of Pozo de Becerra, a short canyon along Hwy 30, 5/1/1977, Henrickson & Lee 15917 (TEX); 37 air mi N of Saltillo, along Hwy 57, N endo of Sierra del Potrero, 9/25/1978, Henrickson & Lee 17635 (TEX); Ca 86 air mi S of Big Bend National Park Basin, S of Sierra Santa Fe del Pino, 7.4 mi W of Rancho Agritos (R. Cimmaron), 8/7/1976, Henrickson & Prigge 15084 (TEX); Ca 32 km WSW of Villa Ocampo in canyon at N base of Cuesta Zozaya, 9/26/1986, Henrickson & Woodruff

20384 (TEX); Road from Monclova westward to Cuatro Ciénegas. 4 mi E of Cuatro Ciénegas, 8/25/1938, Johnston 7121 (GH, UC); Road from Monclova westward to beyond Cuatro Ciénegas. 2 mi NW of Frontera, 8/25/1938, Johnston 7176 (GH); Valley floor E of Puerto Caballo; road from Puerto del Caballo easterly, 16 km across broad valley to the low hills at Tanque Jerico, about lat 27° 34' N, 8/22/1941, Johnston 8334a (GH); San Rocendo Canyon, a tributary of the Rio Grande in far northern end of state, 5/1/1979, Johnston 12456 (TEX); Picachos Colorados, ca lat. 28° 36', 8/11/1940, Johnston & Muller 119 (GH, LL, MEXU); Sierra de las Cruces, eastern foothills 7 mi N of Santa Elena Mine, 8/15/1940, Johnston & Muller 326 (LL); 5 km WNW of Hacienda Magueyal on the Cuatro Ciénegas-Esmeralda road, 5/7/1973, Johnston et al. 10903 (LL, MEXU); Mina El Popo ca 2 km S of Cañon del Diablo on dissected E slope of Sierra del Carmen; ca 19 km by winding road N of Rancho El Jardín, 7/29/1973, Johnston et al. 11911 (LL, TEX); Monclova, 7/20/1939, Marsh (TEX); Monclova, 5/20/1939, Marsh 1812 (GH); 6 mi SW of Hipolito, 8/29/1939, Mueller 3001 (GH, LL, MO, UC); Ca 40 km W of Cuatro Ciénegas, paralleling railroad, on road up to microwave tower, 10/19/1985, Nesom et al. 5266 (TEX); States of Coahuila and Nuevo Leon. [Juraz, about 100 mi N from Monclova on the Sabinas River.?], 9/23/1880, Palmer 793 (GH); Sierra de Parras aprox. 15 km al WNW de Menchaca por el camino al Amparo, 4/13/1981, Rodriguez & Carranza s.n. (TEX); Near Hwy 40, between Torreón and Saltillo, ca 58 mi W of Saltillo, 9/27/1974, Rollins & Rollins 7464 (GH, MEXU, TEX); Cañon Espantosa, western slope of Sierra de Vicente, about 20 km ESE of Cuatro Ciénegas, 3/15/1941, Schroeder 126 (GH); 15 mi SW of Saltillo, Shreve 8740 (US); 12 km E of La India; Llano de Guaje, flats in bottom of bolson near Tanque de La India, about lat 28° 00' N, 8/25/1941, Stewart 1178 (GH, LL); Valleys NE of Sierra del Pino. 10 km W of San Guillermo, 9/19/1941, Stewart 1760 (GH, LL); Eastern foothills of the Sierra de las

Cruces, vicinity of Santa Elena Mines (2 km NW), 10/10/1940, Stewart 251 (GH); Cañon de Tinaja Blanca, eastern slope of the igneous central mass of the Sierra de las Cruces, W of Santa Elena Mines, 6/22/1941, Stewart 588 (GH, LL, MEXU); 2 km E of La Palma; vicinity of La Palma, a ranch in the broad valley NW of the Sierra de las Cruces, near the Chihuahuan boundary about 15 km N of Jaco, 7/5/1941, Stewart 652 (GH); 5 km E of Guimabalete; road from Guimabalete to Acatita, via Laguna del Rey, 9/17/1942, Stewart & Santos 2642 (GH); Base of mountains along eastern margin of Valle de Acatita. Ranchos de las Uvas (3 km NW), 10/13/1942, Stewart & Santos 2995 (GH); Road from Guimbalete SE to Acatita, via Laguna del Rey. Laguna del Rey (SW end), 10/14/1942, Stewart & Santos 3020 (GH); Sierra la Paila, ca 9 air km NNE of Estacion Martes at foot of Cerro Alto, 7/25/1993, Turner et al. 93-140 (MEXU, TEX); Hwy 57, 70 mi N of Satillo, 6/3/1966, Wilson 11364 (TEX); Sierra de San Marcos, areas cercanas a la Poza de la Becerra en Cuatrocienegas, 9/25/1988, Zarate A-4 (TEX). **Mpio. Cuatro Ciénegas:** Rancho Falcón, Cuesta del Dulce, about 12 mi W of Hacienda Berrendo, 8/19/1937, Wynd 719 (GH, MO, NY, US). **Mpio. Parras:** Parras, S of, 10/9/1993, Hinton et al. 23533 (TEX); S of Parras, 10/10/1993, Hinton et al. 23571 (MEXU); S of Parras, 10/10/1993, Hinton et al. 23571 (TEX). **DURANGO:** 21-24 mi S of La Zarca above the Rio Nazas, 10/31/1966, Gentry s.n. (US); 8 km al SSE de Vicente Guerrero, por la carretera a Suchil, 10/13/1980, Gonzalez & Herrera 1440 (MEXU, NY, TEX); Ca 14 air mi WSW of Torreón, 2.5 mi W of Hwy 40 towards Microondas Estación Sapioris, 8/14/1973, Henrickson 12364 (TEX); Ca 54 air km SSE of Torreón in canyon above Estacion Otto in SW side of Sierra de Jimulco near Mina San Jose, 9/12/1980, Henrickson & Bekey 18501b (TEX); Ca 33 air km S of Torreón along DUR B8 between Hwy 40 (vic. of Estación Diego & road W to Santa Jimilco (near San Jose)), 9/12/1980, Henrickson & Bekey 18511 (TEX); +/- 16 air mi SW of Torreón, Coah., on upper road to

Microonda Sapioris, +/- 5 mi SW of León Guzman, the road to the Microondas extending from old Hwy 40, the specific site in a saddle about 1 rd mi below the towers, 10/17/2002, Henrickson & Riskind 23155 (TEX); On low hills 2 mi W of Bermejillo, 9/18/1938, Shreve 8782 (US); Yerbanis, 8/24/1939, Shreve 9134 (GH); Camino Tepehuanas-La Candela, orillas del poblado de Tepehuanes, 9/4/1989, Bolaños & Ramos 195 (MEXU); Tephuanes, 7/28/1944, Fisher 44231 (GH, MO); Tephuanes, 7/28/1944, Fisher 44266 (NY); Ca 1.5 mi N of Estacion Chocolate on Hwy 40, 7/30/1991, Mayfield et al. 1090 (TEX); Tepehuanes, 6/15/1906, Palmer 309 (GH, MO, NY, UC, US). **Mpio. Lerdo:** Cuesta la Fortuna, Sierra Las Noas. Carr. Torreón-Nazereno, 6/16/1983, Villarreal et al. 2254 (TEX). **Mpio. Nombre de Dios:** Las Lomas, 8/29/1979, Gonzalez 1076 (MO). **Mpio. Poanas:** 3 km de La Joya, cerca del Cerro del Sacrificio, 8/23/1984, Chávez 73 (MEXU). Cerro del Sacrificio, 7 km de La Joya, 9/10/1984, Jiménez 17 (MEXU). **Mpio. Rodeo:** Mina la Amparo 6 km al NW de Las Higueras, 9/5/1983, Tenorio et al. 4238 (MEXU); Mina la Amparo 6 km al NW de Las Higueras, 9/5/1983, Tenorio et al. 4238 (TEX). **Mpio. Tlahualilo de Zaragoza:** Tlahualilo de Zaragoza, Ceballos to Mohovano de Lilas, 9/9/1994, Hinton et al. 24734 (TEX). **NUEVO LEON:** Along Nuevo Leon Hwy 102 ca 3.4 rd mi W of jct with Mexico Hwy 53, ca 10 air mi NE of Espinazo, ca 60 air mi NW of Monterrey, 5/19/2002, Chumley et al. 7392 (TEX); 5 mi N of Espinoza, WNW of Monterrey, 5/22/1972, Powell & Turner 2328 (TEX); Off MEX Hwy 53 between Monterrey and Monclova, ca 55 mi NW of Monterrey, 10/10/1974, Rollins & Rollins 74156 (GH, MEXU, TEX). **ZACATECAS:** 26.5 mi W of Camacho, 9/3/1971, Henrickson B6310 (TEX); 13 mi WSW of Jalpa, 8/14/1969, Taylor & Taylor 6282 (NY); Near El Vergel about 14.5 mi WSW of Sombrerete along the Rio Antonio, 8/19/1969, Taylor & Taylor 6282 (US).

USA: NEW MEXICO: International boundary, United States and Mexico; Monument No. 6 to Monument No. 12, 9/22/1892, Wagner 956 (US); [New Mexico], Wright 1694 (GH, MO, NY); Vasey s.n. (NY). **Chaves County:** 1 mi W of Acme. Northeastern limit of Larrea desert in this area, 8/27/1945, Waterfall 6124 (GH, MO, NY). **Dona Ana County:** San Andreas Mts., Jornada Range Reserve, NE of New Well, 8/17/1929, Ellison 807 (MO); Rincon, 9/9/1884, Jones 4167 (NY, RM, US); Tortugas Mt. E of Mesilla Park, 7/15/1906, Standley 545 (MO); Organ Mts., 8/1881, Vasey s.n. (NY, US); 3.6 mi E of Las Cruces, at summit of Tortugas Mtn., 6/6/1981, Ward et al. 81-160 (MO); In the Organ Mountains, 7/15/1897, Wooton 154 (GH, NY, RM, UC); Mesa W of the Organ Mountains. Little Mt., 8/29/1903, Wooton s.n. (MO); Little Mt. near Las Cruces, 9/2/1894, Wooton s.n. (NY); On the mesa W of the Organ Mountains, 8/26/1902, Wooton s.n. (RM, UC); On the Mesa W of the White Mountains. Tortugas Mt., 7/15/1906, Wooton & Standley s.n. (US); On the Mesa W of the Organ Mountains. Tortugas Mt., 8/19/1906, Wooton & Standley s.n. (US); On the Mesa W of the Organ Mountains. Tortugas Mt., 9/1/1908, Wooton & Standley s.n. (US); Potrillo Mts., W. Potrillo Mts., Guzman's Lookout Mtn., south side, 8/23/1986, Worthington 14728 (NY); Bishop Cap, 2 air mi NNW of top of Bishop Cap, 9/5/1988, Worthington 17237 (NY). **Eddy County:** On Eddy County Road 206 ca 10 air mi S of Oil City, 8/23/2000, Chumley & Moore 7314 (TEX); Queen, 8/2/1909, Wooton s.n. (US). **Hidalgo County:** Valley of Sanz [San Simon River], Rutisell s.n. (NY); Apache Hills, slopes about the Apache Mine, 9/2/1985, Worthington 13483 (NY); Animas Mts., approx. 7 air mi SE of Animas, 8/28/1986, Worthington 14849 (NY). **Luna County:** Along N tributary of Starvation Draw, on slope just above drainage, 9/3/1986, Columbus 568 (UC); Victorio Mts., 3 mi S of Gage exit on I-10 at old mining town along limestone ridge, 8/25/1984, Worthington 12452 (NY). **Otero County:** Base foothills, Alamogordo, 5/19/1902, Rehn

& Viereck s.n. (A, RM); Sacramento Mountains, La Luz Canyon, 8/27/1901, Wooton s.n. (US). **Sierra County:** Tierra Blanca, 1/1/1904, Beals s.n. (A); Cedar Spring, 8/27/1895, Mulford 1073 (US). **Socorro County:** Hills S of road from Ben Rentfrow's ranch to "upper crossing of malpais.", 9/13/1923, Eggleston 19430 (US); Socorro, 7/14/1897, Herrick 708 (US); Collected on a knoll 1100 ft from fence at crater site. [Trinity?], 8/30/1965, Hess et al. 503 (NY). **TEXAS:** Mexican Boundary Survey: chiefly in the Valley of the Rio Grande below Doñana, Parry et al. s.n. (NY); Western Texas to El Paso, NM, Wright 563 (GH, NY, US). **Brewster County:** Big Bend entrance, 8/31/1946, Albers 46193 (TEX); Level uplands area E of Bullis Range, on Bullis Gap Ranch, 5/16/1977, Butterwick & Lott 3554 (TEX); Along summit of Bullis Range, just S of Bullis Gap, on Bullis Gap Ranch, 5/18/1977, Butterwick & Lott 3606 (TEX); Along Summit of Bullis Range, ca 25 mi S of Sanderson, w/in Lower Canyons of the Rio Grande, 5/20/1977, Butterwick & Lott 3677 (TEX); Overlooking San Francisco Canyon, ca 4 mi up from the Rio Grande, ca 25 mi S of Sanderson, w/in lower canyons of the Rio Grande, 5/22/1977, Butterwick & Lott 3703 (TEX); On S side of Burro Mesa, Big Bend National Park, 9/23/1966, Correll 33839 (LL); Terlingua Beds, on rd to Agua Frio Ranch from Hwy 118, 6/18/1963, Correll & Wasshausen 27899 (LL); Near Castolon, 5/5/1928, Cory 2171 (GH); 5-1/4 mi NE of Terlingua, 10/27/1938, Cory 31237 (GH); Along Terlingua road in foothills just W Chisos Mountains, 11/27/1946, Cory 3716 (GH); Along the Terlingua road in the foothills just W of the Chisos Mountains, 11/27/1946, Hinckley 3716 (NY); Along Rio Grande near Reagan Canyon, 12/24/1946, Hinckley 3733 (NY); Terlingua Abaja. Chisos Mts., 7/16/1937, Marsh 109 (GH, TEX, UC); 1 mi NW of Boquillas, 9/4/1937, Marsh 313 (UC); Near Boquillas, 6/15/1944, McDougall 2024 (US); Near abandoned wax factory on Rio Grande at mouth of Big Canyon (Reagan Canyon quad), 4/4/1947, McVaugh 7790 (GH, TEX); Chisos Mountains, gravelly mesa

W of mountains, 6/27/1931, Moore & Steyermark 3256 (GH, MO, UC); Chisos Mts., 7/18/1932, Mueller s.n. (TEX); Along Blue Creek, near Trap Mountain, Chisos Mountains, 5/26/1928, Palmer 34191 (MO, NY); ca 70 mi S of Alpine, 7/2/1970, Powell 1971 (TEX); Near Terlingua, N of Reed Plateau, 6/27/1978, Powell 3331 (TEX); Near base of Pinnacles, 21 mi W of Glen Springs, Big Bend National Park, 6/17/1941, Rose-Innes & Moon 1191 (GH, TEX); At Panther Junction, 7/1/1961, Ross 52 (TEX); Rio Grande Village, Big Bend National Park, 8/2/1970, Selander 12 (TEX); Oak Spring run-off area, 8/23/1970, Semple 359 (MO. US); BBNP, Oak Spring run-off area, 8/23/1970, Semple 380 (MO, US); Glenn Spring area, 8/21/1939, Sperry 1550 (GH); In area between Chisos Mountains and Rio Grande River, 6/22/1936, Sperry 154 (US); Glenn Spring area, 8/21/1939, Sperry 1550 (UC); On hills at Stillwells Ranch, Chisos Mountain area, 8/2/1937, Sperry & Warnock 673 (US); Alpine, 8/15/1932, Steiger 1352 (NY); O2 Ranch, 40 mi S of Alpine, 9/15/1932, Steiger 2036 (NY); Chisos Mts, 7/9/1931, Tharp s.n. (TEX); 1 mi E of Santa Elena Canyon, 7/13/1991, Turner 15988 (TEX); 0.4 mi S of Wild Horse Saloon, ca 5 mi N of Study Butte along Hwy 118. 29-25 N, 103-31 W, 9/14/1991, Turner 8 (TEX); Big Bend National Park, Burro Mesa, along rd shoulder. 29-15 N, 103-15 W, 9/14/1991, Turner & Zhao 16029a (TEX); Big Bend National Park, Burro Mesa, along rd shoulder. 29-15 N, 103-15 W, 9/14/1991, Turner & Zhao 16029b (TEX); Big Bend National Park, Burro Mesa, along rd shoulder. 29-15 N, 103-15 W, 9/14/1991, Turner & Zhao 16029c (TEX); At head of Heath Canyon, Dead Horse Mountains, Big Bend National Park, 7/19/1952, Warnock 10783 (TEX); At McKinney Springs, Dead Horse Mountains, Big Bend National Park, 7/19/1952, Warnock 10824 (TEX); At Hot Springs, Chisos Mt. area, 6/8/1937, Warnock 1122 (GH, TEX); On hills about 5 mi N of Terlingua, Chisos Mt. area, 8/31/1937, Warnock 1122 (US); Between Boquillas & Boquillas Canyon, 8/5/1937, Warnock 1123 (TEX); Altuda Point, Glass

Mts., Gage estate, 8/1/1953, Warnock 11374 (LL); At Comanche Spring, Lajitas-Chisos Mt. area, 7/17/1937, Warnock 1207 (TEX); Along road between Todd Hill and Burro Mesa, Big Bend National Park. 3200-3500 ft, 8/1/1955, Warnock 12825 (LL); At head of Boquillas Canyon, Big Bend National Park, 8/10/1955, Warnock 12887 (LL); , 9/12/1937, Warnock 20226 (LL); S side of Emory [Peak?], 8/26/1937, Warnock 20241 (LL); 30 mi S of Alpine on Alpine-Terlingua rd, 6/3/1940, Warnock 20911 (TEX); On low hills near Terlingua, 8/29/1941, Warnock 20971 (LL, UC); Maravillo Cr., 50 mi S of Marathon, 4/3/1938, Warnock 20979 (LL); At Chisos Pens, Chisos Mts. area, 8/2/1937, Warnock 21030 (TEX); 10 mi N of Terlingua, 8/22/1947, Warnock 6872 (TEX); On Tornillo Cr., Big Bend National Park, 9/2/1947, Warnock 7030 (TEX); Alpine, 6/2/1940, Warnock s.n. (TEX); Old Blue, Glass Mts., 7/13/1940, Warnock W114A (TEX); In Santa Helena [Elena] Canyon, 3/19/1941, Warnock & Rose-Innes 513 (TEX); 5 mi W of Terlingua, Warnock et al. 1165 (LL). **Crane County:** 1 mi. W of Upton Co. line, along hwy 329, Turner 15981 (TEX). **Culberson County:** Guadalupe Mountains National Park: S of Nipple Hill, 6/24/1973, Burgess 1025 (TEX); Guadalupe Mountains National Park: canyon ca 0.3 km above mouth, ca 0.7 km N, 3.2 km W of summit of Bush Mountain, 8/17/1974, Burgess 2486 (TEX); Guadalupe Mts. Nat'l Park; plot 8-19-75-I TLB. W escarpment ca. 150 m NW of Cave 8. SW - facing 80% slope. 0.8 km S, 1.0 km W summit of Bush Mountain, Burgess 3865 (TEX); Pine Springs, at base of Guadalupe Mountains, 8/5/1967, Cole et al. 3279 (NY); 26 mi E of Hwy 62-180 along Hwy 652, 5/21/1973, Higgins 6837 (NY); 6/22/1949, Janszen 77 (TEX); On SE base of Guadalupe Peak of Guadalupe Mts., adjacent to rest area along Hwy 180, ca 7 mi NE of jct with Hwy 54, 7/24/1969, Marcks & Marcks 1312 (TEX); Guadalupe Mountains National Park, notch area E of Patterson Hills, 6/17/1973, Northington 642 (TEX); Victorio Canyon, N of Victorio Peak, 6/16/1973, Sikes & Smith 627 (LL, NY); Guadalupe

Mountains, 8/6/1910, Young s.n. (GH); Guadalupe, 8/6/1910, Young s.n. (MO); W of Kent, 8/6/1916, Young s.n. (MO); Near Seven-heart Gap, near Kent, 8/6/1915, Young s.n. (TEX). **El Paso County:** El Paso, 9/22/1901, Bailey 748 (US); 1 mi N of El Paso, 9/23/1944, Barkley 14539A (UC); 1 mi N of El Paso, 9/28/1944, Barkley 14539c (TEX); Franklin Mts., at Canutillo, 7/12/1911, Barlow s.n. (UC,US); Vicinity of El Paso, Benedict 80 (US); In drainage N of Martin Canyon, in southern Hueco Mts., 8/21/1975, Butterwick 3175 (LL); On west edge of El Paso. ("La Frontera" of C. Wright.), 9/28/1959, Correll 22617 (LL); North end of Franklin Mountains, 10/30/1962, Correll 26555 (LL); El Paso, 5/13/1902, Earle 482 (NY); Eastern slope Franklin Mts., 6/29/1921, Ferris & Duncan 2411 (NY); El Paso, 7/17/1922, Fisher 319 (NY); On mesa, El Paso, 10/6/1906, Johnson 3 (NY); On campus of Texas College of Mines, 7/5/1946, Lee 76 (TEX); El Paso, 7/4/1895, Mulford 251 (MO, NY); Near El Paso, 6/19/1926, Palmer 31083 (A, MO); El Paso, 8/4/1920, Schultz 221 (NY); Franklin Mts., El Paso, 9/15/1915, Slater s.n. (US); Vicinity of El Paso, 9/15/1912, Stearns 66 (US); Vicinity of El Paso, Stearns s.n. (NY); Vicinity of El Paso, 9/15/1912, Stearns s.n. (US); On Scenic Drive, Mt. Franklin, 5/30/1947, Warnock 5711 (LL, TEX); 5 mi W of El Paso, 9/8/1947, Warnock 7261 (TEX); El Paso, 9/20/1932, Whitehouse s.n. (TEX); El Paso, NW part of city at small andesite hills 0.3 mi N jct Belvedere with Westwind, 7/16/1986, Worthington 14292 (NY); Three Sisters Hills, about 1.5 air mi N of jct. I-10 with N. Mesa, 8/13/1988, Worthington 16914 (NY). **Hudspeth County:** 10 mi SE of McNary, jct of routes 34 and 80, 10/31/1962, Correll 26611 (LL); foothills of Quitman Mts. 10 mi. W of Sierra Blanca, Warnock 13563 (LL); 10 mi W of Sierra Blanca, Quitman Mountains, 7/7/1955, Warnock 13589 (LL); In S end of the Quitman Mts., 4 mi NE of Indian Hot Springs, 7/1/1943, Waterfall 4849 (GH, MO, NY); SW foot of Malone Mountains, 12 mi W of Sierra Blanca, 8/21/1946, Waterfall 6667 (GH, NY). **Jeff Davis County:** North side of Davis Mts., 1/2 mi S of Kent on Texas Hwy 118, 10/14/1979, Felger & Soreng 5418 (NY); Low Goat Canyon, 7/30/1935, Hinckley 236 (NY); Davis Mountains, near Livermore, 7/15/1936, Hinckley s.n. (GH); Goat Canyon, Mt. Livermore, 7/30/1935, Hinckley s.n. (TEX); Davis Mts., near Indian Lodge, Lundell 13178 (LL, NY); Toward Espy Miller Ranch, 4 mi SW of Valentine, 8/7/1949, Warnock & Turner 8999 (LL); 4-1/2 mi WSW of Chispa, 7/26/1943, Waterfall 5292 (GH, MO, NY). **Kimble County:** Telegraph, 10/8/1916, Palmer 10937 (MO). **Loving County:** On Texas FM Road 652, ca 3.5 rd mi E of the Pecos River, 8/23/2000, Chumley & Moore 7313 (TEX); 5 mi. NE of Red Bluff Dam, Turner 1032 (LL). **Pecos County:** Oilfields NW of Ft. Stockton, 7/28/1958, Bratz & Elliott s.n. (NY); US 285 ca 2 mi NW of Ft. Stockton/, 5/9/1970, Flyr 1407 (MO); 7/4/1943, Tharp 43-744 (TEX); 6/9/1943, Tharp 43-745 (TEX, UC); 7/17/1943, Tharp 43-746 (TEX); 24 mi SW of Ft. Stockton along highway 67 (via IH 10). 39-39 N, 103-16 W, 7/13/1999, Turner 99-442 (TEX); along hwy 40 to 45 mi. SE of Ft. Stockton toward Sanderson, Warnock 13454 (LL). **Presidio County:** Just N of Chinati Peak, between Dead Horse and Pinto Canyon, 6/9/1977, Butterwick & Lott 3808 (TEX); just N of Prospect Peak, ca. 1 1/2 mi. NW of Tres Papalotes in the Solitario, on the Big Bend Ranch, Butterwick & Strong 686 (TEX); along jeep trail leading to the Righthand Shutup, ca 1-1/2 mi SW of McGirke Tanks in the Solitario on Big Bend Ranch, 6/6/1975, Butterwick & Strong 841 (TEX); On Texas FM Road 170 at East Rancherias Road, ca 13 air SE of Redford, 5/13/2000, Chumley & Moore 7306 (TEX); About 12 mi SE of Redford, 4/21/1961, Correll 23695 (LL); On Rio Grande, 5-8 mi SE of Presidio, 5/14/1959, Correll & Johnston 21879 (LL, NY); 2-3 mi NW of Redford, 5/14/1959, Correll & Johnston 21888 (LL); About 12 mi SE of Redford, 4/21/1961, Correll & Rollins 23695 (NY); Fresno Canyon, 25 mi N of Lajitas, 5/29/1938, Cutler 1900 (MO); 2 mi N of Redford, 9/1/1973, Fritz & Riskind s.n. (LL); , 10/6/1932, Greenwood 6 (TEX); Redford, 8/7/1919, Hanson 791 (GH, US); Redford, 8/7/1919, Hanson s.n. (TEX); 12.5 mi E of Redford along Hwy 170 on slopes above the Rio Grande. 29-18 N, 104-01 W, 7/24/1973, Henrickson 11284 (TEX); Between Presidio and Redford on Hwy 170, 5/19/1973, Higgins 6798 (NY); Near Penitas ranch house, about 24 mi S of Marfa, 9/15/1937, Hinckley 1046 (NY); Sierra Tierra Vieja, Brite's, 7/28/1938, Hinckley 1231 (NY); 1/2 mi w/in Presidio County, Chispa-Povenir rd, 6/2/1941, Hinckley 1550 (NY, TEX); Dragged road leading N from main road, 2 mi N Bracks Canyon, 6/10/1941, Hinckley 1644 (US); Sierra Tierra Vieja, slope leading from Vieja Pass into Cottonwood Canyon, 7/16/1941, Hinckley 1974 (NY); Vieja Pass, Tierra Vieja Mts., 7/16/1941, Hinckley 1974 (TEX, US); Overlooking Rio Grande at the mouth of Tapado Canyon about 80 mi S of Marfa, 12/30/1941, Hinckley 2316 (GH, LL, NY); On slope along Marfa-Ruidosa road about 1 mi from western end Pinto Canyon, 7/7/1944, Hinckley 3046 (NY); Along Hwy 647, 8 mi N of Presidio, 8/5/1945, Lundell & Lundell 14294 (LL); 8 mi. N of Ruidosa, foothills SW of Chinati Mt, Mueller 8424 (LL, NY); Near Medina Creek, 9/15/1892, Nealley 159a (US); Chenates region, 1/1/1889, Nealley 471 (US); SE end of Chianti Mts., 2-1/2 mi S of Shafter on Hwy 67. Approx. 104-20 W, 29-48 N, 10/22/1983, Sanders 4147 (TEX); Above the Rio Grande floodplain, 7/7/1948, Schulz 48266 (TEX); Sierra Vieja, Capote Canyon, ca 300 m below falls, 6/28/1973, Sikes & Smith 679 (LL, NY); Along Estaban Canyon, 5/28/1957, Warnock & McBryde 14494 (LL); Foothills of Chenate [Chinati] Mts., 9/9/1914, Young 11 (MO); Foothills of Chenate [Chinati] Mts., 9/9/1914, Young s.n. (TEX). **Reeves County:** About 3 mi E of Saragosa, 6/23/1964, Correll & Hanson 29837 (LL, MO); Barrilla Hills, 20-2/3 mi E of Balmorhea, 9/28/1942, Cory 40544 (TEX); Near Pecos, 10/26/1944, Johnston 46101 (TEX); along Pecos Hwy, ca. 8 mi. N of Saragosa, Warnock 10125 (LL); About 10 mi N of Saragosa towards Pecos, 9/9/1951, Warnock 10190 (LL); 25 mi NW of Pecos, 5/15/1949, Warnock 8559 (LL); 7 mi N of Pecos, 8/22/1942, Waterfall 4236 (GH, NY). **Terrell County:** On mesa 8 mi E of Sanderson, Route 90, 7/7/1958, Correll & Johnston 19371 (LL, MO, NY); 5-10 mi E of Dryden, 7/15/1949, Surratt 111 (TEX); 5 mi SE of Dryden. 30-00 N,102-05 W, 9/14/1991, Turner 5 (TEX). **Val Verde County:** Just [ ] of Pecos River, Hwy 90, 8/26/1967, Langford s.n. (LL); Langtry, 5/15/1913, Orcutt 3131 (MO); 3 mi E of Langtry along Hwy 90, 9/27/1998, Turner 98-437 (TEX); 10-12 mi. N of Del Rio, toward Loma Alta, Warnock 14960 (LL); 10-12 mi N of Del Rio towards Loma Alta. Elev. 1050 ft, 6/22/1957, Warnock & McBryde 14993 (LL); 35 mi N of Del Rio near Loma Alta, 6/7/1957, Warnock & McBryde 15169 (LL). **Ward County:** 5.5 mi E of Barstow, 9/11/1965, Correll 31683 (LL, NY); 5 mi. E of Barstow, Cory 45113 (TEX). **Zapata County:** [Probably in error *fide* BLT] San Ygnacio, 7/20/1925, Tharp 3642 (TEX).

22. *Menodora longifolia* (Steyerm.) Chumley, *stat. nov.*

Basionym: *Menodora decemfida* (Gill. *ex* Hook. & Arn.) A. Gray var. *longifolia* Steyerm., Ann. Missouri Bot. Gard. 19:143, 1932. Holotype: MEXICO: DURANGO: Santiago Papasquiaro, and vicinity, 8/1896, *Palmer 429* (MO!). Isotypes: A!, F, GH!, NY!, UC!, US!

Plants fastigiate ***subherbaceous to suffrutescent perennials***, 32—41 cm tall, with no roots seen, caudex with many branches. ***Stems*** strict, branching throughout, opposite; older wood tan, glabrous, rugose, rimose; younger stems green, shallowly fluted, terete or moderately angled in cross section, glabrous or glabrate to sparsely scabrid, especially at nodes and axils, trichomes often rudimentary (reduced to minute papillae)or if longer, short and hyaline, (0.03) 0.06—0.07 mm; internodes at midbranch (27) 34—56 (66) mm. ***Leaves*** opposite, becoming alternate bracts only remotely in most distal parts of inflorescence, sessile, submembranaceous to subcoriaceous, linear to linear-lanceolate or rarely linear-oblanceolate, occasionally broader, (15) 19.5—31 (36) by 1.2—2.2 (2.8), length to width ratio (10) 12—18.7 (21), apices acute, margins entire, thickened, base attenuate, decurrent, glabrate, often hispidulous at least at base and margins above, and punctate, usually more notably so below, uninervate, nerve prominent abaxially, often with more obscure laterals at least basally, swollen or not at node. ***Inflorescence*** a compound dichasium of 1—15 flowers with opposite branching. ***Pedicels*** (3) 4.4—20.5 (27) mm long, 0.5 (0.8) mm in diameter, glabrous, holding fruit erect, subtended by a narrowly lanceolate to linear bract, bracts occurring in opposite pairs, occasionally singly and alternate. ***Calyx*** tube turbinate, nerved more or less prominently, glabrous or hispidulous, (2.2) 2.3—2.6 (2.7) by (2.4) 2.5—3 (3.1) mm, broadening in fruit to 4.5—4.8 mm; lobes 7—10 (11), (3.4) 4.4—4.9 (4.9) by0.3—0.6 (0.7) mm, thin, not nerved, linear to broadly subulate, hispidulous and punctate, apices acute, margins entire. ***Corolla*** infundibuliform, yellow, tube (4.6) 4.8—5.7 mm, 0.9—1.3 mm at base, opening to (3.4) 3.6—4.5 (5) mm at throat, pilose within; limbs (4) 5, obtuse, rarely acute or mucronate, 10.2—12.2 (12.7) by (4.5) 4.6—5.6 mm, glabrous. ***Stamens*** filantherous; filaments adnate ca 1—2.8 mm below throat, (6.1) 6.4—8.6 (9.1) mm long, glabrous; anthers exserted ca 5.3—6.4 mm, (2.9) 3—3.6 (3.7) by 0.8—0.9 (1.3) mm, often with a short, conical process extending from the connective apically, dorsifixed, latrorse. ***Pollen*** 50—70 µm. ***Ovary*** bicarpellate, each carpel with a single locule and 4 ovules. ***Style*** (12) 12.2—13.6 (13.9) mm, glabrous. ***Stigma*** capitate, bilobed, equalling or just exceeding the anthers. No mature fruit seen.

Very limited distribution at Santiago Papasquiaro and vicinity in Durango, from 1700—1900 m elevation. Flowering Jun.—Sept.

Steyermark (1932) cited a quite morphologically diverse set of specimens for this species. The type (*Palmer 429*) is quite distinct, and the other specimens mentioned in the protologue are quite different. The specimens cited for Texas (both in modern Big Bend National Park, *Havard s.n.*, *Moore & Steyermark 3257*) are referable to *Menodora scoparia*, and Schaffner collections of Potosí are referred to *M. coulteri* and *M. mexicana*. Thus the only authentic material is that of the type.

Menodora longifolia is similar to *M. yecorana*, and they are distinct sister taxa in the molecular phylogeny despite being quite isolated from each other.

SPECIMENS EXAMINED:

MEXICO: DURANGO: Santiago Papasquiaro, state of Durango and vicinity, 8/1896, Palmer 429 (A, GH, MO, NY, UC, US).

23. *Menodora yecorana* Van Devender & B. L. Turner

Phytologia 82 (4): 269, 1997. Holotype: MEXICO: SONORA: Yécora: 3.4 km N of Yécora on road to Agua Blanca, 7/15/1997, *A. L. Reina G. et al. 97-752* (TEX!).

Plants fastigiate suffrutescent perennials, (41) 32.1—76.6 (80) cm tall, with a no roots seen with few branches. ***Stems*** strict, branching remote, opposite, rarely to regularly alternate in inflorescence; older wood tan, glabrous, rugose, pitted, rimose; younger stems green, deeply fluted, with an obvious decurrent groove, terete below, strongly angled above in cross section, punctate, hispidulous at axils and nodes, trichomes short, white or hyaline, 0.05—0.09 mm; internodes at midbranch (2) 6—36 (43) mm. ***Leaves*** opposite, rarely to commonly alternate in inflorescence, sessile, submembranaceous, linear, entire leaves (10) 13.2—22.8 (26.5) by 0.5—4.3 (7), length to width ratio (2.1) 9.5—25.4 (28.3), punctate, most obvious below though sometimes obscure, and glabrate but often very sparsely hispidulous at base and along margins, apices acute, margins entire, base decurrent, uninervate, nerves very prominent abaxially. ***Inflorescence*** a compound dichasium 1—12 flowers, with opposite branching at least initially. ***Pedicels*** (3) 4.2—15.4 (25) mm long, 0.6—0.8 mm in diameter, glabrous, holding fruit erect, subtended by a linear, punctate, glabrate bract, bracts sometimes in opposite pairs but commonly alternate. ***Calyx*** tube turbinate, nerved, glabrous, 3.5—3.9 by 2.9—3.1 (3.1) mm, broadening in fruit to (5.5) 5.2—6.9 (7) mm; lobes 6—8 (9), (4.5) 4.8—7 by0.4—0.5 mm, thin, nerved, linear-lanceolate, glabrous, apices acute, margins entire. ***Corolla*** infundibuliform, yellow, tube 5.5—6.5 mm, 1.3—1.6 mm at base, opening to 3.1—4.8 mm at throat, pilose within; limbs (4) 5, 13.4—13.5 by 4.6—5.1 mm, glabrous. ***Stamens*** 2, filantherous, epipetalous; filaments adnate ca 1.8—2.4 mm, 7.5—8.6 mm long, glabrous; anthers exserted ca 4.8 mm, 3.2—3.7 by 0.8—1.1 mm, with a conical process extending from the connective apically, dorsifixed, latrorse. ***Pollen*** 60 µm. ***Ovary*** bicarpellate, each carpel with a single locule and 4 ovules. ***Style*** 16—16.4 mm, glabrous. ***Stigma*** capitate, exceeding anthers ca 3 mm. ***Fruit*** with cocci globose, circumscissile, glabrous, 8 by 6 mm in diameter; pericarp thin, membranaceous, more or less translucent; each coccus containing 4 seeds, fewer by abortion. **Seeds** obovate, plano-convex to lenticular, (4.3) 4.4—5.2 (5) by 2.3—2.5 (2.5) by 0.7—1.7 (1.5) mm, regularly reticulate.

Limited distribution in the vicinity of Yécora, Sonora, from 1520—1700 m elevation. With flower or fruit Jul to Sep.

This is the sister species to *Menodora longifolia*, and is a rare local endemic growing on volcanic ash substrates (Van Devender and Turner 1997). It is similar in habit and appearance to *M. longifolia*, but is distinctive for its more acicular leaves, punctate stems, and much longer calyx lobes, the latter being reminiscent of those of *M. longiflora*.

SPECIMENS EXAMINED:

MEXICO: SONORA: Mpio. Yécora: 3.4 km N of Yécora on road to Agua Blanca, 7/15/1997, A. L. Reina G. et al. 97-752 (TEX); 3.4 km N of Yécora on road to Agua Blanca, 9/23/1997, A. L. Reina G. et al. 97-1188 (NY); 9.0 km NW of Yécora on road to Mesa Grande, 9/29/1998, T. R. Van Devender et al. 98-1939 (NY).

24. *Menodora scabra* A. Gray

Amer. J. Sci. II. 14:44, 1852. Lectotype (Steyermark, Ann. Missouri Bot. Gard. 19:136, 1932): USA: NEW MEXICO: Sierra Co.: Ojo del Muerto, south of Santa Fe, 8/2/1846, *Wizlizenus 68 (MO!)*.

Plants fastigiate ***subherbaceous to suffrutescent perennials***, (14) 21.3—43 (60) cm tall, with a woody taproot, caudex 5—13 mm diameter with many branches. ***Stems*** erect, branching throughout or remotely, alternate, usually opposite basally but rarely otherwise; older wood tan, gray to black, glabrate to strigillose, rugose, rimose; younger stems green, shallowly to moderately fluted, more so usually above, decurrent groove obscure, terete, only slightly angled, more so above in cross section, glabrate (though often hispidulous in axils) to densely strigillose, trichomes rudimentary and minutely papillate under magnification or more commonly short, white or hyaline, retrorse, (0.04) 0.06—0.09 (0.11) mm; internodes at midbranch (3) 7—42 (78) mm, usually not exceeding the subtending leaves or elongate and leaves remote; rarely afflicted with insect galls. ***Leaves*** alternate, basal 2—4 nodes usually opposite, rarely so to midbranch, becoming alternate bracts in inflorescence, sessile, submembranaceous, linear to linear-lanceolate or linear-oblanceolate, or broader and ovate to obovate, very rarely bifid or trifid, entire leaves (3) 9.6—25.2 (40.9) by (0.5) 1.6—4.2 (8.5), length to width ratio (2) 3.8—9.4 (22), lobed leaves (6.53) 9.4—24.2 (33) by (0.86) 0.8—8.1 (11.56) mm, length to width ratio (1.5) 3.7—8.3 (10.3), width at departure of lowest lobes (0.63) 0.9—3.4 (6.85) mm, ultimate segment 1.2—1.8 mm wide, glabrate (usually at least minutely papillate), or moderately to densely hispidulous, often punctate especially below, apices acute or apiculate, rarely mucronate, rarely obtuse or cordate below, margins entire, thickened, base attenuate or cuneate, decurrent, uninervate, nerves prominent abaxially though often attenuating to apex, swollen or not at node, rarely with obscure lateral nerves. ***Inflorescence*** a terminal compound dichasium with alternate branching of 1—15 flowers. ***Pedicels*** (0.9) 2.7—15.1 (31) mm long, (0.3) 0.4—0.6 (0.8) mm in diameter, glabrous to densely strigillose, holding fruit erect, subtended by a linear to lanceolate bract. ***Calyx*** tube turbinate, glabrous to strigillose, usually punctate, (1.4) 1.6—2.4 (3.6) by (1.4) 1.6—2.3 (3) mm, broadening in fruit to (2.5) 2.8—4.1 (5.1) mm; lobes (4) 9—10 (12), (1.3) 2.6—5 (9.5) by (0.2) 0.3—0.6 (0.9) mm, thin, usually nerved, linear or subulate, hispidulous, apices acute, margins entire. ***Corolla*** infundibuliform, yellow, outer petals often red in bud, tube (2.9) 3.4—5.4 (7) mm, (0.8) 1.1—1.6 (2.1) mm at base, opening to (2.3) 2.7—3.9 (5) mm at throat, pilose or rarely glabrous within; limbs (4) 5 (6), obovate or oblong, apices obtuse, acute, or occasionally mucronate, (4.4) 5.5—8.3 (10.1) by (2.1) 3—4.7 (6.7) mm, sparsely hirtellous in bud becoming glabrate in flower. ***Stamens*** filantherous; filaments adnate (1) 1.2—1.9 (2.3) mm below throat, (2) 2.9—5.2 (6) mm long, glabrous; anthers exserted (0.8) 1.3—3.1 (4), (1.7) 2—2.7 (3.4) by (0.4) 0.5—0.8 (1) mm, rarely with a short linear or conical process extending from the apex of the connective, dorsifixed, latrorse. ***Pollen*** (40) 50—70 (90) µm. ***Ovary*** bicarpellate, bilobed, each carpel with a single locule and 4 ovules. ***Style*** (5.4) 7.1—10.6 (13.4) mm, glabrous. ***Stigma*** capitate, often bilobed, equalling or exceeding the anthers 0.5—3 mm. ***Fruit*** with cocci globose or obovoid, circumscissile, glabrous, (4.4) 5.2—6.8 (8) by (3.2) 4—5.6 (7) mm in diameter; pericarp thin, membranaceous, more or less translucent; each coccus containing 4 seeds or fewer by abortion. ***Seeds*** obovate or rarely ovate, trigonal or less commonly plano-convex or meniscoid to lenticular, (3.9) 4.6—5.5 (6.1) by (1.9) 2.7—3.7 (4) by (0.8) 1.1—1.7 (2) mm, finely reticulate, raphal rib raised and prominent or occasionally not well-developed in some varieties, often scalloped at least abaxially.

Distibuted in northern and central New Mexico west to southern California (peripheral in southern Utah and Nevada) and south to Baja California and northern Sonora; disjunct along the middle Arkansas River in Colorado, from (380) 700—2461 m elevation. Flowering (Mar) Apr—Sep (through mid-Nov, and in early Jan), with fruit Apr—Sep (through Nov and Jan).

This is a widespread and morphologically variable species of open desert grasslands and hillsides. In my concept, this is mostly a species of western North America, being east of the Continental Divide only in central and northern New Mexico and Colorado. The species consists of four varieties, distinguished mostly by habit, size, leaf shape and relative leaf and internode lengths, and occupying fairly distinct geographic regions. Most of the varieties come together in the region surrounding the Continental Divide, along with *Menodora laevis,* and determinations of specimens in this region can be problematic. The type locality for *M. scabra* lies in this zone in Sierra County, New Mexico, at an old watering hole (Ojo del Muerto; now usually under the waters of Elephant Butte Reservoir except in very dry years) along the old Spanish trail (the Jornado del Muerto) from Las Cruces to Santa Fe; Turner (1991) cited the locality in error as being in Santa Fe County.

Gray did not indicate the type of the species in his description, and two of the syntypes mentioned in the protologue were later referred to different species: *Wright 563* (GH) = *M. laevis*; and *J. Gregg 527* (GH) = holotype of *M. scoparia*.

The four varieties can be distinguished by the following characters:

1. Leaves relatively short and broad, lanceolate or oblanceolate, length to width ratio usually 5 or less; plants usually freely branching throughout ....24c. ***M. scabra* var. *sonorensis***

1. Leaves linear to linear-lanceolate or linear-oblanceolate, length-to-width ratio usually 5 or greater; plants usually branching only proximally near the base, and distally for the inflorescence

    2. Plants usually less than 30 cm tall; internodes and leaves relatively uniform in length ....24a. ***M. scabra* var. *scabra***

    2. Plants usually 30 cm or more tall; internodes elongate, often dramatically increasing in length to midstem

        3. Plants usually strigillose; leaves increasing in length to midstem, often longest there; internodes usually surpassed by or approximate to the

apices of subtending leaves; calyx lobes usually 10 (rarely fewer); ....24d. ***M. scabra* var. *occidentalis***

3. Plants usually glabrate; leaves largest below, often becoming slightly or greatly reduced in size above; internodes usually greatly exceeding the subtending leaves; calyx lobes usually less than 8 (rarely 10) ....24d. ***M. scabra* var. *glabrescens***

24a. *Menodora scabra A. Gray* var.*scabra*

Plants fastigiate ***subherbaceous to suffrutescent perennials***, (14) 17.4—26.6 (31) cm tall. ***Stems*** erect, branching remote, rarely throughout, alternate, usually opposite basally; younger stems green, glabrate to densely strigillose, internodes at midbranch (6) 8—18 (25) mm, usually shorter than the subtending leaves, making the leaves approximate and relatively crowded, internodes and leaves fairly uniform in size throughout, only slightly longer at midstem. ***Leaves*** alternate, usually opposite basally becoming quickly alternate, linear to linear-lanceolate or linear-oblanceolate, very rarely bifid or trifid, (3) 11.8—26.3 (33.9) by (1) 1.5—3.5 (5.7), length to width ratio (3) 5.7—10 (12.5), glabrate to hispidulous, usually punctate most obviously so below. ***Calyx*** lobes (5) 9—11 (12).

Distributed in northern and central New Mexico west to the Colorado Plateau in northern Arizona and peripherally in southern Utah, southeastern California and southeastern Nevada, with disjunct populations in central Colorado and Baja California, from (492) 1320—2400 m elevation. Flowering (Apr) late May to Sep (through mid-Nov, and in early Jan), with fruit (from May) Jun to mid-Sep (through Nov, and Jan).

SPECIMENS EXAMINED:

MEXICO: BAJA CALIFORNIA NORTE: West slope of Cerro Piñón, 3 mi N of El Alamo, 5/30/1970, Moran 17646 (LL, RSA, UC); Sierra Juárez, north fork of Cañada el Rincón, 7/4/1976, Moran 23600 (MEXU); Sierra de Juarez, ca 1 mi S of Japa, SW of La Rumorosa, on an unnamed dirt road, 5/27/1990, Neel & White s.n. (TEX); Japa. Lower California, 7/25/1883, Orcutt 926 (UC). **Ensenada:** 3 mi W of Santa Catarina, 64 mi SE of Ensenada, 8/21/1961, Broder 593 (US).

USA: ARIZONA: 7/21/1896, Crampton s.n. (US); 1/1/1869, Palmer 69 (US). **Apache County:** 5 mi W of 2-story Trading Post on Navajo Rte. 68 near Window Rock, first canyon N of hwy, 7/11/1961, Bohrer 636a (UC); White Mountains, 6/23/1930, Drushel 8477 (US); 12 mi N of White R., White Mountains, 6/23/1930, Goodman & Hitchcock 1302 (GH, MO, NY, RM, UC). **Coconino County:** Rim, Grand Canyon, 7/6/1912, Condit s.n. (UC); 2 mi S of Grand Canyon, 7/22/1933, Degener & Park 4413 (NY); Tusayan National Forest, 8/7/1912, Douthitt 170 (RM); 5 mi N of Williams, Hargrove & Schroeder s.n. (MO); About 1/2 mi NW of hellhole Bend on Little Colorado River gorge, W of Cameron, 5/26/1994, Hevron 2143 (MEXU); Grand Canyon, along road to Hopi Point, 7/1/1913, Hitchcock 104 (US); Near Flagstaff, 6/23/1901, Leiberg 5555 (US); In the vicinity of Flagstaff, 7/4/1898, MacDougal 218 (GH, NY, UC, US); Red Wall, Kaibab Trail, Grand Canyon National Park, 5/23/1938, Nelson & Nelson 1549 (RM); Flagstaff, Purpus 8057 (MO, UC, US); 10 mi S of Grand Canyon, 7/13/1892, Wooton s.n. (US). **Gila County:** 10 mi W of Fort Apache, 6/15/1937, Allen 906 (UC); 14 mi SW of Ft. Apache and 1/2 mi S of Black River, 7/28/1965, Hess 351 (UC). **Greenlee County:** Duncan Plains, 10/1/1900, Davidson 444a (GH). **Mohave County:** Handcock Tank, Kanab [Kaibab] Plateau, Grand Canyon National Monument, Toroweap, 6/15/1954, Cottam 14004 (GH, US); Peach Springs, 7/6/1883, Rusby 718 (MO, UC). **Navajo County:** Ft. Apache, Bear Canyon, 6/15/1932, Fish 25 (UC); White Mountains, 8/10/1903, Griffiths 5389 (US); Chalcedony Park, 7/15/1897, Hough 34 (GH, MO, US); Petrified National Forest, 6/25/1935, Maguire & Maguire 12198 (RM); Between Holbrook and Lupton, 5/22/1934, McKelvey 4585 (A); Holbrook, 8/17/1896, Zuck s.n. (US). **Pima County:** Santa Catalina Mts. [Mt. Lemmon, named for his wife; 35 km NE Tucson, this variety for this locality doubtful], 5/1/1881, Lemmon 164 (UC). **Santa Cruz County:** The[Appleton-Whittell] Research Ranch just S of Tucson [near Elgin]; East Mesa, just E of gate leading to Forest Service land, 9/1/1988, Elias et al. 12085 (NY). **Yavapai County:** 4 mi ESE of Camp Verde, sandy flats ca 1/2 mi N of main road between white bluffs, 6/23/1979, Ertter & Strachan 2935 (NY); E side of large wash 4.5 mi ESE of Camp Verde on N side of main road, 6/24/1979, Ertter & Strachan 2945 (NY); Coconino National Forest. Stoneman Lake Rd, 1 mi E of Hwy 79. Beaver Creek watershed, 8/15/1967, Feddema 3682 (RM); Ash Fork, 6/20/1903, Griffiths 4767 (US); Prescott, 7/16/1903, Griffiths 4882 (US); Cedar Glade, 6/16/1920, Jones 87 (GH); Clemenceau, 5/25/1922, Jones s.n. (MO, UC); Cedar Glade, 6/16/1922, Jones s.n. (UC); 8.1 mi E of Sedona on 174, 6/4/1967, Mears 1822 (TEX); One-half way between Ashfork and Seligman, Hwy 66, 5/26/1960, Miranda & Deaver 5736 (UC); 1.1 mi N75°W of Anderson Butte along Bill Gray Road (FS761), 12 mi N of Bridgeport, 9/10/1984, Morefield & Schaack 2559 (NY); Coconino National Forest: Beaver Creek Ranger Station, 6/28/1955, Pase 439 (RM). **CALIFORNIA: San Bernardino County:** Mesa south slopes New York Mts., 5/10/1939, Alexander 415 (UC); 4th of July Canyon, New York Mts., 5/5/1940, Alexander & Kellogg 1340 (UC); Half way up 4th of July Canyon, New York Mountains., 5/11/1940, Alexander & Kellogg 1399 (GH, UC); Barnwell, 5/1/1911, Brandegee s.n. (UC); ca 7.5 mi E of Cima in New York Mts., on S-facing slopes on NW-SE trending Canyon W of Fourth of July Canyon, 6/4/1973, Henrickson 10522 (LL, NY); E. Mojave Desert, New York Mountains: W branch of Fourth of July Canyon, 6/21/1973, Thorne & Tilforth 44120 (MO, NY). **COLORADO: Fremont County:** Along foothills road 10 mi N of Cañon City between Cañon City and Colorado Springs, 7/3/1921, Bethel s.n. (GH, RM); Along Fremont Road 132 ca 0.9 rd mi N of jct with Fremont Road 123, ca 6 air mi ENE of Cañon City, 8/18/2001, Chumley 7366 (TEX); Along Fremont Road 120 ca 7 air mi E of Florence, ca 1.6 rd mi W of jct with US Hwy 50, 8/18/2001, Chumley 7367 (TEX); At entrance to Red Canyon Park, off Fremont Road 9 ca 9 rd mi N of Cañon City, 8/16/2001, Chumley & Goodson 7363 (TEX); Florence to Colorado Springs, 9/1/1921, Clokey 4235 (RM, UC); East of Cañon City, 7/3/1921, Clokey et al. 4236 (MO, NY, RM, UC, US); 18 mi NE of Cañon City, 5/28/1954, Harrington 7307 (MO); 30 mi S of Colorado Springs, 6/14/1941, Livingston 481 (TEX); at rd. jct. to Red Canyon Campground 11 mi N of Cañon City on Co. Rd. 9, 7/17/1984, Neese 15942 (NY, RM); Between Cañon City and Colorado Springs, 6/20/1927, Osterhout 6840 (NY, RM); Between Cañon City and Colorado Springs, 6/16/1928, Osterhout 6909 (MO, RM); Florence, 6/15/1912, Ramaley 9777 (RM). **Pueblo County:** Off Old Colorado Hwy 96, near its terminus on south side of Pueblo Reservoir, ca 5 air mi S of Pueblo West, 8/18/2001, Chumley 7368 (TEX); Along Colorado Hwy 96 ca 4.2 rd mi W of park headquarters at Pueblo Reservoir, 8/18/2001, Chumley 7369 (TEX); 4 mi SW Pueblo, Arkansas River bottoms, 9/4/1943, Ewan 15324a (NY); Pueblo, 1/1/1873, Greene s.n. (GH); Upper end of Pueblo Reservoir, S of reservoir, 6/14/1978, Warnock 809 (TEX); South Pueblo. Goodnight Ranch, 8/6/1883, Woodward s.n. (GH). **NEW MEXICO:** [New Mexico], Wright 1694 (GH, NY, US); 1847, Fendler 693 (GH, NY, UC, US); Rusby s.n. (A, NY); Thurber 693 (GH). **Bernalillo County:** Cibola National Forest: vicinity of Cedro Ranger Station Pasture, 7/13/1967, Gierisch 3324 (RM); Albuquerque, 9/4/1894, Herrick s.n. (NY); Albuquerque, Howard s.n. (MO). **Catron County:** Wash near Paddy's Hole, 7/28/1924, Eggleston 20354 (NY); 8 mi W of Continental Divide, near Tularosa Creek, 7/2/1927, Goddard 813 (UC); 2 mi S of Glenwood, 5/30/1993, Turner 93-33 (TEX); San Augustin Plains, 13 mi S of Datil, 7/9/1965, Weber & Salamun 12772 (NY, TEX). **Grant County:** 15 mi NW of Redrock, without collector, s.n. (NY); Bluffs of Little Dry Creek, NW of Buckhorn, 6/3/1985, Barneby 17990 (NY, US); Silver City, 1/1/1911, Beard s.n. (MO); Hills east of Silver City, 9/15/1927, Gooding 4394 (RM); Mogollon Creek, 6/12/1935, Maguire 11965 (NY); Pinus altus [Pinos Altos], 8/7/1895, Mulford 807 (NY, US); Copper Mines, 7/15/1857, Thurber 232 (GH, NY); [Copper Mines.], Thurber s.n. (NY); 5 mi W of Silver City, 7/4/1906, Wooton s.n. (US). **Guadalupe County:** By Hwy 54, 25 mi NE of Vaughn, 7/17/1975, LeDoux & Dunn 1861 (MO, NY). **Hidalgo County:** Monument No. 40, Mex. bound. line.[In packet: "Upper corner monument, parallel 31° 47'"], 5/9/1892, Mearns 252 (US); Big Hatchet Mts., 2 air mi NE from the top of Big Hatchet Peak in canyon draining east, 9/19/1993, Worthington 22438 (NY). **Luna County:** Along US 180 10 mi NW of Deming, 5/5/1990, Helmkamp 234 (TEX). **McKinley County:** Ft. Wingate, 7/15/1880, Rusby 255 (MO, NY, UC, US). **San Miguel County:** At head of Hermosa Canyon, 2.8 mi S of Rte. 104, 18 mi E of Las Vegas. Crystal Pasture, N fenceline, near ranch road at gate to Mogote Trap, 8/21/1982, Hill & Levandoski 12133 (NY); Santa Fe National Forest and Vicinity: along Arroyo Leguino just below the northwest end of Meseta de los Ladrones, ca 7.5-8 air mi E of Villanueva; ca 21 air mi S of Las Vegas. Also S3 SE1/4, 7/11/2004, Nelson 61606 (RM); Santa Fe National Forest: Sangre de Cristo Mountains and vicinity: From North San Ysidro NNE to lower Apache Canyon. At Forest boundary, 5/30/2004, Reif 9622 (RM); Santa Fe National Forest: Sangre de Cristo Mountains and vicinity: Anton Chico. NM Hwy 85 at northern forest boundary, 1.5 air mi S of Bernal. Also S11 SE1/4, 5/30/2004, Reif 9684 (RM); Between Anton Chico and Las Vegas, 10/1/1913, Rose & Fitch 17653 (NY); Between Anton Chico and Las Vegas, 10/1/1913, Rose & Fitch 17653 (US); Near Pecos, 8/15/1908, Standley 4967 (GH); Near Pecos, 8/15/1908, Standley 4967 (MO, NY, US). **Sandoval County:** Eastern slope of Sandia Mountains, Las Palomas, 6/18/1914, Ellis 372 (NY, US); Sandia Mountains, near La Madera, 6/18/1914, Ellis 372 (MO); Golden, 7 mi S, 8/15/2001, Neff 01-08-15-01 (TEX). **Santa Fe County:** Galisteo, 8/23/1926, Arséne 15819 (UC); 2 mi E of Santa Fe, 7/28/1926, Arséne & Benedict 16755 (US); La Glorieta, 9/15/1879, Brandegee 11936 (MO); Santa Fe, 7/20/1898, Earle 74 (NY); Near Santa Fe, 9/8/1881, Engelmann s.n. (MO); Santa Fe National Forest: ca 5 air mi W of Rowe, vicinity of S.D. Jacinto bench mark, 1/14/2004, Hartman 79222 (RM); Santa Fe, 7/8/1897, Heller & Heller 3826 (GH, MO, NY, US); 25 mi S of Golden, 7/24/1938, Hitchcock et al. 4218 (RM, UC). **Sierra County:** Bear Den Canyon at edge of riparian area about 4 km N of Rhodes Canyon, 8/28/1991, Anderson & Morrow 5096 (TEX); Jornada del Muerto. [Ojo del Muerto], 8/1846, Wislizenus 68 (MO); Kingston, Black Range (Emory Pass), 6/22/1985, Worthington 13294 (NY). **Socorro County:** About 19 mi due E of Socorro on Mesa Redonda, 8/13/1977, Edwards & Reitzel 4783 (NY); Plains E of Datil on Hwy 60, 7/17/1973, Higgins 7749 (NY). **Torrance County:** I-40, W of mile marker 224 E of Moriarity, 6/29/1986, Walter & Walter 11185 (MO). **NEVADA: Lincoln County:** Deer Lodge Canyon Road, 6/28/1980, Williams 80-153-9 (NY). **UTAH:** Southern Utah, Northern Arizona 1877, Palmer 65 (GH, MO, NY, US). **Beaver County:** Hamlin Valley. Slopes E of valley, 5/24/1987, Franklin 4846 (NY, RM). **Garfield County:** About 8 mi SE of Escalante, along Hole in the Rock road, Alvey Wash drainage, 6/25/1965, Holmgren et al. 2033 (GH, NY, TEX). **Kane County:** 4 mi S

Glendale, 6/20/1940, Maguire 18885 (RM). **Washington County:** Cane Spring Mountains, Purpus 6228 (NY, UC, US).

24b. *Menodora scabra A. Gray* var. *glabrescens* A. Gray in S. Watson

Cat. Pl. Wheeler Exp. 15, 1874. Lectoype (Turner, Phytologia 71:5:352, 1991): USA: ARIZONA: without locality or date, *Wheeler s.n.* (GH!).

Menodora scabra A. Gray var. *longituba* Steyerm., Ann. Missouri Bot. Gard. 19: 141, 1932. Holotype: USA: ARIZONA: Maricopa Co.: Massatzal [Mazatzal] Mountains, 5/5/1867, *Smart 213* (GH!).

Plants fastigiate ***subherbaceous to suffrutescent perennials***, (30) 30.5—49.8 (60) cm tall. ***Stems*** strict, branching remote, alternate, opposite basally but rarely to midbranch; younger stems green, glabrate (often hispidulous in axils) to somewhat densely strigillose below and glabrate above, rarely strigillose throughout; internodes often crowded basally, lengthening dramatically to near midbranch, often with alternating long and short internodes, (3) 17—56 (78) mm at midbranch, usually exceeding the subtending leaves. ***Leaves*** alternate or opposite, usually opposite at least basally to near midbranch and alternate above, sessile or subpetiolate, submembranaceous, rarely subcoriaceous, linear to narrowly elliptic tending toward either slightly linear-lanceolate or linear-oblanceolate, often more linear above and obovate or spatulate below, usually largest just above basalmost nodes, rarely near midbranch but usually slightly to greatly reduced above, (3) 8.3—24.8 (40.9) by (0.5) 1.3—3.6 (5.7), length to width ratio (2.7) 4.1—10.1 (22), glabrate to hispidulous, often glabrate above, occasionally punctate below. ***Calyx*** lobes (4) 5—7 (10).

In the central highland transition zone between the Colorado Plateau and Sonoran Desert in Arizona, in the eastern Mohave Desert of southern California and in Baja California Norte, from (369) 760-1784 m elevation. Flowering (late Mar) Apr to Sep (Oct), with fruit mid May to Oct.

This taxon was formerly recognized as *Menodora scoparia* in western North America, but I restrict use of that species name to individuals of the Chihuahuan Desert region east of the Continental Divide. Though Steyermark had reviewed a number of specimens of the western members of *M. scoparia*, he did not contrast differences between those of the west versus those from the east. In general, the western plants recognized here are a little more robust, larger, taller plants than their eastern counterparts, with larger leaves that occasionally are not extremely reduced above. This form is prevalent throughout the Arizona and California part of the range, and is occasional in Baja California. There, however, the plants tend to be a bit smaller, more like the eastern *M. scoparia*, with broader leaves. A number of specimens appear to be intermediate between the scoparioid form and a more scabroid form (e.g., *Moran 17646* (LL, RSA, UC), which I have referred to *scabra*; *C. R. Orcutt 926* or *s.n.*). The group in Lower California is certainly worth more study and clarification.

The type (and to my knowledge only specimen ever identified) of *Menodora scabra* var. *longituba* is indistinguishable from the material of *glabrescens*, and Steyermark routinely annotated specimen sheets of simiilar character from eastern Arizona as var. *ramosissima*. In the east, this taxon seems to intergrade with both var. *scabra* and what I have recognized below as var. *sonorensis*.

SPECIMENS EXAMINED:

MEXICO: BAJA CALIFORNIA NORTE: San Julio Cañon, Lower California, 4/20/1889, Brandegee s.n. (GH); Las Huertas, 5/19/1889, Brandegee s.n. (UC); Agua Dulce, 5/16/1889, Brandegee s.n. (UC); El Rancho Viejo, 4/24/1889, Brandegee s.n. (US); Canyon del Diablo, to the N and W of Picacho del Diablo (Cerro La Encantada), eastern flank of Sierra San Pedro Martir. 4.5 mi up canyon from its mouth, 6/17/1954, Chambers 632 (UC); Jacumba. Lower California, 7/9/1922, Fisher 36 (US); 3.2 mi NW of Rosarito, 6/5/1963, Moran 11185 (UC, US); Sierra Juarez, Portezuelo de Jamau, 10/2/1966, Moran 13656 (UC); Sierra Juarez, south slope of Cerro Chichi de la India. [Cerro Tetas de la India], 8/31/1968, Moran 15556 (UC); Sierra San Borja, southeast slope of Cerro el Sauco, 3/27/1960, Moran 8096 (UC, US); Sierra San Borja, east slope of valley of San Juan, 6/8/1962, Moran 9734 (GH, UC, US); Cantillas Mts. Lower California, 7/25/1900, Orcutt 926 (GH); Cantillas Mts, Lower California, 8/1/1883, Orcutt 949 (GH); Cañon Cantillas, 7/7/1884, Orcutt s.n. (NY); Cantillas Cañon. Lower California. [Cañon El Tajo], 8/1/1883, Orcutt s.n. (UC); Flora of Lower California, Parry's Pinesy [?], 7/4/1884, Orcutt s.n. (UC, US); About 7 mi W of El Rosarito, W of S end of Sierra San Pedro Mártir, 6/5/1963, Thorne 32083 (GH, UC); ca 2 mi S of La Rumorosa, 11/12/1983, Thorne & Wisura 57420 (MO); S of La Rumorosa: 3.3 mi S on Laguna Hanson Road, 5/9/1985, Thorne & Wisura 60538 (MEXU); At El Banco, oasis on eastern flank of Sierra San Pedro Martir, between San Felipe Desert and Los Emes, 5/11/1941, Wiggins 9849 (US).

USA: ARIZONA: [without date or locality], Wheeler s.n. (GH); Barney, 8/20/1921, Jones s.n. (UC). **Cochise County:** Pinery Creek, Chiricahua Mts., 8/15/1896, Crampton s.n. (US). **Gila County:**Ca 6 airline mi NW of Rye, 6/11/1993, Atwood & Anderson

18105 (NY); Off Forest Road 583 (road to Tonto State Park) ca 0.7 mi W of jct with US Hwy 87, 8/11/2001, Chumley & Vanden Huevel 7361 (TEX); Mesa near Rock and Rye creeks, Collum 68 (GH), MO, NY, US); Apache Trail and adjacent region: Mazatzal Mts. on road to Amethyst Mine, 5/11/1929, Eastwood 17071 (GH, UC); Roosevelt Dam, 5/17/1919, Eastwood 8671 (GH, UC, US); Tonto National Forest: 4.5 mi W of Strawberry, 8/17/1976, Gierisch 3766 (RM); Bluff above Natural Bridge, 1 mi N, 9/28/1935, Gooding s.n. (UC); Roosevelt Dam, 8/3/1911, Gooding 720 (GH); Natural Drainages Experimental Area A, lower Parker Creek drainages, Sierra Ancha Mountains, 9/4/1946, Gould & Hudson 3863 (GH, NY, UC); Cherry, 7/16/1922, Jones s.n. (UC); Near Miami, 7/16/1931, Peebles 7945 (US); Near the weather station at Parker Creek Station. Sierra Ancha, 7/12/1958, Wagner 165 (UC). **La Paz County:** In vicinity of old Smithsonian Observatory, at summit of Harquahala Peak, Harquahala Mountains, 9/26/1955, Tucker 2868 (UC). **Maricopa County:** Massatzal [Mazatzal] Mountains, 5/5/1867, Smart 213 (GH); Sunflower, 8/2/1980, Taylor & Taylor 29431 (NY). **Mohave County:** Vicinity of Kingman, 1/1/1926, Braem s.n. (A); Crozier, 10/1/1927, Braem s.n. (A); Oatman, 4/21/1931, Eastwood 18187 (US); Yucca, 5/17/1884, Jones 3924 (A, NY, US); Kingman, 9/18/1935, Kearney & Peebles 12597 (US); Peach Springs, 7/6/1883, Rusby 5292 (NY, UC, US); 20 mi from Kingman, 5/30/1893, Wilson s.n. (UC, US). **Pinal County:** Arboretum grounds, 5/24/1935, Whitehead 1274 (UC). **Yavapai County:** 6 mi SW of Prescott along Hwy 89, Prescott National Forest, 9/5/1991, Atwood 17043 (MO, NY); Ft. Whipple; Skull Valley, 6/4/1865, Coues & Palmer 223 (MO); 31. 9 rd mi E of I-17, along Bloody Basin Road, 4/22/1984, Hodgson 2837 (NY); Above Cornville, 8/20/1921, Jones s.n. (UC); Prescott, 7/17/1927, Peebles et al. 4261 (US); Copper Basin, 8/25/1894, Toumey 206 (NY); Prescott, 8/24/1894, Toumey s.n. (UC); Prescott, 7/31/1911, Wooton s.n. (US); Prescott, 7/29/1896, Zuck s.n. (NY). **CALIFORNIA:**

[without locality], Cooper s.n. (US). **Riverside County:** North base of Eagle Mts., 5/21/1941, Alexander & Kellogg 2208 (GH, UC); Lost Horse Mine Road Joshua Tree National Monument, 5/30/1941, Cole 839 (UC). **San Bernardino County:** Flat north slope Clark Mt., 6/24/1939, Alexander 823 (UC, JEP); Mitchell's Caverns, Providence Mts., 5/15/1937, Beal 293 (JEP); Cave's trail, Mitchell's Caverns, Providence Mts., 5/17/1937, Beal 313 (JEP); Hill below Mitchell's Caverns, Providence Mts. [Bird Canyon noted in packet.], 7/3/1938, Beal 561 (JEP); Fountain Canyon, Mohave Desert, Providence Mts., 6/15/1941, Beal 938 (JEP); Fountain Canyon, Providence Mts., Mohave Desert, 6/16/1940, Beal s.n. (GH, JEP); Providence Mts., 6/6/1902, Brandegee s.n. (UC); Fort Mojave, Cooper s.n. (GH); Mitchell's Caverns, Providence Mts., 5/4/1937, Jepson 18169 (JEP); Cedar Canyon, between New York and Providence Mts., eastern Mojave Desert, 5/31/1952, Munz 17450 (NY); Vicinity of Bonanza King Mine, east slope of Providence Mountains, Mojave Desert, 5/23/1920, Munz et al. 4264 (NY, RM, US); Leastalk near Mojave Desert, New York Mts., 6/3/1915, Parish 10260 (JEP); New York Mts. near Leastock, 6/3/1915, Parish 10268 (UC); E. Mojave Desert, Providence Mts.: Globe Canyon, N of mets. ca 7 mi NE of Kelso (by road); upper part of canyon below mine, 6/19/1973, Thorne & Tilforth 43933 (GH, MO, NY); E. Mojave Desert, Providence Mts.: Mitchell Caverns State Park, large canyon NW of park headquarters, 6/20/1973, Thorne & Tilforth 44000 (NY); E. Mojave Desert, New York Mts.: Near mouth of Sagamore Mine, 6/21/1973, Thorne & Tilforth 44154 (NY); Coulton. [Colton], 5/15/1880, Vasey 362 (MO, NY, US); Mojave Desert, W slope of Providence Mts., 5-3/10 mi E of Hayden (UPRR) or 9/10 mi below Tough Nut Mine, 5/27/1941, Wolf 10761 (NY, TEX, UC); Mojave Desert, Clark Mt., 1.8 mi E of Pachalka Spring, 1st Canyon to E, 10/5/1935, Wolf 7593 (UC). **San Diego County:** Jacumba, 5/29/1903, Abrams 3641 (A, GH, MO, NY, UC, US); Desert Tower, E of Jacumba, 4/19/1962, Dempster 1908

(JEPS); Jacumba, 6/25/1935, McMinn 4008 (UC); 3 mi E of Jacumba. 32-37.25 N, 116-08.25 W, 5/22/1966, Moran 13136 (LL, UC); Southern part of San Diego County, Palmer s.n. (GH); San Felipe, 6/15/1880, Parish & Parish 435 (MO, NY); Jacumba, near the boundary monument, 7/8/1931, Wolf 2281 (UC). **NEVADA: Clark County:** Near south end of Highland Range, Piute Valley, 5/28/1992, Marrs-Smith BLM-49 (NY).

24c. ***Menodora scabra A. Gray*** var. ***occidentalis*** **Chumley**, *var. nov.*

Menodorae scabrae *A. Gray var.* glabrescens *A. Gray similis sed internodiis* (5) 9—24 (33) mm, *scaberulentis, plerumque brevis quam folia; folia* (3) 10.1—29.4 (39.2) *longis et* (1.3) 1.6—4.2 (5.6) mm *latis, hispidus, punctatus. Holotype*: USA: ARIZONA: Gila County: Salt River Mountains. 4/3/1932, Gillespie 5581 (GH!). Isotypes: NY!, UC!, US!.

Plants fastigiate ***subherbaceous to suffrutescent perennials***, 27—46 (60) cm tall. ***Stems*** erect, branching remote, occasionally throughout, alternate, rarely opposite basally; younger stems green, strigillose to densely so; internodes often alternating long and short, (5) 9—24 (33) mm at midbranch, internodes and leaves usually increasing in length to midbranch, internodes usually surpassed by the apices or approximate to the length of subtending leaves. ***Leaves*** alternate, rarely opposite or subopposite basally to midbranch, sessile, submembranaceous, linear or linear-lanceolate to linear-oblanceolate, occasionally broader (especially below) and elliptic, very rarely bifid or trifid, (3) 10.1—29.4 (39.2) by (1.3) 1.6—4.2 (5.6) mm, length to width ratio (2) 4.6—9.9 (12.4), hispidulous, punctate at least below. ***Calyx*** lobes (5) 10 (12).

Distributed in the Sonoran Desert in western Arizona and northern Sonora, from 380—689 (2068) m elevation. Flowering (Mar) Apr—mid-May with fruit late Apr to Jul.

In form, this plant greatly resembles individuals of var. *glabrescens*, and is distinguished largely by the relative lengths of the internodes and leaves; in this taxon, the leaves are generally as long or longer than the internode they subtend. In Steyermark's concept of *scabra*, these are mostly referable to his polymorphic conept of var. *ramosissima.*

SPECIMENS EXAMINED:

MEXICO: SONORA: Cerros de los Tanques, ca 3.2 km SSW of Quitobaquito, southernmost of 3 granitic cerros (small mountains). Near summit (common from near base to summit), 2/10/1989, Felger & Broyles 89-21 (MEXU); On south side of Sierra Cipriano, 0.5 km E of hwy, 18 km SW of Sonoryta on MEX Hwy 8, 3/30/1988, Felger & Zimmerman 88-221 (MEXU); North end of the Sierra El Viejo in the large canyon containing the Mina Santa Cruz, 25 mi SW of Caborca, 3/7/1983, Sanders et al. 3493 (MEXU).

USA: ARIZONA: Gila County: Salt River Mountains, 4/3/1932, Gillespie 5581 (GH, NY, UC, US). **Maricopa County:** Tempe; SW1/4 of Sec 1, 4/17/1935, Davis s.n. (TEX); Tempe, 4/21/1892, Gaume & Blaschka s.n. (GH); White Tank Mountains Regional Park, Mesquite Springs Canyon, 5/5/1969, Keil 4561 (NY); Phoenix, 5/18/1897, Kuntze s.n. (NY); South Mountain Park, near W end, 4/17/1988, Landrum 6000 (NY); Corner Hidden Valley Road & Skyline Drive, Cave Creek, 4/3/1974, Lehr 1185 (NY). **Mohave County:** ca 2 mi S of Wikieup along US Hwy 93, 5/23/1995, Turner & Turner 95-123 (TEX). **Pima County:** Childs Mountain, Cabeza Prieta National Wildlife Refuge, 32-26-10 N, 112-56-10 W, 4/9/1993, Felger & Seminoff 93-289 (TEX). **Pinal County:**

Sacaton, Gilman 296 (UC); W of Queen, 4/26/1930, Wolff & Dana 1882 (US). **Yavapai County:** Paved road on W side of Lake Pleasant approx. 5.0 rd mi N of jct with AZ 74, 5/14/2003, Moore 231 (TEX); Bradshaw Mts., Purpus s.n. (UC). **UTAH: Washington County:** Near the Pine Valley Campgrounds, 7/21/1973, Higgins 7887 (NY).

24d. ***Menodora scabra A. Gray* var. *sonorensis* Chumley**, *var. nov.*

Menodorae scabrae *A. Gray var.* ramosissima *Steyerm. similis sed* (20) 20.9—52.3 (80) cm *alta, internodiis* (3) 7—24 (38) mm; *folium lanceolatus, oblanceolatus, vel elliptico-ovatis,* (3) 9.8—20.3 (33.4) *longis et* ((1.7) 2.4—5.2 (8.5) mm *latis, glabris vel sparse hispidus, punctatus; corollae tubo* 2.8—5 mm*, limbae* (5.3) 5.6—8.3 (10.1) *mm longis; pistillo* (6) 6.9—9.9 (11.1) mm. *Holotype*: ARIZONA: Pima Co.: Foothills, west side of Baboquivari Mountains, 4/17/1935, Aven Nelson & Ruth Nelson 1549 (RM!). Isotype: (GH!, MO!, NY!, UC!).

Plants fastigiate subherbaceous to suffrutescent perennials, (20) 20.9—52.3 (80) cm tall. ***Stems*** erect, branching throughout, rarely only remotely, alternate though usually opposite basally; younger stems green, moderately to densely strigillose, rarely glabrate; internodes commonly regularly spaced but often alternating long and short, (3) 7—24 (38) mm at midbranch, usually not exceeding the subtending leaves (though rarely greatly so). ***Leaves*** alternate, opposite basally, lanceolate or oblanceolate, often more narrow to linear or broader and elliptic to ovate or obovate, rarely bifid, (3) 9.8—20.3 (33.4) by (1.7) 2.4—5.2 (8.5) mm, length to width ratio (1.5) 2.9—5.3 (6.7) glabrate (minutely papillate), moderately to densely hispidulous, or sparsely hirtellous, often punctate. ***Calyx*** lobes (7) 9—10 (12).

Distributed in the eastern Sonoran Desert of southeast Arizona and northeast Sonora, to the Continental Divide, from 646—946 (2461) m elevation. Flowering (from Mar) May and Aug to Sept., with fruit late Apr to May (through Jul) and Aug tot Sep (Oct).

This variety was commonly ascribed by Steyermark to his var. *ramosissima* or var. *laevis*, depending on the stature of the plant. Its broader lanceolate or oblanceolate leaves distinguish it from the other varieties of *Menodora scabra*, but it may intergrade with *M. laevis* in the region around the Continental Divide. The essential character that separates *M. laevis* is its continuous, foveolate seed coat, as opposed to the reticulate seed coat of *M. scabra*, and unfortunately in the contact zone, I have seen few specimens with mature seed.

SPECIMENS EXAMINED:

MEXICO: SONORA: Hwy 83 Nogales, US-Mexico border. Santa Ana, 6/21/1977, Dwyer 14102 (MEXU, MO); 15 rd mi S of Agua Prieta, 2/7/1960, Felger 3980 (MEXU); Cerro del Viejo SW of Caborca, 10/10/1954, Gentry 14439 (US); Hwy 15 S of Santa Ana, 8/10/1957, Solbrig & Ornduff 4367 (GH); Region of the Rio De Bavispe, Northeastern Sonora: Colonia Morelos, 9/25/1941, White 4576 (GH, NY, US); 9 mi W of Pozo Cerna, 10/4/1932, Wiggins 6042 (US); 8 mi E of Magdalena, 9/14/1934, Wiggins 7187 (A, UC, US).

USA: ARIZONA: Dutch Charley's Ranch, near Monument 88, 8/13/1893, Mearns 1868 (NY, US); [w/o locality], 1/1/1884, Pringle s.n. (US). **Cochise County:** 3/8 mi N of Tombstone, 7/22/1953, Gardner & Fletcher 93 (US); Bowie, 9/22/1884, Jones 4330 (A); Rustler's Park, Chiricahua Mountains, 8/28/1966, Tate & Lehto 562 (NY). **Graham**

County: On the mesas at Camp Grant, 5/4/1867, Palmer 206 (MO). **Navajo County:** Ft. Apache, Hoyt s.n. (NY). **Pima County:** Desert Botanical Laboratory, Tucson. [1675 West Anklam Road], 1/1/1905, [without collector] 44 (US); W side of Tucson Mountains, adjacent to the wash at bottom of Contzen Pass, 4/10/1978, Barker 78-38 (LL); Martinez's Ranch; 16 mi W of Tucson, 3/31/1940, Brass 14261 (GH, MO, NY); In field adjacent to west-bound access road of Interstate Hwy 10, ca 1/4 mi W of exit 281 and US Hwy 83, ca 21.5 mi SE of Tucson, 8/26/2000, Chumley & Moore 7318 (TEX); Tucson, 8/29/1931, Demaree 8012 (MO); 5-1/2 mi SE of Mountainview, on the Tucson-Benson highway, 4/16/1938, Foster 163 (GH); Near Sells, Papago Res., 7/27/1931, Gilman 7968 (US); Tucson Mountain. Vicinity of Tucson, 4/11/1913, Greenman & Greenman 4 (MO); On trip to Tucson Mt., 3/7/1901, Griffiths 2436 (NY); Near Tucson, 8/21/1932, Harrison & Kearney 8916 (US); E of Vail, 4/27/1942, Harvey s.n. (LP); Papago Reservation, 5/7/1930, Jones 26448 (MO); Sierrestas [Sierrita] Mts., W of Tucson. [45 km SW of Tucson], 4/15/1881, Lemmon 164 (GH); San Baboquivari Mountains, vicinity of ranger station and slopes to the north, 4/17/1935, Maguire 10740 (GH, NY); Vicinity of Colossal Caves, 5/28/1935, Maguire 11703 (NY); Tucson, 4/15/1937, Meebold s.n. (NY); NE slope of Tucson Mountains in Picture Rock Wash, 4/14/1992, Merello & Brunner 207 (MO); Foothills, west side of Baboquivari Mountains, 4/17/1935, Nelson & Nelson 1549 (GH, MO, NY, RM, UC); Outskirts of Tucson, 4/25/1935, Nelson & Nelson 1618 (NY, RM); Tumamoc Hill, Tucson, 5/6/1909, Parish s.n. (A); Hills near Tucson, 5/15/1885, Pringle 15602 (MO); Hills near Tucson, 5/17/1883, Pringle s.n. (GH, NY, US); S foothills of Santa Catalina Mts., Redington Road, 4/8/1978, Reeves 6673 (NY); Near Tucson, 8/6/1914, Rehder 228 (GH); In the vicinity of Tucson, Laboratory Hill, 4/27/1910, Rose et al. 13788 (US); Sienega, S. Arizona, 8/15/1874, Rothrock 561 (GH, US); Tucson, Tumamoc Hill, 9/20/1916, Shreve

4988 (UC); 3 mi S of Sells on road to Topowa, 8/23/1973, Spellenberg & Willson 3602 (NY); Tucson; mesas, 5/12/1903, Thornber 2317 (GH, NY, TEX);Tucson, 5/22/1903, Thornber 448 (MO, NY, UC, US); Tucson, 8/27/1901, Thornber s.n. (UC); Tucson, 4/20/1892, Toumey 206 (A); Tucson, 5/15/1892, Toumey 206a (US); 4 mi S of Mission San Xavier, 8/23/1941, Wiggins & Rollins 61 (MO, NY). **Pinal County:** Table Top Mts., between Indian Butte and Table Top, Indian Butte Quad, 4/11/1981, Butterwick & Hillyard 7241 (TEX). **Santa Cruz County:** Nogales, 8/28/1927, Peebles 4725 (US). **Yavapai County:** Congress Junction, 5/1/1903, Jones s.n. (MO, US).

Excluded Species

Menodora integrifolia (Cham. & Schltdl.) Steud. var. *angulare* (Vahl) Kuntze, Rev. Gen. Plant. 3.2:197, 1898 = *Jasminum angulare* Vahl

Table 1. Summary of accepted taxa in *Menodora* with partial synonymy and distribution; older synonyms (*Bolivaria*, etc.) are not included - see species treatments for full synonymy and references.

Accepted taxon	**Names in synonymy**	**Distribution**
M. africana Hook. subsp. *africana*		Africa: E South Africa, S Botswana
M. africana subsp. *australis* (Steyerm.) Chumley, *comb. nov*.	*M. heterophylla* var. *australis* Steyerm.	Africa: E South Africa, S Botswana
M. coulteri A. Gray	*M. coulteri* var. *minima* Steyerm. *M. helianthemoides* var. *engelmannii* Steyerm. *M. hintoniorum* B. L. Turner	North America: central Mexico
M. decemfida (Gill. *ex* Hook. & Arn.) A. Gray		South America: Argentine pre-cordillera
M. gypsophila B. L. Turner		North America: central Mexico
M. helianthemoides Bonpl.	*M. helianthemoides* var. *parviflora* Greenm. *M. helianthemoides* var. *magniflora* Steyerm. *M. magniflora* (Steyerm.) B. L. Turner	North America: central Mexico
M. henricksonii Chumley var. *henricksonii, sp. nov*.		North America: central Mexico
M. henricksonii var. *confusa* Chumley, *var. nov*.		North America: central Mexico
M. heterophylla Moric. ex DC.		North America: USA, NE Mexico
M. integrifolia (Cham & Schltdl.) Steud.	*M. trifida* (Cham & Schltdl.) Steud. *M. integrifolia* var. *trifida* (Cham & Schltdl.) Kuntze *M. pinnatisecta* Steyerm. var. *pinnatisecta* *M. integrifolia* var. *pinnatisecta* (Steyerm.) Burkart *M. pinnatisecta* var. *missionum* T. Meyer *M. integrifolia* var. *odonelliana* T. Meyer *M. hassleriana* Chod. *M. chloragantha* (J. Rémy) Steyerm. *M. pinnatifida* Mart.	South America: Argentina, central Bolivia, E Paraguay, SW Brazil, Uruguay
M. intricata T. S. Brandegee	*M. intricata* var. *purpusii* Steyerm.	North America: central Mexico
M. jaliscana B. L. Turner		North America: central Mexico
M. juncea Harv.		Africa: W South Africa
M. laevis Wooton & Standl.	*M. scabra* var. *laevis* (Wooton & Standl.) Steyerm.	North America: central Mexico
M. linoides Phil.		South America: central Chile
M. longiflora A. Gray	*M. hispida* Palmer *M. pubens* A. Gray *Menodoropsis longiflora* (A. Gray) Small	North America: W Texas, N Mexico
M. longifolia (Steyerm.) Chumley, *comb. nov*.	*M. decemfida* var. *longifolia* Steyerm.	North America: W Durango, Mexico
M. mexicana A. DC. in DC.	*M. potosiensis* Henrickson ex B. L. Turner	North America: central Mexico
M. muellerae Rehd.		North America: central Mexico
M. pulchella Markgr.		South America: high elevation Argentina-Bolivia
M. scabra A. Gray var. *scabra*		North America: N Arizona, N New Mexico
M. scabra A. Gray var. *glabrescens* A. Gray in S. Wats.		North America: Baja California, S California, central Arizona
M. scabra var. *occidentalis* Chumley, *var. nov*.		North America: W Sonoran Desert
M. scabra var. *sonorensis* Chumley, *var. nov*.		North America: E Sonoran Desert

Table 1. (continued)

Accepted taxon	Names in synonymy	Distribution
M. scoparia Engelm. *ex* A. Gray		North America: Chihuahuan Desert
M. spinescens A. Gray var. *spinescens*		North America: NE Mojave Desert
M. spinescens var. *mohavensis* Steyerm.		North America: S Mojave Desert
M. spinescens A. Gray var. *bahensis* Chumley, *var. nov.*		North America: Baja California, Mexico
M. robusta Benth.		South America: N Patagonia
M. tehuacana B. L. Turner		North America: central Mexico
M. yecorana Van Devender & B. L. Turner		North America: NW Mexico

Table 2. Statistics for floral presentation size for species and recognized infraspecific taxa in *Menodora*. Presentation is the diameter of the floral face as presented to a potential pollinator, and was calculated as 2X corolla limb length + diameter of throat.

Taxon	**Sample Size**	**Median (mm)**	**Mean (mm)**	**Standard Error**	**Standard Deviation**	**Range (mm)**	**Min (mm)**	**Max (mm)**	**Confidence (95.0%)**
africana subsp. africana	14	19.50	20.32	0.79	2.97	9.50	16.50	26.00	1.72
africana subsp. australis	7	22.00	20.57	1.67	4.43	10.00	15.00	25.00	4.10
coulteri var. coulteri	9	22.00	21.30	2.04	6.12	21.00	12.00	33.00	4.71
coulteri var. minima	9	12.00	12.48	0.82	2.46	8.65	8.85	17.50	1.89
decemfida	10	20.54	22.78	2.01	6.36	20.50	13.53	34.03	4.55
gypsophila	4	17.23	17.30	0.16	0.33	0.67	17.04	17.71	0.52
helianthemoides	10	19.93	20.56	1.72	5.45	17.88	13.41	31.29	3.90
helianthemoides var. magniflora	7	26.58	26.41	1.91	5.05	14.82	20.91	35.73	4.67
henricksonii	6	22.49	22.39	1.69	4.15	11.35	16.00	27.35	4.36
henricksonii var. confusa	2	19.87	19.87	3.63	5.13	7.26	16.24	23.50	46.12
heterophylla	14	18.83	18.81	0.72	2.68	10.34	13.41	23.75	1.55
integrifolia	55	14.16	14.69	0.48	3.58	14.17	8.34	22.51	0.97
integrifolia var. integrifolia	19	15.69	15.66	0.82	3.58	11.92	10.59	22.51	1.73
integrifolia var. odonelliana	5	11.98	12.65	1.55	3.47	9.52	8.50	18.02	4.31
integrifolia var. pinnatisecta	18	15.20	14.93	0.87	3.69	13.27	8.34	21.61	1.83
integrifolia var. trifida	13	13.89	13.71	0.91	3.28	13.55	8.45	22.00	1.98
intricata	10	16.61	15.67	1.70	5.37	16.84	7.16	24.00	3.84
juncea	13	33.00	31.38	2.02	7.29	26.00	14.00	40.00	4.40
laevis	27	17.00	17.47	0.49	2.56	11.37	12.63	24.00	1.01
linoides	10	25.50	24.75	2.07	6.55	19.00	15.00	34.00	4.68
longiflora	14	24.54	24.17	0.96	3.58	13.75	15.25	29.00	2.07
longifolia	5	25.86	26.46	0.97	2.16	5.69	24.17	29.86	2.69
mexicana	13	28.12	25.21	2.05	7.39	22.69	14.00	36.69	4.47
muellerae	7	17.00	17.00	0.95	2.52	7.00	13.00	20.00	2.33
pulchella	5	20.00	19.40	1.78	3.97	10.00	14.00	24.00	4.94
robusta	12	19.45	19.09	1.05	3.64	11.16	12.20	23.36	2.32
scabra	51	17.21	17.12	0.43	3.04	11.34	11.99	23.33	0.85
scabra var. scabra	11	16.00	16.87	0.78	2.58	8.45	13.63	22.08	1.73
scabra var. glabrescens	21	17.12	16.97	0.80	3.65	11.34	11.99	23.33	1.66
scabra var. occidentalis	7	17.75	17.26	0.63	1.68	4.44	14.55	18.99	1.55
scabra var. sonorensis	12	17.39	17.52	0.91	3.14	9.71	13.36	23.07	1.99
scoparia	17	21.00	21.05	1.20	4.94	21.00	10.00	31.00	2.54
spinescens var. spinescens	11	6.75	6.41	0.45	1.48	5.36	3.14	8.50	0.99
spinescens var. mohavensis	7	12.14	12.16	0.89	2.36	7.08	9.45	16.53	2.18
tehuacana	9	20.10	19.88	1.46	4.38	13.06	12.81	25.87	3.37
yecorana	2	30.81	30.81	0.75	1.07	1.51	30.05	31.56	9.59

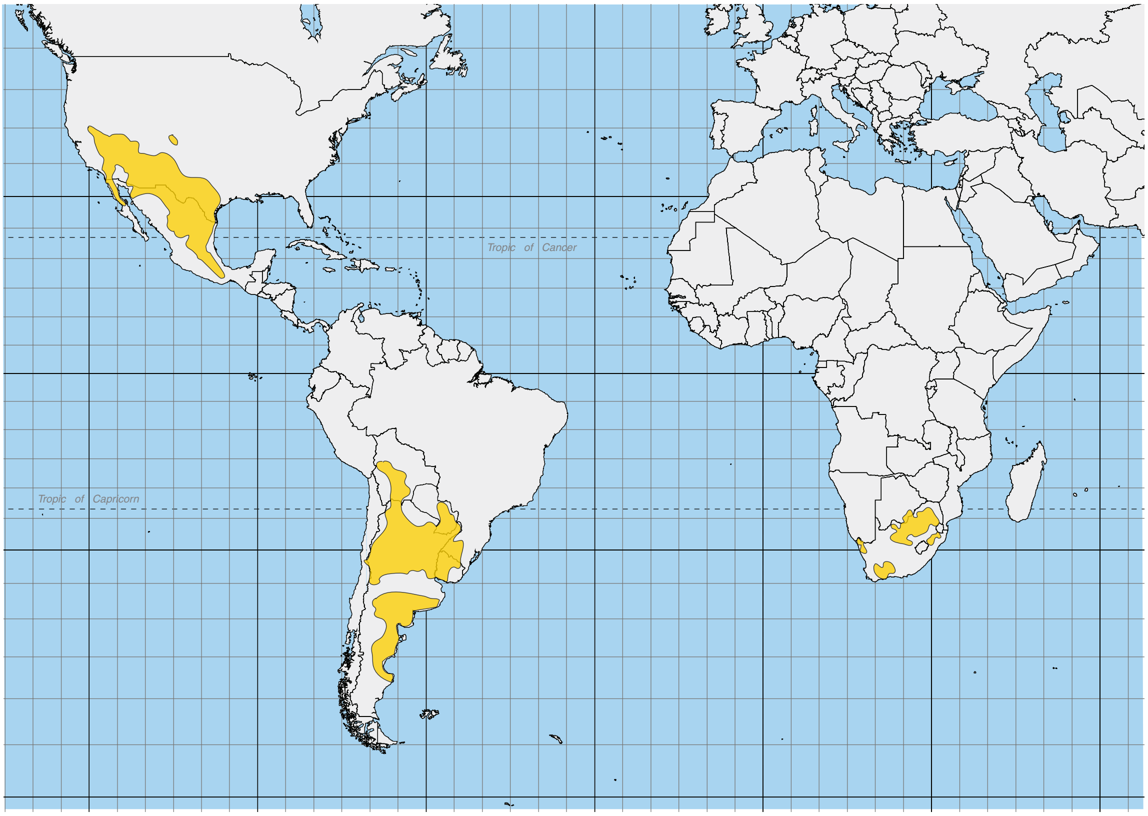


Fig. 1. Worldwide distribution of *Menodora*.

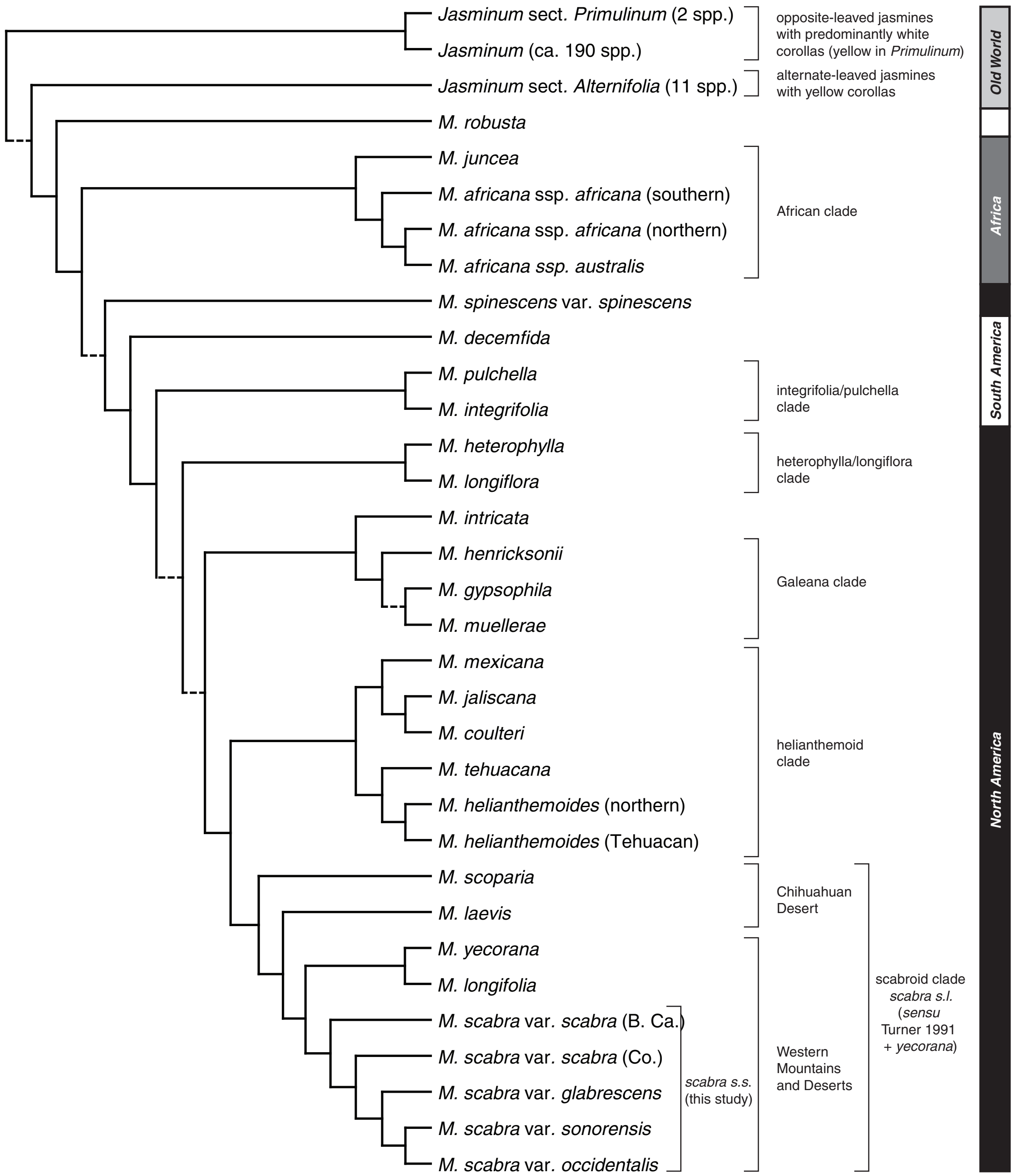


Fig. 2. Evolutionary diagram of species relationships in *Menodora* and their relationship to *Jasminum*, based on the results of a molecular phylogenetic study of the group using a combined data set of nuclear and chloroplast markers under maximum likelihood. Dashed lines indicate branches with weak support. Classification and nomenclature of species and subsecific ranks is that provided in this study. Not included in this scheme are *M. linoides* of Chile and the two varieties of *M. spinescens* for which suitable material was either unavailable or has only recently become available.

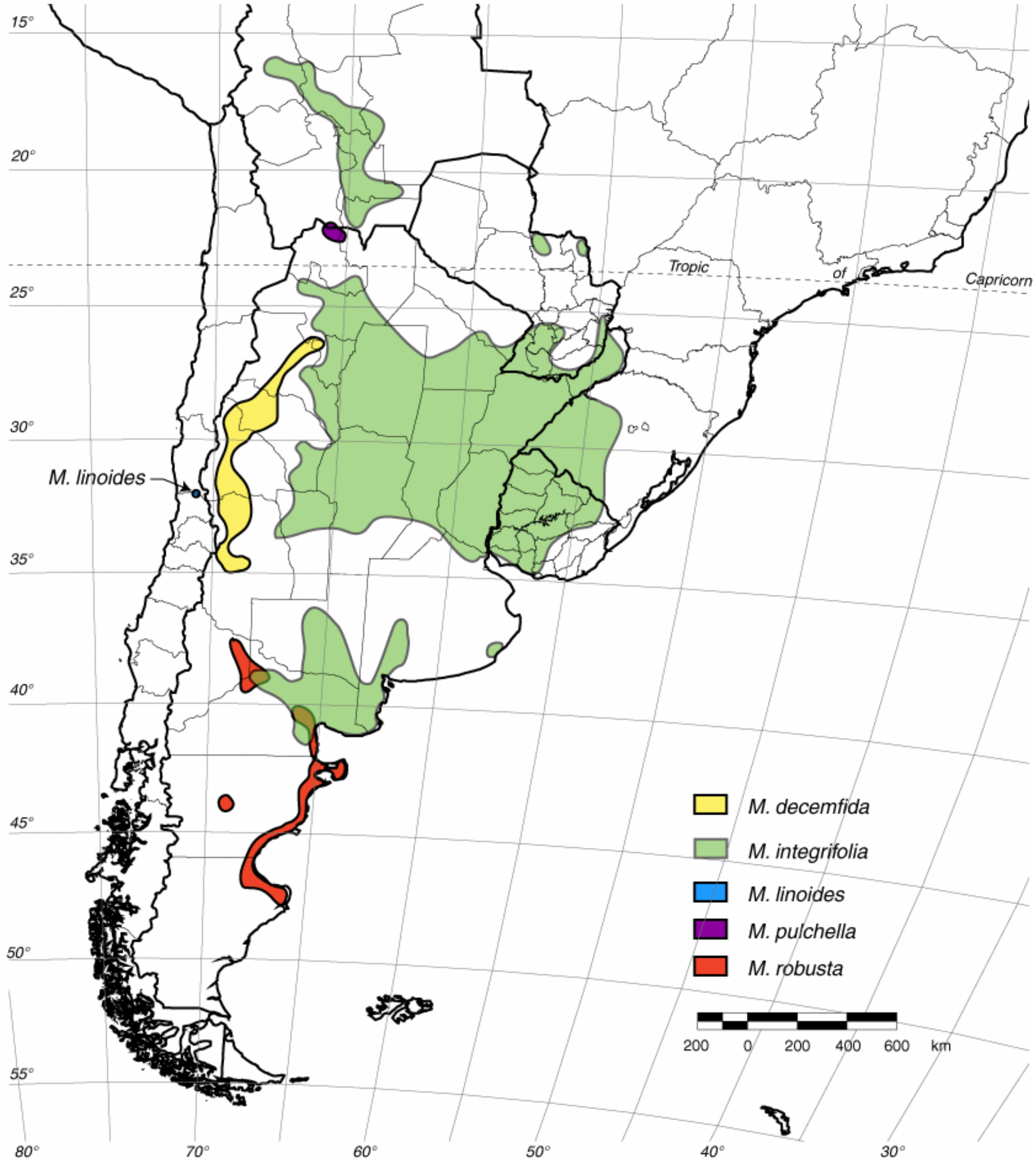


Fig. 3. The distribution of *Menodora* in South America.

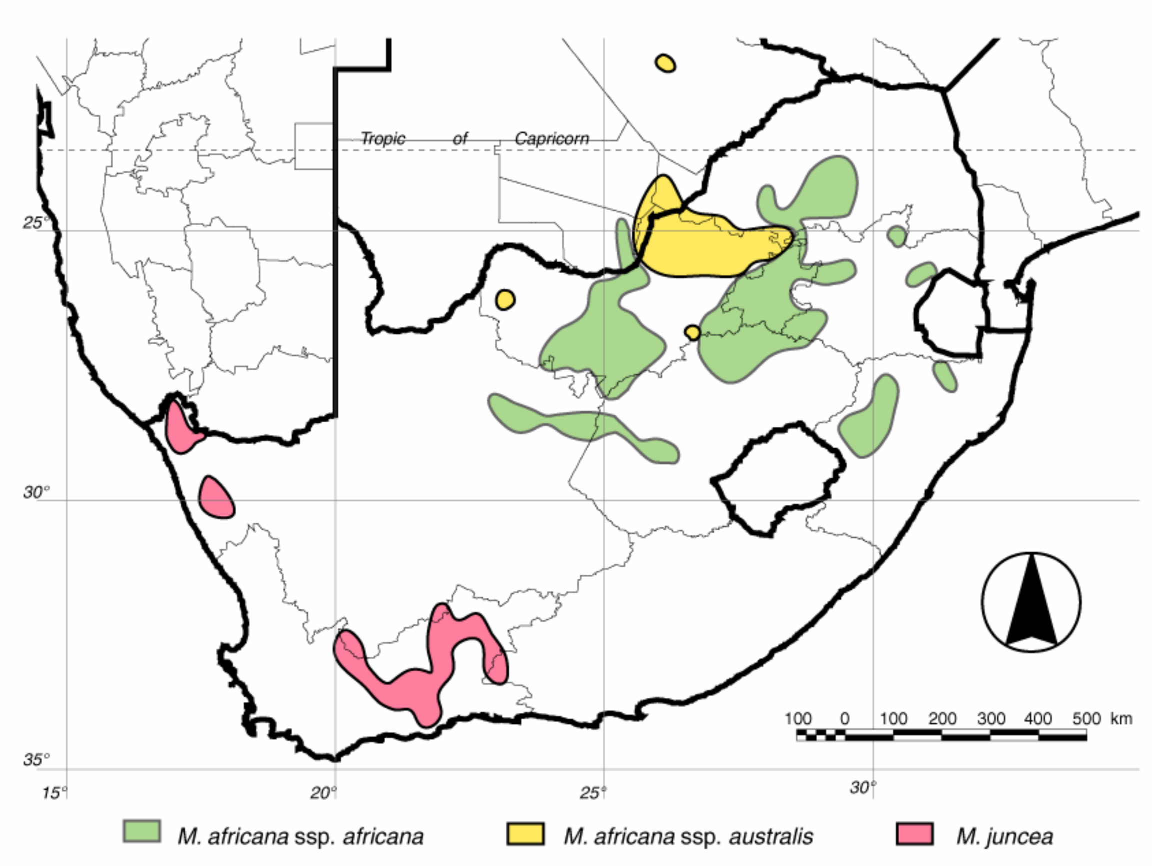


Fig. 4. The distribution of *Menodora* in southern Africa.

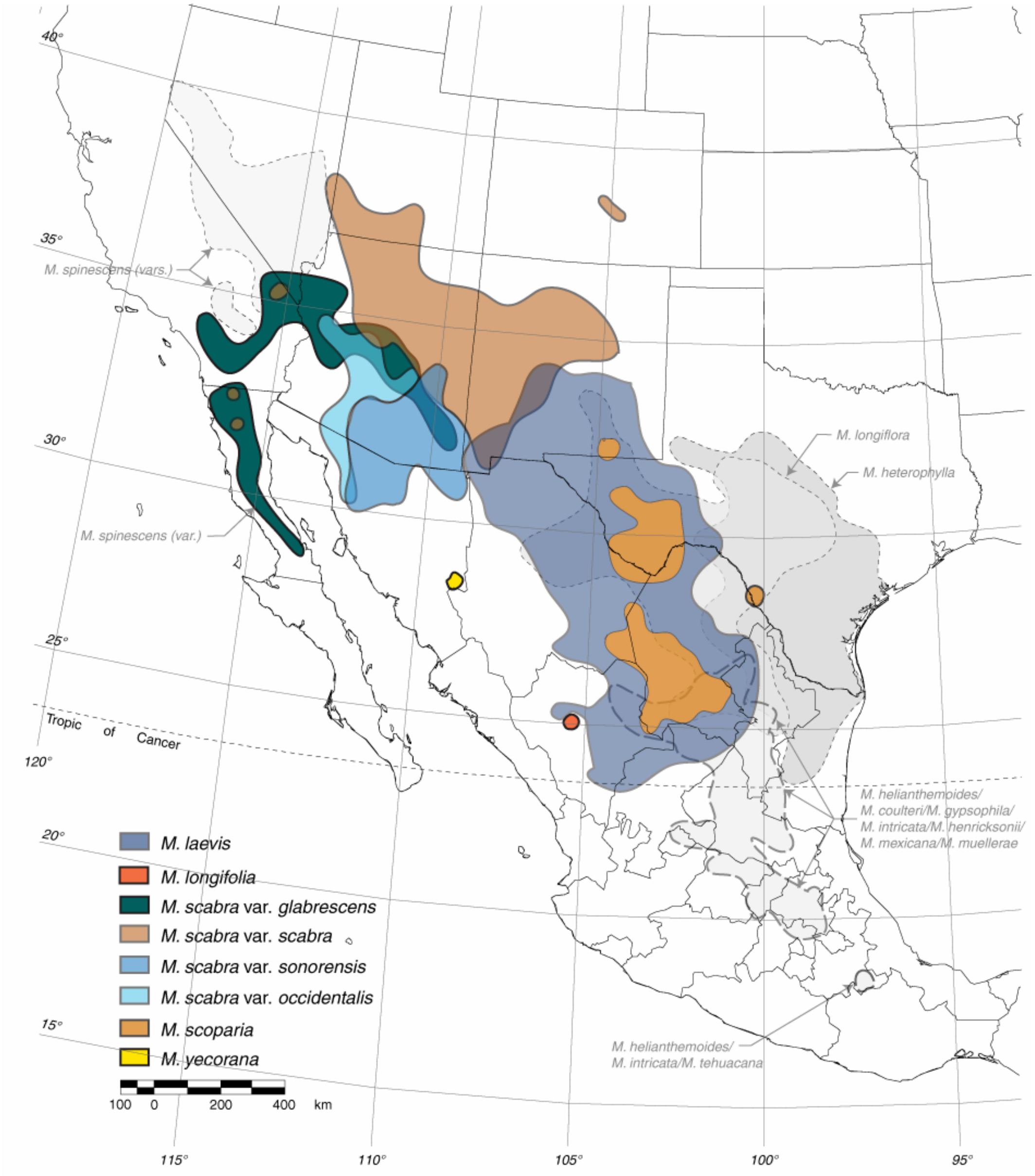


Fig. 5. Distribution of the scabroid menodoras in North America. The distribution of other species or species groups is indicated by dashed lines (see Figs. 6 and 7). The distributions of the varieties of *M. scabra* overlap to some extent, and some morphological intergradation is apparent in these zones, particularly in the region close to the Continental Divide in southwestern New Mexico and southern Arizona. Otherwise, *M. scabra* overlaps to a limited extent the ranges of *M. spinescens* in California, Nevada, and Baja and *M. laevis* in New Mexico. The range of *M. laevis* overlaps those of most of the eastern species except *M. intricata, M. mexicana, M. helianthemoides* and *M. tehuacana*, all of which occur farther to the south.

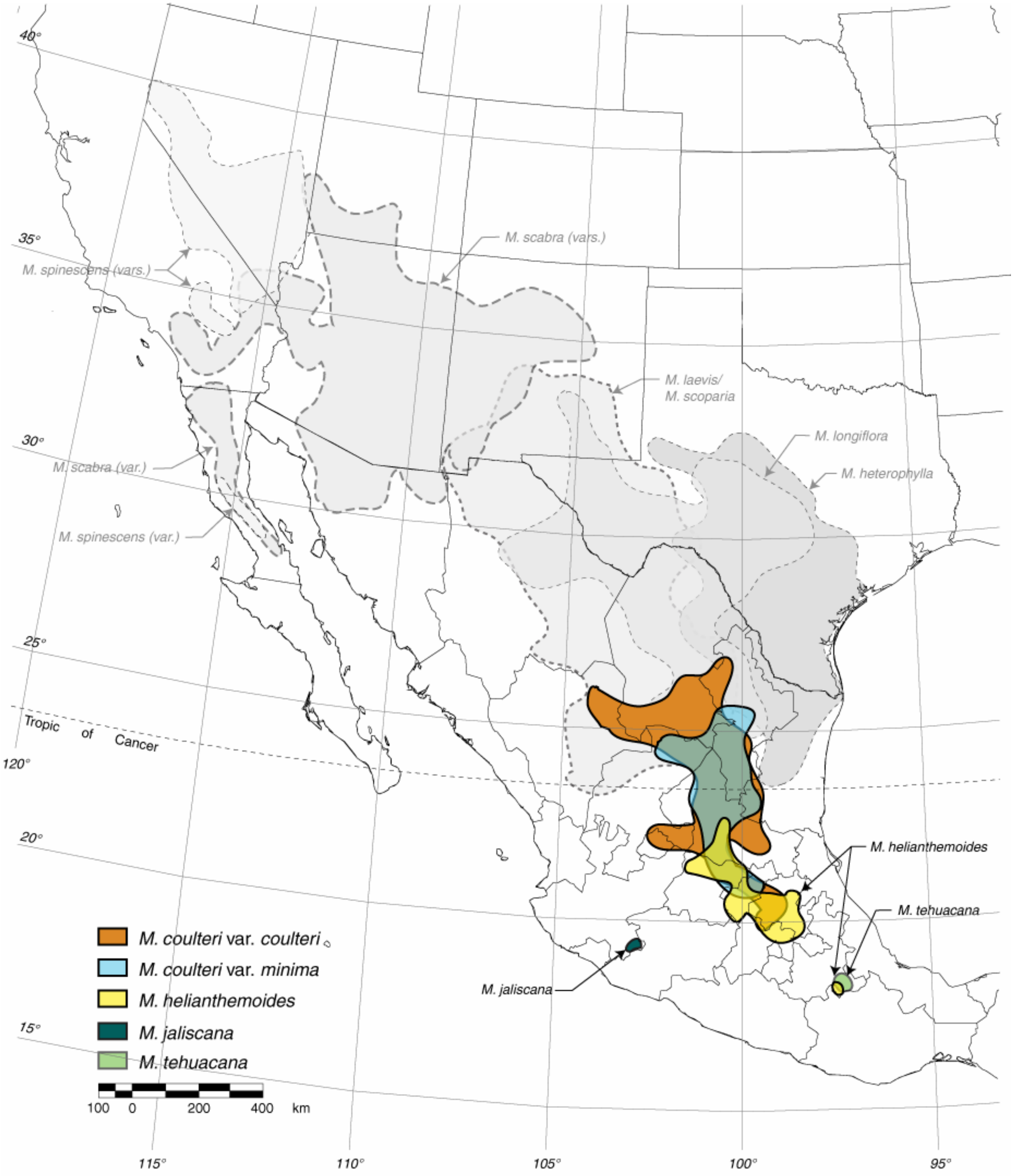


Fig. 6. Distribution of *Menodora helianthemoides* and most of its close relatives in central Mexico.

Fig. 7. Distribution of *Menodora spinescens* in western North America and, in the east, of *M. heterophylla, M. longiflora,* the Galeana group of species *(M. intricata, M. muellerae, M. henricksonii,* and *M. gypsophila),* and *M. mexicana*.

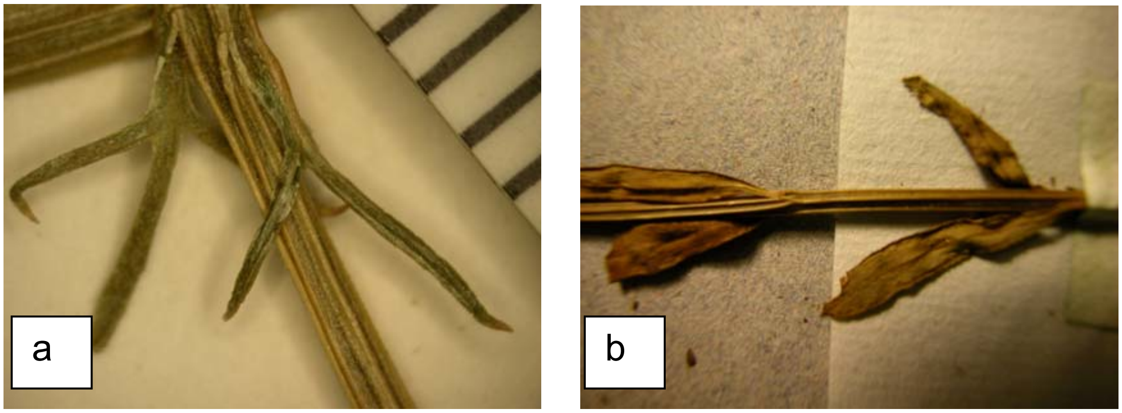


Fig. 8. Stem fluting. *a) Menodora intricata* (left; *Purpus 5016*, US), and *b) M. mexicana* (right; *Andrieux s.n.*, G-DC).

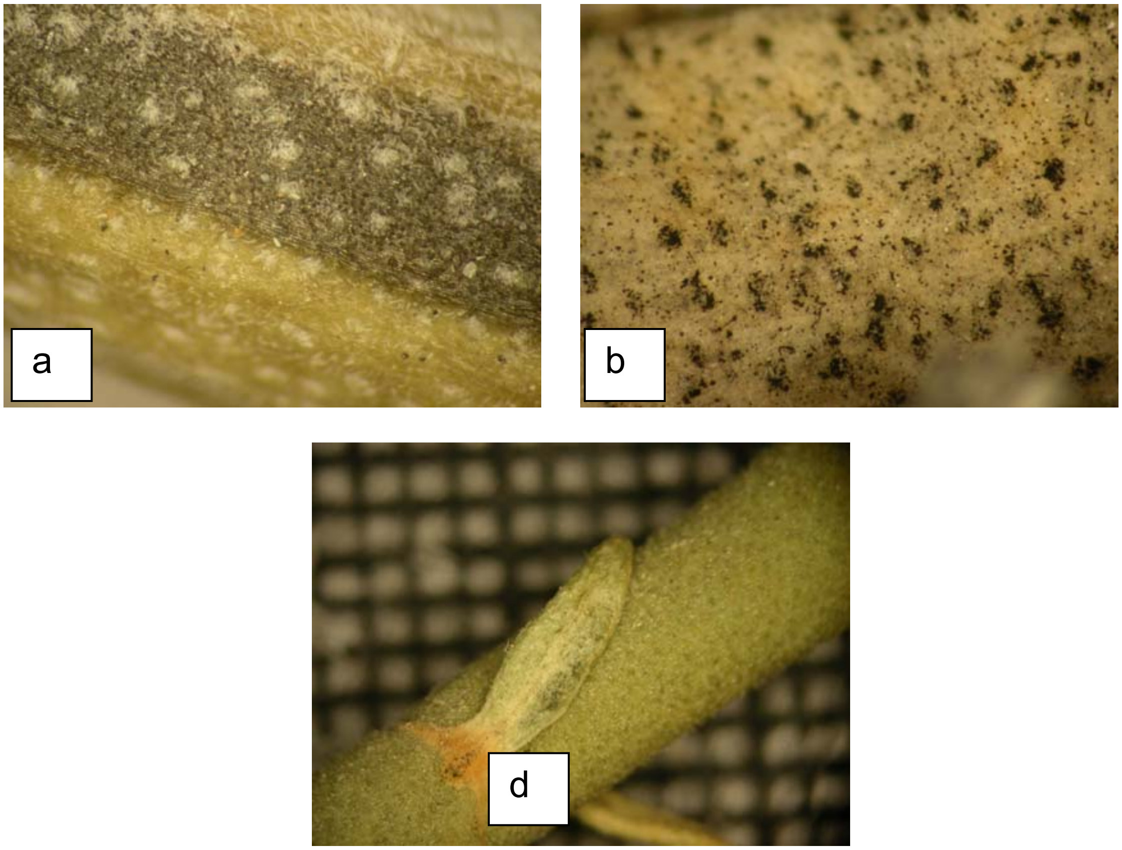


Fig. 9. Stomatal crypts. a) lenticel-like appearance of crypts on green stem of *M. spinescens* (*Chumley 7346*, TEX) , b) on older wood of *M. spinescens* (*Chumley 7347*, TEX), c) cross-section of crypt on *M. spinescens* (from Gibson, 1983), d) stem of *M. robusta* (*Chumley 7422*, TEX); crypts appear as shallow pits.

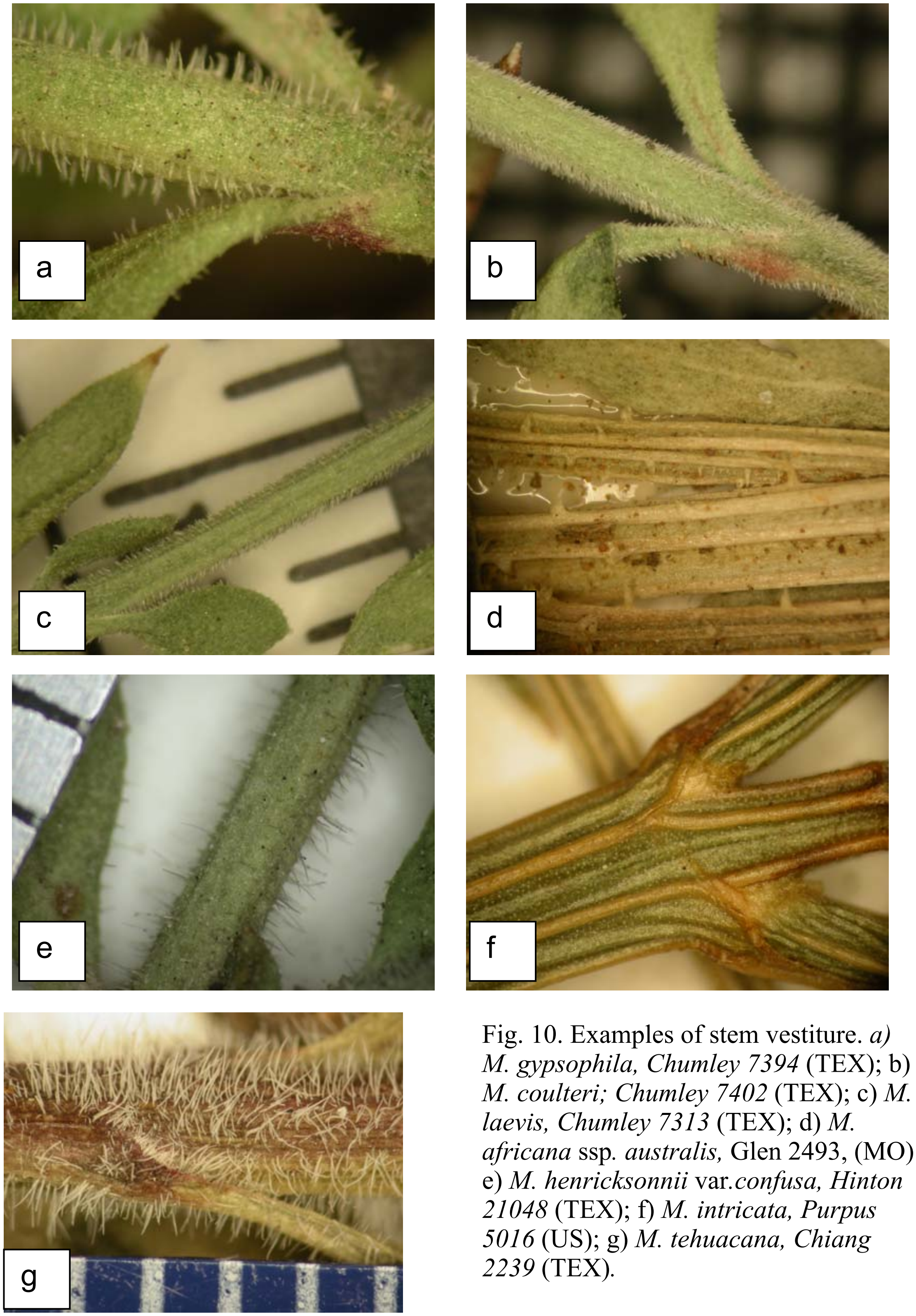


Fig. 10. Examples of stem vestiture. *a) M. gypsophila, Chumley 7394* (TEX); b) *M. coulteri; Chumley 7402* (TEX); c) *M. laevis, Chumley 7313* (TEX); d) *M. africana* ssp. *australis,* Glen 2493, (MO); e) *M. henricksonnii* var.*confusa, Hinton 21048* (TEX); f) *M. intricata, Purpus 5016* (US); g) *M. tehuacana, Chiang 2239* (TEX).

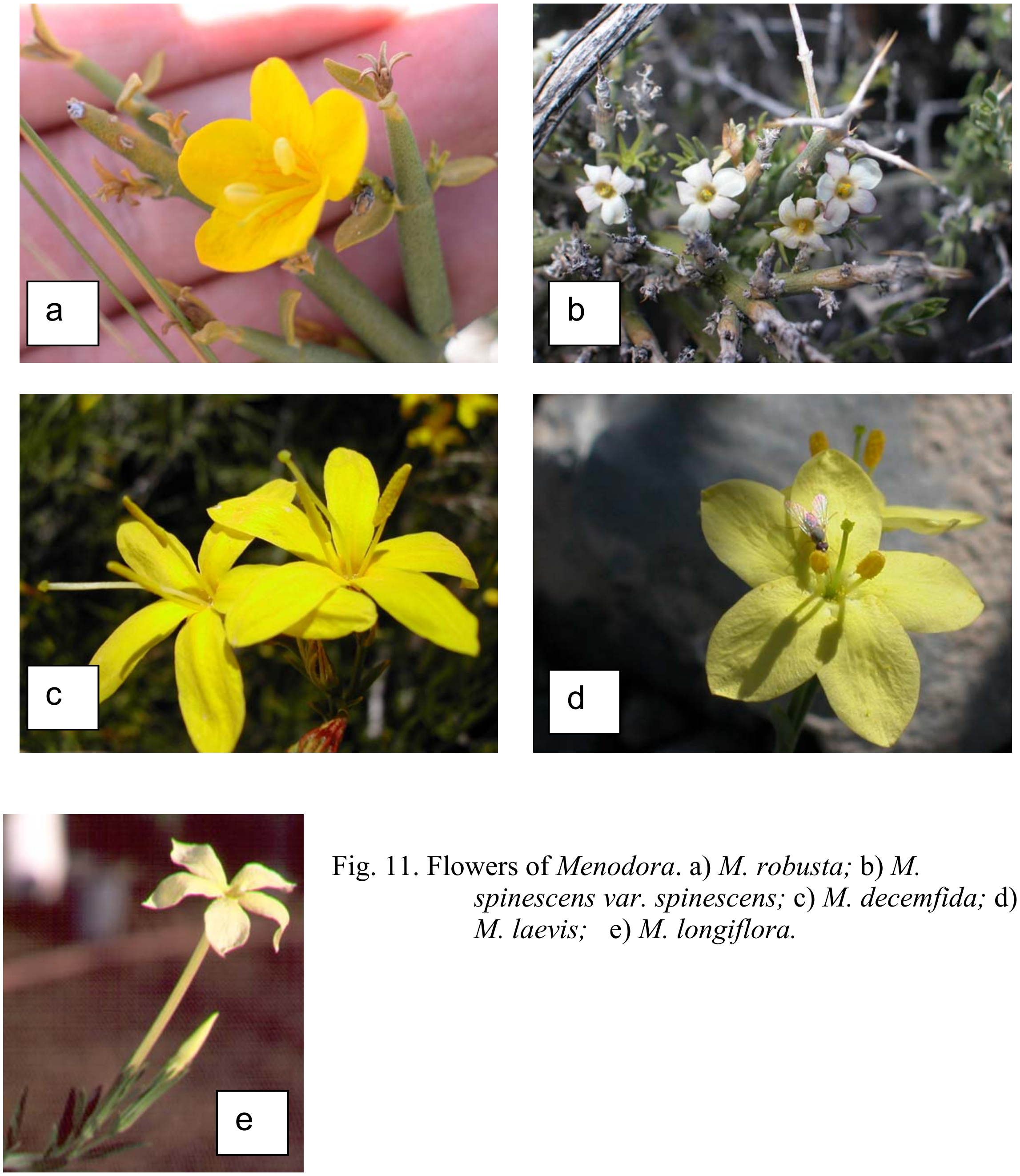


Fig. 11. Flowers of *Menodora*. a) *M. robusta;* b) *M. spinescens var. spinescens;* c) *M. decemfida;* d) *M. laevis;* e) *M. longiflora.*

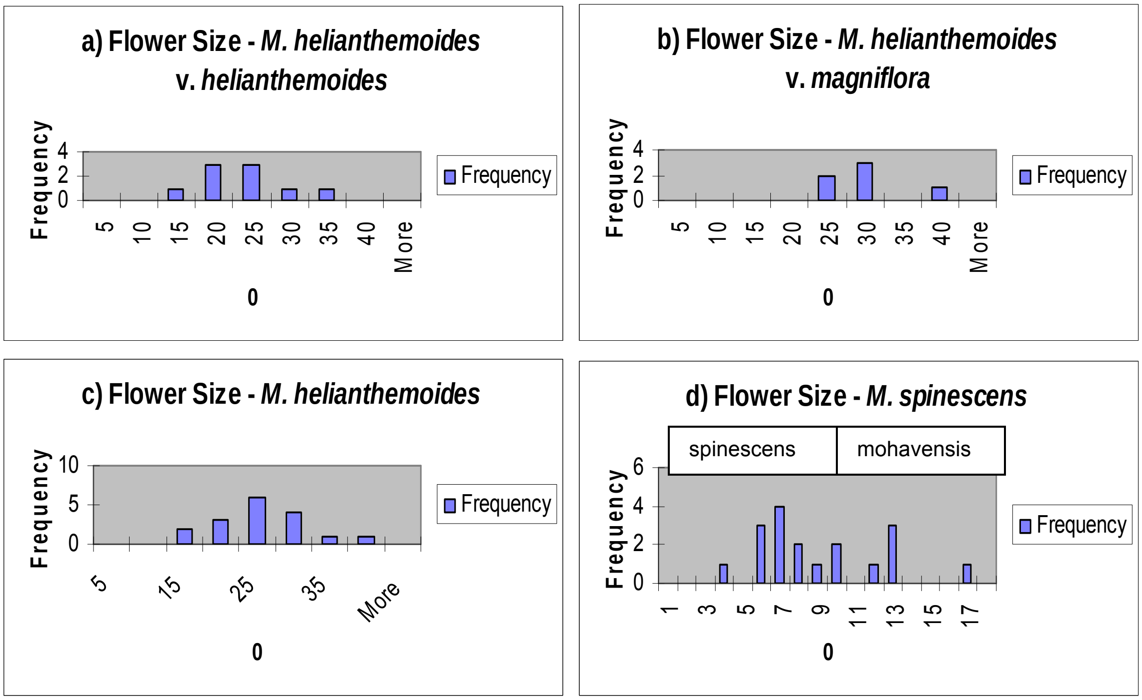


Fig. 12. Histograms showing the frequency distribution of floral presentation size (2X corolla lobe length + diameter of throat) for two representative taxa. a) Histogram for M. helianthemoides s.s. (incl. var. parviflora). b) Histogram for the larger flowered form var. *magniflora*. c) Histogram for *M helianthemoides* s.l. (including var. *magniflora*); distribution approaches a more normal curve. d) the more or lesss bimodal distribution found in *M. spinescens*, representing differences between the two varieties; the two approach but do not overlap in size..

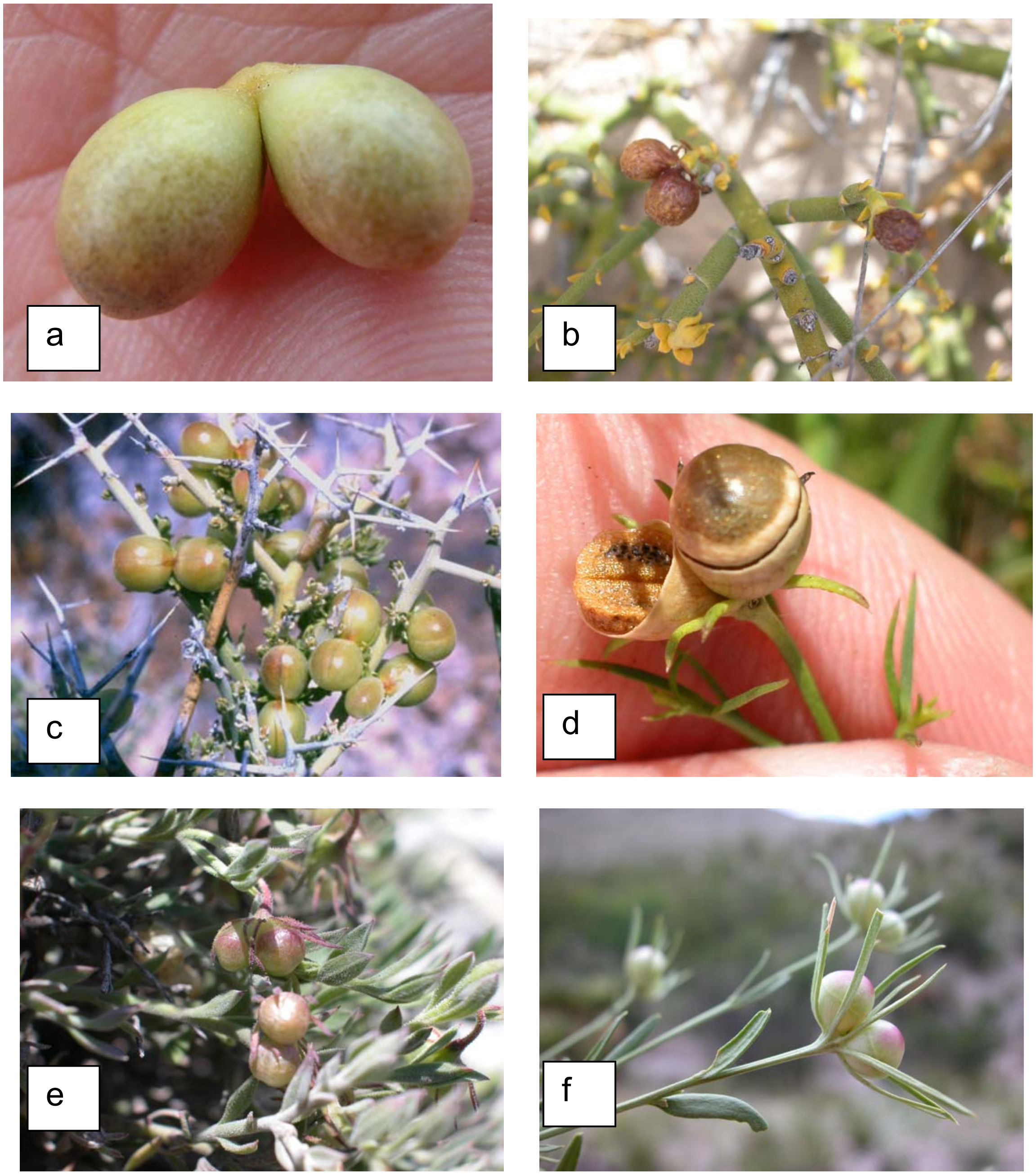
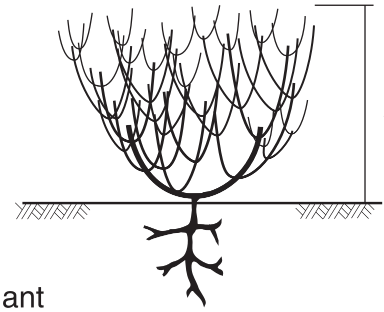
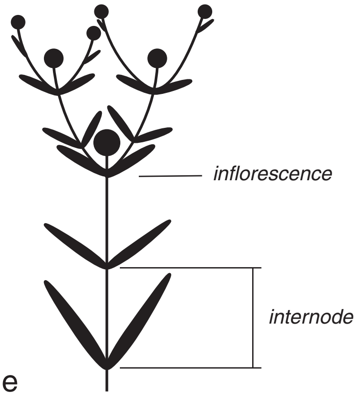


Fig. 13. Fruit of *Menodora*. a) Bilobed capsule of *M. robusta* removed from receptacle, showing the basal connection between the cocci; b) *M. robusta*; c) *M. spinescens* var. *spinescens*, note vertical suture; d) *M. integrifolia;* e) *M. gypsophila;* f) *M. longiflora.*

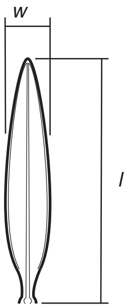
Fig. 14. Measurements taken in this study. l = length , w = width, h = heighth. a) plant height; b) internode taken at first full internode below branching for inflorescence; c) and d) leaf measurements, u = width of ultimate leaf segment; e) calyx and corolla measurements; f) style and stamen measurements; g) coccus measurements; and h) seed dimensions.



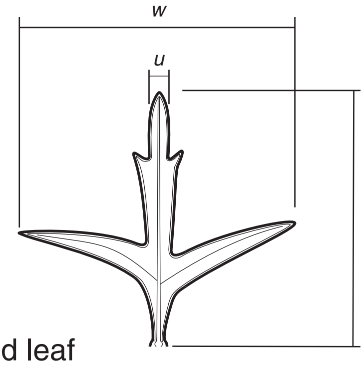
a) plant



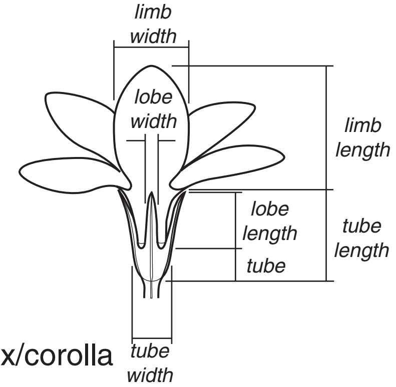
b) internode



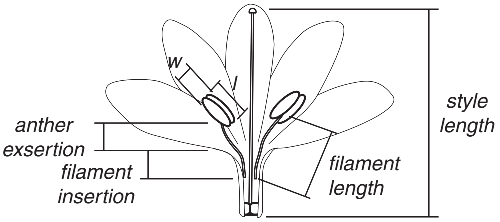
c) entire leaf



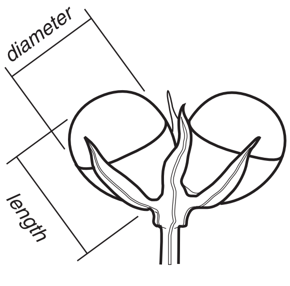
d) lobed leaf



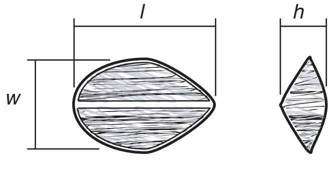
e) calyx/corolla



f) gynoecium/androecium



g) coccus



h) seed

Chapter 4: The complete chloroplast genome sequence of *Pelargonium* × *hortorum*: Organization and evolution of the largest and most highly rearranged chloroplast genome of land plants

INTRODUCTION

The recent proliferation of chloroplast genomic data has confirmed what had earlier been demonstrated through many restriction site mapping studies, that gene content, gene order, and genome organization are largely conserved within land plants (Palmer 1991; Raubeson and Jansen 2005). These observations are particularly true of angiosperm chloroplast genomes, owing to their extensive sampling. The tobacco chloroplast genome (Shinozaki et al. 1986), as the first to be completely sequenced, is most often the model against which newly sequenced genomes are compared, and it is indeed typical of most angiosperms in length, structural partitions and their relative sizes, gene content, and gene order. In angiosperms, chloroplast DNA (cpDNA) is typically a molecule of 120-160 thousand base pairs (kb) with a quadripartite organization consisting of two copies of an inverted repeat (IR) of about 20-28 kb in size separating two single copy regions of 80-90 kb (the large single copy region or LSC) and 16-27 kb (the small single copy region or SSC). In angiosperms, the genome usually encodes four rRNAs, 30 tRNAs, and around 80 unique proteins. Most genes are found in the single copy regions, but the rRNAs and 10-15 protein and tRNA genes are duplicated within the IR.

Deviations from the conserved gene order are typically the result of either changes in the extent of the IR or inversions (Palmer 1991; Raubeson and Jansen 2005). Changes in the extent of the IR take the form of expansions or contractions. A change made at one IR boundary will be reflected as an insertion or deletion in the other copy of the IR, thus altering the gene order. Small changes of one to several hundred nucleotides are quite common and may not affect gene order, but larger ones may do so quite dramatically, as in the expansions of 12 kb in *Nicotiana acuminata* (Goulding et al. 1996), 11.5 kb in Berberidaceae (Kim and Jansen 1994), and 11 kb in *Lobelia thuliniana* (Knox and Palmer, 1999). Contractions are less common (Raubeson and Jansen 2005) but have been documented in Apiaceae (Plunkett and Downie 2000). The loss or near loss of the IR in conifers (Lidholm et al. 1988; Strauss et al. 1988; Raubeson and Jansen 1992; Wakasugi et al. 1994), papilionoid legumes (Palmer et al. 1987; Lavin, Doyle, and Palmer 1990), *Erodium* and *Sarcocaulon* (Geraniaceae) (Price et al. 1990) may represent the extreme of IR contraction. Successive expansion-contraction events or multiple contractions may also be one way in which genes are translocated to different regions of the genome, as has been suggested in adzuki bean (Perry et al. 2002).

Inversions are occasional features within chloroplast genomes, and large ones have been found in Asteraceae (22.8 kb) (Jansen and Palmer 1987; Kim, Choi, and Jansen 2005), *Oenothera* (54 kb) (Hachtel, Neuss, and Vomstein 1991; Hupfer 2000), and Fabaceae (50 kb) (Palmer, Osorio, and Thompson 1988; Bruneau, Doyle, and Palmer 1990; Doyle et al. 1996). Rearrangements involving inversions are usually limited to a single event or at most a simple series of events (Palmer 1991; Downie and Palmer 1992), as in the Ranunculaceae (Johansson and Jansen 1991; Johansson and Jansen 1993; Hoot and Palmer 1994; Johansson 1999) and Poaceae (Howe et al. 1988; Doyle et al. 1992; Katayama and Ogihara 1996).

Complex rearrangements involving multiple events are quite rare, but examples have been identified among conifers (Lidholm et al. 1988; Strauss et al. 1988; Raubeson and Jansen 1992; Wakasugi et al. 1994), legumes (Palmer and Thompson 1981; Palmer, Osorio, and Thompson 1988; Milligan, Hampton, and Palmer 1989), campanuloids

(Cosner et al. 1997; Cosner, Raubeson, and Jansen 2004) and the related lobelioids (Knox, Downie, and Palmer 1993), and geraniums (Palmer, Nugent, and Herbon 1987). Of these highly rearranged genomes, only two pine species have been completely sequenced to date (Wakasugi et al. 1994, Noh et al. 2003 unpublished accession NC_004677). An evolutionary scenario for pines based on mapping data (Strauss et al. 1988) suggested a minimum of two deletions (one of which represents a contraction involving one entire copy of the IR) and four inversions; expanding this to reflect the greater detail of the sequenced pine genomes requires two small IR shifts and three additional inversions (Figure S1a, Appendix 2). The sequenced genome of the parasite *Epifagus* can also be considered highly rearranged, but its rearrangements are mostly due to the large deletions that have severely reduced its genome along with a single small inversion (Wolfe, Morden, and Palmer 1992). Study of each of these groups may have much to teach us about the pattern, mode, and mechanisms of genome evolution in the chloroplast (Palmer 1990).

In this study, we present the complete nucleotide sequence of the chloroplast genome of the common garden geranium (*Pelargonium* × *hortorum* L. H. Bailey; Geraniaceae) and compare it to other genomes. This genome was previously found to be unusually large and highly rearranged (Palmer, Nugent, and Herbon 1987). This initial study estimated the genome size to be about 217 kb, or about 50% larger than usual, and concluded that most of this size increase was the result of a three-fold increase in the size of the IR, with consequent reduction of both single copy regions. Gene order was found to be highly rearranged relative to tobacco; a minimum of six inversions were hypothesized in addition to the aforementioned tripling of the IR size. Two families of dispersed repeats (later characterized by Palmer (1991) as potentially novel DNA) were detected. These novelties also appear to have contributed to the genome expansion, and recombination between them was proposed as a possible cause of the inversions. Our study has largely confirmed size estimates for the genome and its partitions, but found that both the rearrangements and the "families" of repeats are far more complex than had been anticipated in the earlier study. We propose a model of genome evolution in which inversions, small and large changes in the extent of the IR, and insertions of duplicated sequence account for much of the increase in size and rearrangement of gene order of the genome.

MATERIALS AND METHODS

Methods for DNA isolation, sequencing, and analysis have been described previously (Jansen et al. 2005), but a brief summary is provided here. Detailed protocols for library creation and sequencing are available at http://www.jgi.doe.gov/sequencing/protocols/prots_production.html.

Commercially available plants of *Pelargonium* × *hortorum* cv. 'Ringo White' (Mower s.n., 4 Sept. 2003 (TEX)) were obtained locally and grown in a greenhouse. Purified cpDNA was isolated with a modified DNAse I method (Kolodner and Tewari 1972) from 500 g of fresh leaf tissue taken from several plants. The isolated DNA was sheared into three kb fragments using a Hydoshear device (Gene Machines). These fragments were then end-repaired, gel isolated, and ligated into pUC18 to create a DNA library. These clones were introduced into *E. coli* by electroporation and plated onto nutrient media with antibiotic selection. Resulting colonies were randomly selected and processed robotically for end sequencing using Big Dye (Applied Biosystems) chemistry on an ABI 3730 XL. A total of 4,608 sequencing reads were generated, which were processed with phred and assembled with phrap (Ewing and Green 1998; Ewing et al.

1998). The quality of sequencing reads and the assembly were verified by eye with Consed 13.0 (Gordon, Abajian, and Green 1998) and Sequencher 4.2 (Gene Codes Corp., 2003).

Gaps that remained in the assembled draft sequence were filled by primer walking on PCR amplified templates. No sequences from the SSC region were recovered in the draft sequence and it was thus necessary to develop a PCR strategy to sequence through the entire region. IR boundaries were also verified by sequencing across them. In all, approximately 20 kb of additional sequencing was necessary to complete the genome. All primer sequences are shown in Table S1, (Appendix 2).

Upon completion of sequencing and final assembly, genes were annotated using DOGMA (Wyman, Jansen, and Boore 2004) and direct BLAST comparisons (Altschul et al. 1990). For annotation purposes, the first base of the genome was defined as the first base of the LSC region where *trnH* is found and the plus or ‘A’ strand is designated as the strand on which *rbcL* is encoded. Annotations are based on nucleotide and amino acid similarity and are not experimentally verified. Additional open reading frames were assessed using EditSeq 5.06 (DNASTAR Inc., 2003) and NCBI’s OrfFinder <http://www.ncbi.nlm.nih.gov/gorf/gorf.html>. Initial ORF searches were limited to frames of 99 bp or longer, and only those with BLAST hits to genes of known function or recognized ORFs were considered further.

Exact microsatellite repeats were examined using Msatfinder ver. 1.6.8 (Thurston and Field 2005) with thresholds of seven repeat units for mononucleotide simple sequence repeats (SSRs) and five repeat units for all other SSRs. Larger repeats were examined using REPuter (Kurtz and Schleiermacher 1999; Kurtz et al. 2001), using a minimum window size of 21 and a Hamming distance of 4.

Mega3 (Kumar, Tamura, and Nei 2004) was used for calculations of GC content and codon usage for comparison of the chloroplast genome of *Pelargonium* to others. The GenBank annotations for the chloroplast genomes of *Spinacia oleracea* (NC_002202), *Arabidopsis thaliana* (NC_000932), *Medicago truncatula* (NC_003119), *Lotus corniculatus* var. *japonicus* (NC_002694), and *Oenothera elata* subsp. *hookeri* (NC_002693) were used for these comparisons.

RESULTS

GENERAL CHARACTERISTICS OF THE GENOME. The chloroplast chromosome of *Pelargonium* × *hortorum* is the largest terrestrial plant chloroplast genome sequenced to date and can be represented as a circular molecule of 217,942 base pairs (bp) (Fig. 1; GenBank accession DQ897681). This is only slightly larger than previously estimated (Palmer, Nugent, and Herbon 1987). The genome has the stereotypical chloroplast quadripartite organization featuring two copies of a 75,741 bp IR separating a LSC region of 59,710 bp and a SSC region of 6,750 bp; these are also very close to the 1987 size estimates. In comparison with other genomes, these are about 3×, 2/3, and 1/3 of the usual sizes, respectively. Approximately 46.8% of the genome encodes proteins, 1.4% encodes tRNAs, and 4.3% encodes ribosomal RNA. The non-coding regions (pseudogenes, spacers, and introns) account for the remaining 48.5% of the genome. GC content is 39.6% overall, 41.1% in protein and RNA coding regions, and 38.1% in non-coding regions. These GC values fall within the range of variation previously reported for chloroplast genomes, and among the five genomes selected for direct comparison are most similar to those of *Oenothera* (Table S2. Appendix 2). Within the protein coding regions, both *Oenothera* and *Pelargonium* also share a similar pattern of codon usage, and generally have a slightly higher GC content at all positions (Tables S2 and S3, Appendix 2).

GENE CONTENT. Gene content is similar to that found in other angiosperm chloroplast genomes, although the total number of genes is dramatically higher due to duplications caused by massive IR expansion. The *Pelargonium* genome contains 76 unique protein genes (39 of which are duplicated within the IR, along with the first exon of *ndhA*), four rRNA genes (all of which are duplicated in the IR), and 29 tRNA genes (eight are duplicated in the IR, including *trnfM*-cau, which has a third copy in the LSC). The total number of identified genes encoded is thus 161, with 51 genes duplicated within the IR. The average size of intergenic spacers is 368 bp.

Identification of the RNA polymerase subunit alpha subunit gene (*rpoA*) proved to be difficult. As previously reported (Palmer et al. 1990a; Palmer et al. 1990b; Downie et al. 1994), three different candidate sequences with similarity to *rpoA* are located in the region surrounding *ycf2* in the IR (Fig. 2). We initially recognized three different fragments [α (ca. 650 bp), β (190 bp), and γ (415 bp)] each of which shares less than 40% sequence identity to homologous regions of *Arbabidopsis rpoA*. The β fragment is itself a partial repeat and extension of the last 80 bp of the α fragment, and the γ fragment overlaps the β by 84 bp. Duplications of the α and β fragments are important elements of the three large repeats found in the second major repeat association (discussed below). Each of the three large repeats contains slightly different open reading frames (ORFs; *ORF574*, *ORF332*, and *ORF365*) each containing both the α and β fragments. These ORFs have a conserved protein domain structure with similarities to RNA polymerase, and thus these may represent highly divergent *rpoA* genes. The γ fragment is also contained within a fourth ORF (*ORF221*). It is possible that one or all of these ORFs may retain functionality, but this was not determined in this study.

Two genes (*ΨinfA* and *Ψycf15*) appear to be present in the genome only as pseudogenes. The first is a fragment of *infA* (translation initiation factor 1), and has been previously reported as a pseudogene in a number of lineages, including *Pelargonium* (Millen et al. 2001). The second, *Ψycf15*, appears to be highly divergent, truncated and has multiple internal stop codons. Truncated *ycf15* genes have been identified in a number of recent chloroplast genomic studies (Schmitz-Linneweber et al. 2001, Goremykin et al. 2003, Kim and Lee 2004, Steane 2005) and its functionality has been questioned.

Three tobacco chloroplast genes (*sprA*, *accD*, and *trnT*-ggu) have not been detected in *Pelargonium*. Of these, the small plastid RNA *sprA* (Vera and Sugiura 1994) has been identified solely within the Solanaceae (Schmitz-Linneweber et al. 2002), where its functionality remains unknown (Sugita et al. 1997). In contrast, *trnT* and *accD* are a part of the normal complement of chloroplast genes, but they have not been detected in *Pelargonium*. In typical chloroplast genomes, *trnT* is found about halfway between *trnE*-uuc and *psbD*, while *accD* is between the genes *rbcL* and *psaI*. In *Pelargonium*, these bracketing genes (*trnE, psbD*, *rbcL*, and *psaI*) are quite remote from each other, and therefore the regions where the missing genes normally reside are not intact. The losses of *trnT* and *accD* thus coincide with rearrangement endpoints (see Fig. 1 and discussion below). The loss of *trnT*-ggu is not reflected in codon usage however, as it seems to utilized in *Pelargonium* at the same rather uniform level found in all other genomes examined (Table S3, Appendix 2).

In addition to *ΨinfA,* and *Ψycf15,* 17 other pseudogenes have been identified within the genome, and all of these represent partial to full duplications of nine functional genes (*rpl33, trnfM, rps14, rrn16, rpl23, rps11, petD, rpoB,* and *rpoC1*). Pseudogenes *ΨtrnfM, Ψrrn16, Ψrpl23, Ψrps11 and ΨpetD* are small, 27-164 bp high-identity fragments of their parent genes (all of these except *ΨtrnfM* are duplicated within the IR). *ΨrpoB* and *ΨrpoC1* appear as a 124 bp unit repeat that consists of the 3′ end of *rpoB*, the 5′ end of *rpoC1*, and the short intervening spacer. Except for an 11 bp deletion in the *rpoB* segment, this repeat has 97% identity with its ancestral region in the LSC. For convenience, we have designated this fragment as *ΨrpoB/C1*. It is a three member family, and all are duplicated within the IR. Both *Ψrpl33* and *Ψrps14* also represent small repeat families. Four copies of *Ψrpl33* are found in diverse parts of the genome. Two of these occur in the *psaI-trnN* spacer in the IR, and represent 5' and 3' fragments of *rpl33*; these could represent a single, degenerate duplication of *rpl33*. Both other copies of *Ψrpl33* lie in the LSC, with the first being a near-full copy of the functional gene and found at the first breakpoint for genome rearrangement following *trnE*. The remaining copy appears to be a degenerate 3' fragment that follows the functional copy of the gene. The two copies of *Ψrps14* are identical full-length copies that differ from the functional gene at only two bases, one of which induces an internal stop. The first of these follows the functional copy of the gene in the LSC, while the second is far downstream, inverted and duplicated in the IR close to the ends of the LSC.

An additional ORF containing the IR-duplicated 5′ *ndhA* exon was designated as *ORF188*. Although fragmentary sequence identity with ORFs from other genomes was found, we have not annotated these features due to the lack of overall sequence and length conservation. However, the *trnA* intron contains two sequences with homology to previously recognized mitochondrial products in *Citrus* [*ACRS* (Ohtani, Yamamoto, and Akimitsu 2002)] and *Phaseolus* [*pvs-trnA* (Woloszynska et al. 2004)], and we have designated these as *ORF56* and *ORF42*, respectively.

Alternate start codons are found in *rps14, rps19*, *psbL* and *ndhB*. Of these, the GUG and ACG starts found in *rps19* and *psbL* respectively are commonly noted across a broad spectrum of angiosperm chloroplast genomes. The GUG start in *rps14* appears to be unique to this genome, however. An AUU start is suggested for *ndhB*, although this inference is problematic. In the normal starting position for *ndhB* (in comparison with other genomes), an ACG start is found, but this is followed by two stop sequences at the third and sixth codons. Given that *ndhB* transcripts are known to be subject to extensive RNA editing in many land plants, (Freyer, Kiefer-Meyer, and Kössel 1997), and that editing can repair internal stops (by means of U→C edits at the first nucleotide of the codon) (Wolf, Rowe, and Hasebe 2004), it seems probable that these sites are edited. While U→C editing has been demonstrated in the chloroplasts of bryophytes (Yoshinaga et al. 1996, Kugita et al. 2003) and ferns (Wolf, Rowe, and Hasebe 2004), it has not been reported for seed plant plastids, and only rarely in angiosperm mitochondria (Gualberto et al. 1989, Schuster et al. 1990). Editing would restore the start and the second stop to the conserved amino acids, but would result in a novel amino acid in the third position. Due to the lack of supporting experimental evidence at this time, however, we conservatively assign an alternate start codon 30 bp downstream.

Fifteen genes (six tRNAs and nine proteins; eight of these are duplicated in the IR) contain introns, all of which maintain conserved intron boundaries. Three genes (*clpP*, *ycf3*, and the transpliced *rps12*) contain the usual complement of two introns each. The ribosomal protein genes *rps16* and *rpl16* have each lost their solitary introns. The latter loss was noted previously in the Geraniaceae in *P. hortorum* and a species of *Erodium* (Downie and Palmer 1992; Campagna and Downie 1998). All introns are Group II introns, with the exception of the sole Group I intron found in *trnL*-uaa.

Small insertions and deletions (indels) relative to *Spinacia* are present in 32 genes, discounting length variation commonly seen at the 3′ terminus. The variable and large hypothetical coding frames *ycf1* (7,659 bp) and *ycf2* (6,333 bp) both have numerous indels, and while alignment of the former is nearly impossible outside of its terminal sequences, in the latter we estimate 48 indels ranging from 3-195 bp, although there are questionable alignments in several regions. Similar results for *ycf2* in *P. hortorum* were reported by Downie et al. (1994). Other genes with multiple indels include the *23S* rRNA gene (five insertions of 4-95 bp, two deletions of 4-7 bp), *rpoB* (five insertions of 3-15 bp and three deletions of 3-9 bp), *rpoC1* (nine insertions of 3-18 bp), *rpoC2* (seven insertions of 3-21 bp and four deletions of 6-9 bp), and *rps18* (eight insertions of 3-27 bp). A 17-bp insertion induces a brief frame shift about 800 bp into *rpoC1*, but this is corrected six bp downstream by a one bp insertion.

NUCLEOTIDE POLYMORPHISMS. We observed a number of sequence polymorphisms using a criterion of a minimum of two independent high quality sequence reads that deviated from the consensus sequence (Table S4, Appendix 2). Nine instances of single nucleotide polymorphisms were identified, of which two are duplicated within the IR for 11 in total. Two of these occur in intergenic spacers in the IR, and three others are non-synonymous changes found within protein-coding genes in the LSC. A single dinucleotide polymorphism was observed in the spacer between *rps16* and *trnQ*-uug. Eleven length polymorphisms in mononucleotide simple sequence repeats were observed, two of which are duplicated in the IR. Only one of these falls within a coding region (*rps4*). Another one was originally thought to alter the coding frame for *ndhK* relative to that of tobacco, but a survey of other genomes showed this region to be highly variable, and thus it may not be part of the gene. An alternate start site was selected downstream in a more conserved region.

Gene Order. In addition to its unusually large size, this genome is highly rearranged in comparison with the conserved gene order shared by tobacco and most other angiosperms (Palmer, Nugent, and Herbon 1987) (Fig. 1). The rearrangements include inversions, apparent translocations, deletions and insertions of duplicated sequence. Considering only the order of genes and pseudogenes, 35 breakpoints are present, not including those duplicated within the second copy of the IR (an additional 23) or the inferred deletions of *trnT* and *accD*.

Gene order is conserved within 26 blocks of genes (Fig. 1). These blocks range from about 30 bp to 30 kb, and contain from one to 25 genes or pseudogenes. The largest blocks that appear in a similar relative arrangement and orientation to those of tobacco are two blocks within the LSC (blocks 1 and 8-9 in Fig. 1) and a block of SSC genes (block 25-26) (the contiguous blocks 8-9 and 25-26 are segregated due to the occurrence of blocks 9 (*rbcL*) and 26 in the IR). The IR is by far the most rearranged structural partition in the genome with almost two thirds of the observed breakpoints. Relative to tobacco, the SSC is the least altered partition (other than in size). Its only major changes are the translocations of *ndhF* (block 22 in fig.1) and *rpl32* (block 23) into different locations in the IR and the major expansion of the IR (block 26) to include all of *ycf1*, *rps15*, *ndhH* and part of *ndhA*.

Two-thirds of the recognized breakpoints fall within five small parts of the genome (three of these are in the IR), and these coincide with the regions where two different associations of repetitive elements are found (i.e., the two repeat families of Palmer et al. 1987). These are the regions falling between: 1) *trnY* and *ycf3*, 2) *rps14* and *psbD*, 3) *rbcL* and *psaJ*, 4) *psaI* and *trnN*, and 5) the region surrounding *ycf2*. Regions 1-4 correspond to what we designate as association members 1.1-1.4 of the first repeat association, and region 5 contains association members 2.1-2.3 (Fig. 1) of the other repeat association. Rather than simple families of repeats, however, these regions, particularly those of the first association, are composite assemblages of heterogeneous elements. A few unique elements (e.g., genes like *rps18*) and 10 small dispersed repeat fragments duplicated from other regions of the genome are present, but most of the repeat elements are contained solely within these regions and are probably derived from more "local" elements.

The first repeat association (members 1.1-1.4) is the most complex, and corresponds to the nine-member family of Palmer et al. (1987). It accounts for 15 of the breakpoints noted above, and is most readily recognized by the presence of *rpl33*, *trnfM*-cau, *rps14* and their respective pseudogene copies. Six large repeats (*a*, *b*, *c*, *d*, *e* and *f* in Fig. 3) can be recognized among the members of this association, and these fall into two classes: repeats associated with *rpl33* (*a*, *c* and *f*) and those associated with *rps14* (*d, b* and *e*); copies of *trnfM* are associated with both classes. A compositional and structural comparison of the association members can be seen in the percentage identity plots or PIPs (Schwartz et al. 2003) shown in Figure 3. As can be seen, the functional *rpl33* gene and its nonfunctional copies occur in several widely dispersed locations. The transcriptional linkage of the relatively short *rpl33*-*rps18* operon (blocks 12 and 13, Fig. 1) is clearly disrupted. Despite the fact that *rpl33* has been duplicated at least 3-4 times (depending on interpretation, and excluding the IR), none of these copies is associated with *rps18*, and neither gene is associated with their respective upstream or downstream partners as found in tobacco. Unlike *rpl33* and *rps18*, however, copies of both *rps14* and *trnfM* are found in two different ancestral arrangements each, one of which is shared. The arrangement of *ΨtrnfM-trnG* in member 1.1, the position of the functional copy of *rps14* at the terminal end of the *psaA*-*psaB* operon in member 1.2 (see Fig.1), and the arrangement of *Ψrps14-trnfM* in member 1.3 all represent the ancestral gene order as found in tobacco. In addition to the gene/pseudogene duplications present, four small dispersed repeats (repeats *g-j*, Table S5, Appendix 2) that represent small fragments (28-63 bp) of genes (*Ψrrn16, Ψrpl23*) or spacers (*trnV-16S*, *rpl20-rpl32*) from diverse other parts of the genome are present. Further, as can be seen from the PIP comparisons in Figure 3, parts of the intergenic regions (including what we have designated as repeat *b*) have a very complex repeat structure; this complexity is still under study and has not yet been completely characterized.

The second repeat association (members 2.1-2.3; Fig. 2) is much simpler, and corresponds to the eight-member repeat family of Palmer et al. (1987). This association accounts for 13 of the breakpoints mentioned previously, and is best characterized by the presence of the *rpoA* α and β fragments and the ORFs that contain them. Unlike the first association, there is only a single basic repeat unit, which consists of three common elements (*ΨrpoB/C1, rpoA*α and *rpoA*β), although members 2.1 and 2.3 share three additional elements (a 162 bp duplication of 3′ *rps11*, a 34 bp fragment with 88% identity to the *petB* intron, and an 81-88 bp fragment with 95% identity to a piece of the *5S-4.5S* spacer). Members 2.2 and 2.3 are inverted in orientation relative to 2.1, and share sequence identities of 76% and 93% with member 2.1, respectively, in the regions where they are alignable. The lower identity of member 2.2 is due to a truncated and essentially unalignable spacer between *ΨrpoB/C1* and the *rpoA*α fragment. In addition to the three elements noted above, member 2.2 also lacks about 800 bp of sequence that follows the *rpoA*β fragment in members 2.1 and 2.3; instead this region is occupied by the *rpoA*γ fragment. Member 2.3 appears to be framed by two short direct repeats otherwise found only in the *5S-4.5S* spacer, and immediately upstream in the *ycf2* spacer is a short, 37-bp fragment (repeat *l*) from a different region of the *5S-4.5S* spacer (95% identity). This is also in the opposite orientation relative to the two direct repeats.

SIMPLE SEQUENCE REPEATS. We found a total of 440 exact or perfect microsatellite repeats within the *Pelargonium* genome (Table S6, Appendix 2). The great majority of these (387) are 7-17 bp mononucleotide adenine or thymine runs, and slightly more than half of the latter belong to the shortest class of only seven bp. Only six dinucleotide repeats of five units were found, and all of these are in the inverted repeat (three repeats with their complements). No other microsatellite types were detected.

Microsatellites are relatively evenly distributed throughout the genome (Fig. 1). Almost two thirds (280) are found within the IRs; the remaining third fall largely within the LSC region, with only 15 found in the SSC. Slightly more than half (245) occur within intergenic spacers, and roughly a third (157) occur in coding sequences. While introns represent only a small percentage of the genome's length, 38 SSRs are found within their boundaries, on average about two per intron.

LARGER REPEATS. Using REPuter, we further identified 6,698 repeats of 21 bp or larger with a sequence identity of greater than 80% within genome. The bulk (5,474, or 82%) are smaller repeats of 21-30 bp, and a large number of these are at least in part inexact mononucleotide SSRs that typically are interrupted by a transitional base or bases; many if not all of the previously discussed SSRs may be contained within this class. Despite the greater size of this genome, the number of repeats in this size class is remarkably uniform in comparisons with several other taxa for which genomic data are available (Fig. 4). However, this class represents 94% or more of the repeats in those other genomes. *Pelargonium* thus has a significantly larger number of 31 bp or larger repeats, having more than 3.6 times as many as *Oenothera*, and more than 35 times as many as *Spinacia*.

The sheer number of smaller repeats precludes a useful discussion of them here. We choose to focus on the classes of 31 bp or more. Upon closer examination, we found that 87% of the repeats in these classes (1,065, including almost all of the largest class) are associated with the two repeat associations discussed above. The remaining 158 large repeats were ultimately reduced to nine pairs of dispersed repeats (31-104 bp) and six small, localized families of 15-33 bp tandem repeats with 4-12 repeats each (repeats *p-z, a1-a4,* Table S5, Appendix 2). Nine additional dispersed repeats (repeats *g-o*, Table S6, Appendix 2) were also identified whose only other occurrence is in the repeat associations (see below) and their duplicates in the IR.

Analysis of this larger class provides some insight into how REPuter may overestimate repeat numbers. REPuter uses pairwise comparisons to recognize repeats, and this is the basis of the count; the number of unique pairs is counted, not the actual number of repeats. A repeat with multiple copies will thus be over-represented. REPuter may also compound this by recognizing several nested or overlapping series of repeats within a given region containing multiple repeats. For example, beginning in the 3' end of *rps*19, there is an 8-unit tandem repeat that extends 101 bp into the adjoining spacer. The basic repeat unit is 27 bp, with a degenerate unit of 21 bp. REPuter failed to identify the basic unit, and recognized 21 overlapping or nested repeats in this region. Similar situations are found in *ycf1*, *ycf2*, and the *5S*-*4.5S* spacer.

DISCUSSION

GENERAL CHARACTERISTICS. The chloroplast genome of *Pelargonium* × *hortorum* is remarkable for its overall size, the relative sizes of its IR and single copy regions, the number of rearrangements and repeats found within it, and the presence of a set of highly divergent *rpoA-like ORFs*. This study has largely confirmed the earlier size estimates (Palmer, Nugent, and Herbon 1987) for the genome and its organizational partitions, the placement of the LSC-IR boundaries, and the occurrence of two “families” of dispersed repeats, and has provided a much greater level of detail into the composition and structure of these repeats and the extent of gene order rearrangements.

GENE CONTENT. Despite the vast increase in size of the genome, gene content is almost identical to that of other angiosperms, with only two genes, *accD* and *trnT-ggu*, having been lost. *accD* has also been lost in a number of lineages including grasses (Katayama and Ogihara 1996), Lobeliaceae (Knox and Palmer 1999), and *Trachelium* (Campanulaceae; (Cosner et al. 1997). As in *Pelargonium*, the loss of *accD* in both the Lobeliaceae and *Trachelium* is associated with proximity to rearrangement endpoints. Similarly, the loss of *trnT* in *Pelargonium* also occurs at an inversion endpoint. The presence of tRNAs has been often noted at such endpoints in grasses, and rearrangements in the region surrounding *trnT*-ggu in grasses suggest two independent inversions (Howe et al. 1988; Hiratsuka et al. 1989; Shimada and Sugiura 1989). With the exception of the wide-scale loss of tRNAs in the parasites *Epifagus* (Morden et al. 1991; Wolfe, Morden, and Palmer 1992) and the related *Orobanche* (Lohan and Wolfe 1998), tRNA loss seems to be very rare within land plants. Of the sequenced chloroplast genomes, such loss has been documented only in the fern *Adiantum* (Wolf et al 2003), where both *trnL-caa* and *trnK-uuu* were reported as lost. The former gene was later found to be restored through RNA editing, however (Wolf, Rowe, and Hasebe 2004) and it is possible that *trnT* may similarly be lurking undetected somewhere in the genome of *Pelargonium*.

The lack of a readily recognizable *rpoA* gene is made more interesting by the fact that there are potentially three different open reading frames that could encode it. The sequences and lengths of all three *rpoA*-like ORFs are very different from those known in other flowering plants, and it is possible that all of these ORFs represent nonfunctional, degenerate forms of the gene. The transfer of *rpoA* to the nucleus and its subsequent loss in the chloroplast has been reported in mosses (Sugiura 2003; Goffinet et al. 2005), and its loss has also been noted in the parasite *Cuscuta*, where it is thought to be related to the loss of photosynthesis (Krause, Berg, and Krupinska 2003). However, another study finds no evidence of a gene transfer to the nucleus in *Pelargonium* × *hortorum* and suggests that the chloroplast *rpoA* is still functional despite its extreme divergence (Kuhlman, Calie, and Palmer, in prep.). In light of this, the question becomes which, or possibly how many, of these ORFs may be transcribed and translated in the genome. Each of the three ORFs differs from the others in sequence and length, indicating at the least different selective pressures on each or at most a lack of constraint on sequence evolution in some. In addition, *rpoA* is normally co-transcribed as the terminal gene of the S10 operon. Although we do not know if it is transcribed, ORF574 occupies this position in the genome. The other ORFs, being well outside the operon as well as in a different orientation, would need to gain independent promoters and regulatory elements in order to be expressed. This may have happened at least once in this genome, if we make the reasonable assumption that both *rpl33* and *rps18* were restored to function after the breakup of their operon. The designation of one or any of these ORFs as *rpoA* is thus problematic without experimental evidence of transcription.

The discovery of the *rpoA*γ fragment downstream and out of frame with the α fragment was suggestive of the possibility that an intron had invaded the gene, The situation seems analogous to that of *Euglena*, where *rpoA* was not initially identified (Hallick et al. 1993), but was later found to be both highly divergent and interrupted by the presence of an intron or introns (Sheveleva, Giordani, and Hallick 2002). Though we identified possible splice sites, the brevity of the intervening sequence (about 340 bp) would have necessitated a highly reduced secondary structure, and we could not find a folding even with the highly reduced structural requirements of a Group III intron as found in *Euglena*.

Similar to the situation with *rpoA*, *rps14* occupies the terminal position in its operon and has also been duplicated twice. The presumably functional gene is found in its traditional position following *psaB*, inferring that the operon is intact. The two copies of *Ψrps14* are isolated not only from the operon but from each other, and differ from the functional gene at only two bases, one of which induces an internal stop. Repair of the stop codon by RNA editing would result in a different amino acid at that position when compared to the presumably functional gene (assuming a U→C edit at the first nucleotide of the stop codon, as in *Adiantum*; see Wolf, Rowe, and Hasebe 2004). Repair of the stop to restore amino acid identity would require a G→U edit at the second position. Moreover, both *Ψrps14* copies would also need to gain new promoters and regulatory elements for expression. Since a functional copy is present, it seems unlikely that these two additional copies are expressed, but this has not been tested experimentally.

In the assessment of potential open reading frames, we found a great deal of conserved sequence with similarity to various ORFs that have been previously characterized in other genomes. However, we very rarely found conservation over the full length of the reading frame, and often longer ORFs from other genomes were recognizable only as a truncated series of smaller reading frames with limited sequence similarity in *Pelargonium*. For example, *ycf68* or *ORF133* has been commonly noted in the *trnI-gau* intron of grasses, but in *Pelargonium*, three different small ORFs account for most the larger hypothetical coding frame. Restoration of the entire frame by RNA-editing of stop codons seems unlikely as these three ORFs are out of frame with respect to each other. Even ORFs among such closely related taxa as *Atropa* and *Nicotiana* are poorly conserved (Schmitz-Linneweber et al. 2002), and thus caution seems advisable in the recognition of potential ORFs.

While potential reading frames were quite numerous, we have chosen to conservatively note only those with similarities to genes of known function. In addition to ORFs we designated for the potential *rpoA* genes and the partial duplication of *ndhA* in the IR, we found only two other such instances, and both of these occur within the *trnA-ugc* intron in the IR. The first of these, *ORF56*, has also been identified in the chloroplast genome of *Calycanthus* (Goremykin et al. 2003). It is nearly identical (99%) to the mitochondrial ACR-toxin sensitivity (*ACRS*) gene of *Citrus jambhiri* Lush., and its presence has been noted in a number of chloroplast and mitochondrial genomes (Ohtani, Yamamoto, and Akimitsu 2002). The second ORF (*ORF42*) is a truncated 3′ fragment of another mitochondrial gene, *pvs-trnA* or *ORF98*, which is associated with a group of mitochondrial genes that impart cytoplasmic male sterility in a species complex of cultivated *Phaseolus* (Fabaceae) (Woloszynska et al. 2004). The situation of these two ORFs seems analogous to that of the many conserved sequences identified in our assessment of other ORFs, in that a BLAST search (Altschul et al. 1997) of GenBank reveals a large number of taxa with conserved chloroplast sequence of varying lengths and sequence identity. The lack of overall conservation across plant lineages suggests that while there may be some constraint on these sequences (e.g., constraints imposed by secondary structure of the intron), these ORFs probably do not represent functional genes in this genome, and it remains to be shown whether they are transcribed and translated.

NUCLEOTIDE POLYMORPHISMS. Given that the genus *Pelargonium* is known to have biparental inheritance of plastids (Baur 1909; Tilney-Bassett 1973; James et al. 2001), it is remarkable that there are relatively few examples of heteroplasmy found in this study (Table S4, Appendix 2), although this might be the result of varying patterns of inheritance (Tilney-Bassett and Birky 1981; Tilney-Bassett and Amouslem 1989). Most of the observed polymorphisms were present in low copy numbers relative to the consensus sequence, and the majority were located in the large single copy region. While these observations could represent real polymorphism within an individual, we did not attempt to determine experimentally if they could be errors that were introduced during clone propagation, sequencing or PCR. Further, since multiple individuals were sampled for DNA isolation, it is possible that these might represent differences between individuals of cultivar 'Ringo White.'

There are also polymorphisms in our sequence for *ycf2* when compared to that of Downie et al. (1994). These include two dinucleotide differences, six single nucleotide differences, a six-bp region with differing insertion points of an adenine, and a 20-bp region in our sequence with three single base insertions that cause a temporary frame shift. Our sequence through the regions where these occur has a minimum 6× coverage, so error on our part does not seem probable. These polymorphisms may represent cultivar differences, in that the Downie et al. (1994) sequence was generated from the *PstI* clone bank of cultivar 'Irene' used by Palmer et al. (1987). Similar polymorphisms are found in the *rpoA*-like sequences from that clone bank (Kuhlman, Calie and Palmer, unpublished data), and while we cannot rule out the possibility of error in these manually generated (Sanger dideoxy with ^{35}S) sequences, additional support for cultivar differences can be seen in the differing organization of the *ycf2* region (Fig. 2). These organizational differences suggest either that rearrangements have continued within historical times since the divergence of these two cultivars, or that these hybrids may have been produced from different parental strains. *Hortus Third* (Bailey and Bailey 1976) cites *P. hortorum* as a "cultigen [cultivated form] of complex hybrid origin, largely derived from *P. inquinans* and *P. zonale*." The "complex origins" of these hybrids may thus be reflected in the sequence and structural differences between the two cultivars.

GENE ORDER, REPEATS, AND REPEAT ASSOCIATIONS. The size of the genome, its gene order, and the number and placement of repeats are all intimately connected. As inferred by Palmer et al. (1987), the increased size of the genome is largely due to gene duplication in the gross expansion of the IR, although the two repeat associations account for about 10% of the total length. While changes in the IR boundaries are common [the "ebb and flow" (Price and Palmer 1993; Goulding et al. 1996)], large-scale changes are not. Assuming a tobacco-like ancestral chloroplast genome, we can construct an evolutionary model in which a series of eight IR boundary shifts (a minimum of three contractions and five expansions) and six inversions (minimum) accounts for most of the major rearrangements (Fig. 5) found in the IR. Two small ebb-and-flow contractions (or a small and a large contraction, steps *b* and *c*, Fig. 5) of the IR are all that is necessary to explain the placement of *trnI* at the beginning of the LSC, and a third can be invoked for the loss of the large ORF (*ORF350* in tobacco) representing the duplicated portion of *ycf1* between *ndhF* and *trnN* (block 25f, step *b*, Fig. 5). Several waves of expansion can then be played out that largely fit the current structure of the genome. These events explain the translocation of several conserved blocks of genes in the IR. Thus both large and small-scale changes in the IR boundaries appear to have played an important role in restructuring gene order in *Pelargonium*.

It is possible that the IR could have been lost or severely reduced in size and content at some point. However, the necessary sequence of contractions and expansions seems to require the presence of both copies, at least until fairly late in the process when the composition and order of the IR was very much as it is today. While the large size of expansions and contractions suggested here might have been a series of smaller, ebb-and-flow events, we see little evidence of this.

In addition to changes in the IR boundaries, inversions have played an important role in the evolution of the modern *Pelargonium* genome. In the simple model presented in Fig. 5, we hypothesize a minimum of only six inversions: 1) *psbD-ycf3* (blocks 3-7), 2) *psaI-rps18* (blocks 11-13), 3) re-inversion of *psbD-psbZ* (block 3), 4) re-inversion of *rps18* (block 11), 5) inversion of *ndhF-trnN* (blocks 20-21), and 6) 50 kb inversion of most of the newly expanded IR from *rpl20-trnN*. Upon re-examination of the data on the basis of this model, we discovered that inversions 3, 4, and 5 are each flanked by small inverted repeats (repeat *a6*, repeat *j* of repeat member 1.4, and repeat *a5*, respectively, Table S5, Appendix 2; the 24 bp inverted repeat that originally flanked *ndhF-trnN* has the appearance of a direct repeat due to the subsequent larger inversion). We found no clear cases of such artifacts correlated with the other repeats, but analyses of these features is ongoing, and these could have been obscured either by sequence evolution or superimposition of other events. With the latter in mind, it is important to note that inversions 1-4 are all adjacent to the locations of the first major repeat association, and important elements of those repeats were at least historically adjacent to or a part of these inversions. While Palmer et al. (1987) were unable to recognize that these repeats represented rearrangements themselves due to the limited resolution of filter hybridization, they had noted their placement near the ends of detected inversions and suggested recombination between them as the major cause of those inversions. Despite our failure to identify the small inverted repeats predicted to occur at all of these boundaries, this is still probable. The complexity of the repeats suggests that they have been subject themselves to a series of evolutionary events, and these could have obscured or eliminated signals of past events.

Our simple model of inversion and IR expansion shown in Fig. 5 does not account for the composition or arrangement of the repeat associations. These high complexity regions are a unique feature of this genome and account for many of the rearrangements present as well as the majority of the larger, non-microsatellite repeats detected. The two associations have no common elements, but do share a few common characteristics. Both are involved with duplication of a gene or genes (in particular, *rpl33*, *rpoA*, *rps14* and *trnfM*) and at least the potential disruption of operons. Both contain a number of pseudogenes. Both involve elements that appear in novel combinations, and these combinations are duplicated and inverted. Many of the elements are endemic to the region of genome space in which they occur, but a few fragments from widely dispersed locations are present as well. The latter elements are typically drawn from otherwise non-repetitive regions without rearrangements.

The proximity of *rpoA* and *rpl33-rps18* at the ends of IR expansions suggests that these expansions possibly in conjunction with inversions could have disrupted their respective operons; similar situations are noted in *Trachelium* (Cosner et al. 1997) and *Vigna* (Perry et al. 2002). The repeat associations could be simply a record of the transcriptional recovery of functional genes lost in the breakup of these operons. While we cannot completely explain the complexity found in the repeat associations by these processes of inversion and IR shifts alone, these could have caused the genomic instability that allowed these regions to evolve.

The rearranged chloroplast genome of pines lacks the complexity of these repeat associations, but inversions and IR shifts have played a major role in its organizational evolution (Fig. S1; Appendix 2). Adapting the evolutionary model of Strauss et al. (1988) to fit the genome organization of *Pinus thunbergii* (Wakasugi et al. 1994), three IR shifts (a small contraction, a small expansion, and a large contraction resulting in the near complete loss of the IR) and seven inversions (Fig. S1a, Appendix 2) are required to explain the current organization of the *Pinus* chloroplast genome. Alternatively, it is also possible to posit multiple IR expansion-contraction events (seven contractions, five expansions) in conjunction with only three inversions (Fig. S1b, Appendix 2). While each of these evolutionary scenarios emphasizes a different process, both depend upon a mixture of inversions and IR boundary shifts to account for the reorganization of the genome. While much of the reorganization of the *Pelargonium* genome can be explained by these processes as well, it seems that a third process is necessary to explain the complexity found there.

Much of our thinking about the high complexity regions could be simplified by the invasion of a duplicative transposable element or some mechanism that produces similar results. With the exception of the degenerate transposon in *Chlamydomonas* (Fan, Woelfle, and Mosig 1995), tranposons are not known in plastid genomes. An alternative explanation for the rampant duplication and inversion could be retroposition (Palmer 1991). Retroposition (reverse transcription of an RNA transcript, in this case with the intron spliced out, to a cDNA, followed by recombination with the primary DNA sequence) has also been suggested as one method by which introns are lost (Dujon 1989; Bock, Hermann, and Fuchs 1997). Palmer (1991) notes that the presence of short dispersed pseudogene sequences may support the idea of random incorporation of cDNAs. Such a process could account for the seemingly random incorporation of non-regionally endemic DNA into the hotspot regions, but not why the more endemic elements (e.g., *rpl33*) are themselves repeated so often. Given the nature of these repeat associations, it is very likely that they are subject to both intra- and intermolecular recombination, and this could also result in duplications (Howe et al. 1988).

In figures 6 and 7, we extend the simple model of evolution presented in figure 5 to the special cases involving the two repeat associations by adding putatively ancestral duplications. In each of these models, we make two simplifying assumptions. First, we assume that duplications occurred prior to any other rearrangements (i.e., inversions and IR shifts) that directly involve the duplicated elements, and second that these are not just simple tandem duplications of a single gene, but involve various duplications of one or several elements. Evidence for the latter is that both *rps14* and *trnfM* are duplicated in two different putatively ancestral arrangements. Once these duplications were in place, then a relatively simple series of seesaw-like inversions and IR boundary displacements, some of which create orphan sequence fragments, could account for almost all of the current structure we see in these regions. In combining all of these evolutionary models, a total of eight IR shifts, 12 inversions, and eight duplications are required at a minimum to explain the structure of the modern *Pelargonium* genome.

If our assumption of the sequential priority of duplications is correct, then it may be that duplications involving *rpoA* and *rpl33* could have interrupted their respective transcriptional operons rather than the processes of inversion and IR shifts mentioned earlier. Similarly, duplication of *rps14* may have disrupted its operon as well. Thus these duplications may have caused the genomic instability that resulted in numerous inversions and IR boundary shifts.

Understanding of the processes involved in the evolution of these highly complex regions will require the continued close examination of the smaller repeats, as well as the sequencing of several closely related genomes with fewer rearrangements. While the number of repeats based on the REPuter analysis may be greatly exaggerated, there seems to be a previously undocumented presence of many repeats of less than 30 bp in all genomes examined. Despite the problem of numerical overestimation, the number of repeats in all of the examined genomes appears to be more or less uniform despite differences in size, structure and content. A cursory examination reveals that many of these lesser repeats consist of imperfect SSRs or combinations of SSRs, and this could be a background of evolutionary noise. However, preliminary analysis shows that similarly structured repeats do seem to play a role in rearrangements with inversions and possibly in changes of the IR (Goulding et al. 1996). Given this background level of repeats, the question might not be why is *Pelargonium* so highly rearranged, but why aren't rearrangements more common in all chloroplast genomes.

In summary, the chloroplast genome of *Pelargonium* × *hortorum* is both the largest and most rearranged genome yet sequenced among land plants. The large increase in size and the number of rearrangements are correlated with a series of large expansions of the inverted repeat and inversions. These may have resulted in the disruption of transcriptional operons, and genes involved in these disruptions form the core units of a series of large, complex repeats that are unique characters of this genome. These repeat regions are hotspots for sequence duplications (including many non-functional gene copies or pseudogenes), inversions, and the incorporation of a few other repetitive elements from elsewhere in the genome. In addition to the two major processes of inversion and large shifts in IR boundaries, a process of sequence duplication may be at work, possibly including the invasion of transposons, a relatively regular process of retroposition, and/or frequent recombination. Despite the major increase in size and complexity, the gene content of this genome is similar to that of other angiosperms. Exceptions to this are the losses of *accD* and *trnT-ggu*, the large number of pseudogenes associated with large repeats, the recognition of two ORFs in the *trnA* intron previously identified from mitochondrial genomes, and a set of three different ORFs that each potentially encode a highly divergent *rpoA* gene.

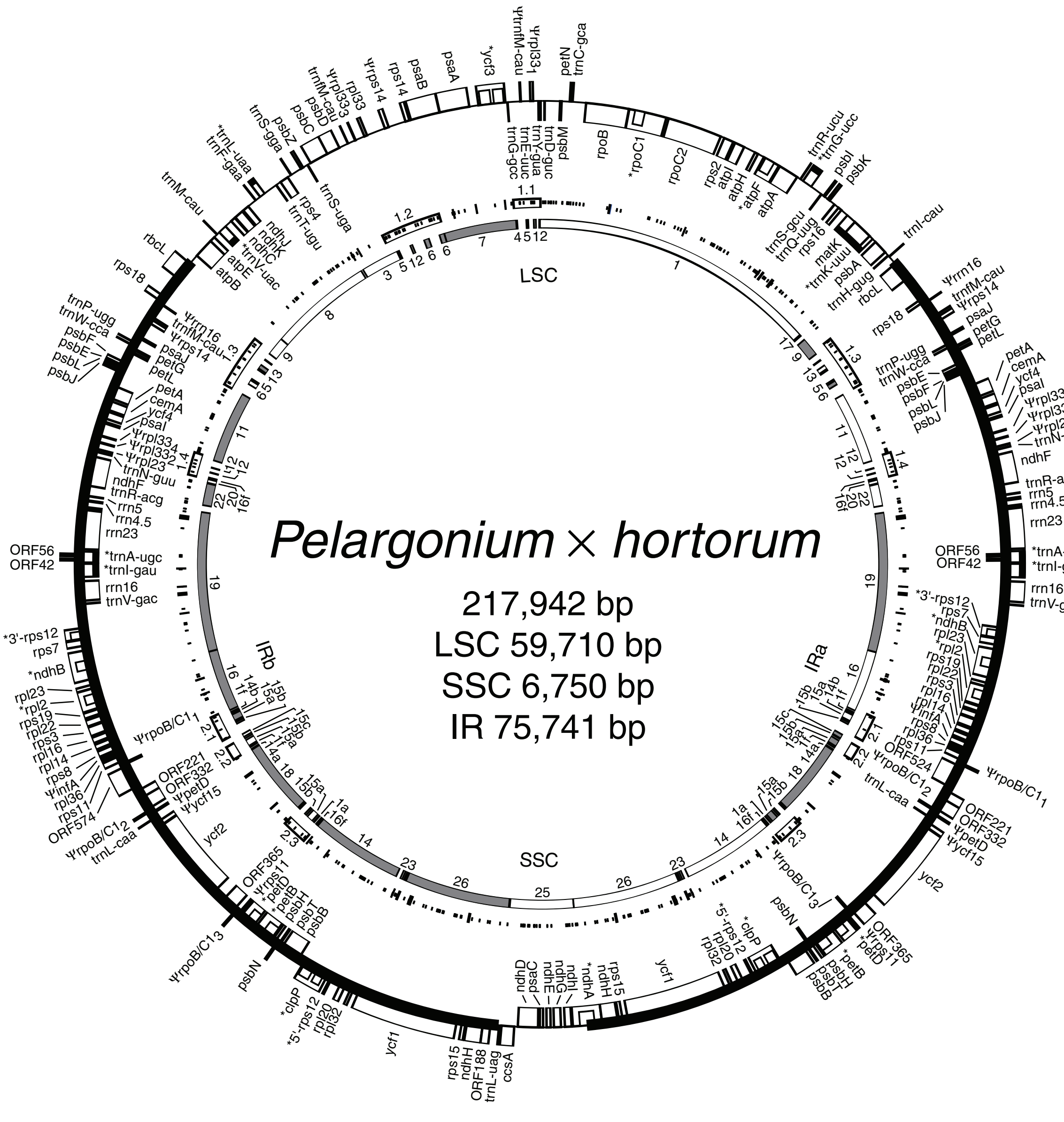


Fig. 1. Map of the chloroplast genome of *Pelargonium* × *hortorum* L. H. Bailey. Middle ring shows the locations of exact SSRs (small hash marks), larger repeats (large hash marks), and the two major repeat associations (1.1-1.4; 2.1-2.3). Interior ring details rearrangements with blocks of genes numbered in the order in which they appear in tobacco; inversions are shaded. * indicates genes with introns.

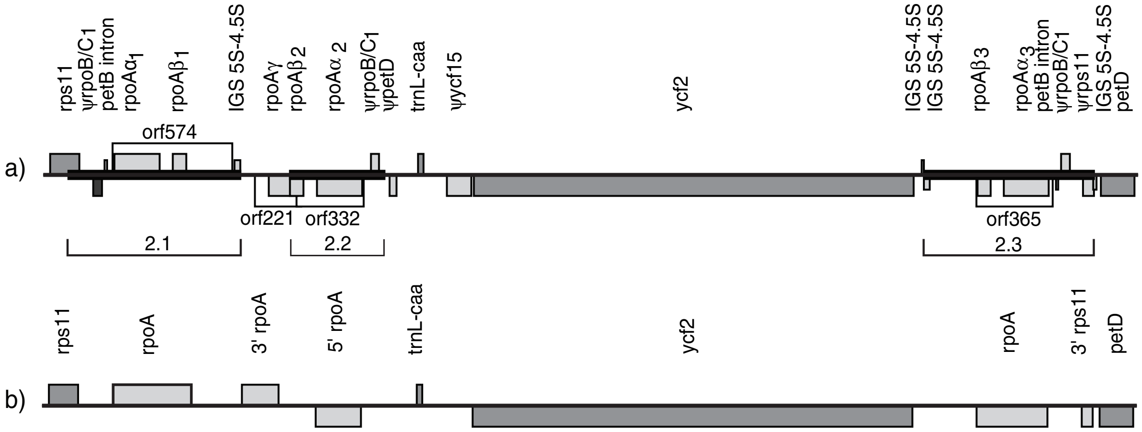


Fig. 2. The region surrounding *ycf2* (a) as determined in cv. 'Ringo White' of our study and (b) as previously reported in cv. 'Irene' in earlier studies (Palmer et al., 1990a and 1990b; Downie et al. 1994). Black bars in a) indicate the repeat association members 2.1-2.3.

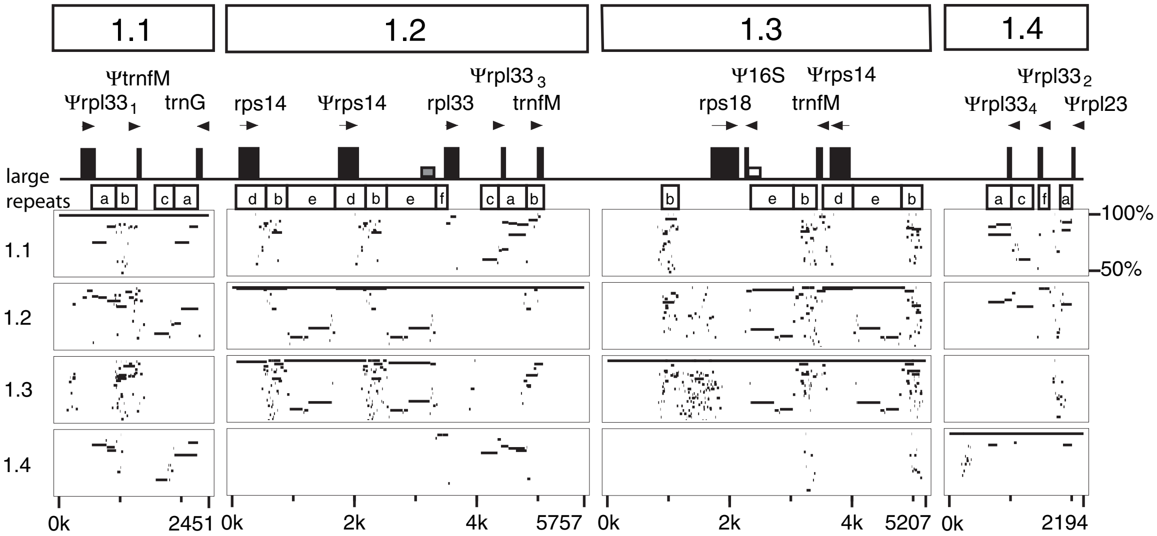


Fig. 3. Percentage identity plots from MultiPipMaker showing identities within and between each of the four members of repeat association 1. Large repeats are labeled a-f.

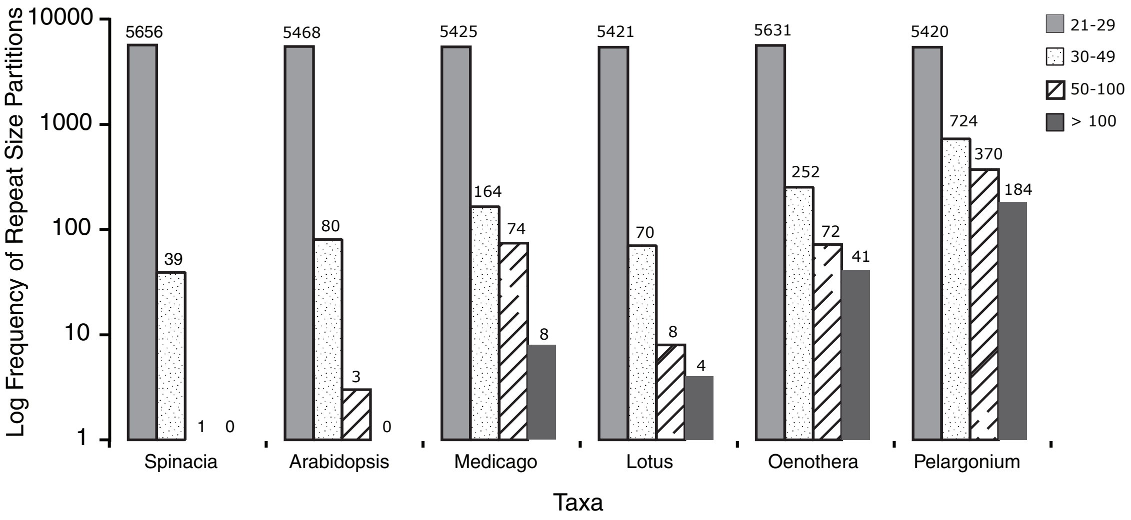
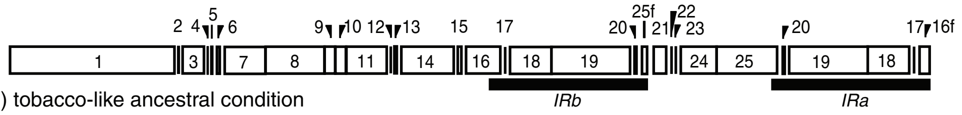
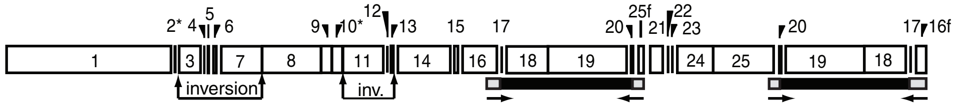


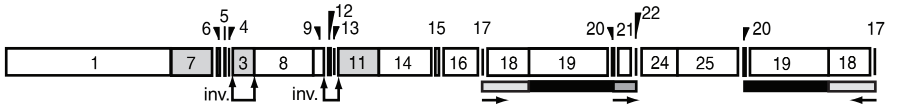
Fig. 4. Histogram of repeat size frequency in *Pelargonium* and five other chloroplast genomes. Repeat size classes are 21-30 bp; 31-50 bp; 51-100 bp; > 100 bp.



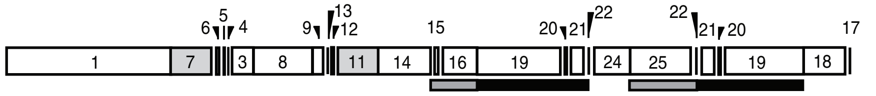
a) tobacco-like ancestral condition



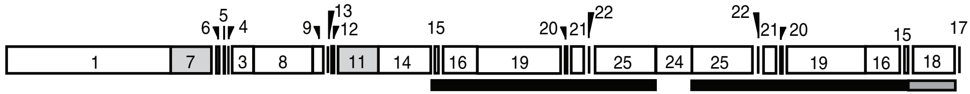
b) two inversions, two small IR contractions, loss of trnT and accD (*)



c) two inversions, a small IR expansion into SSC, large IR contraction in LSC

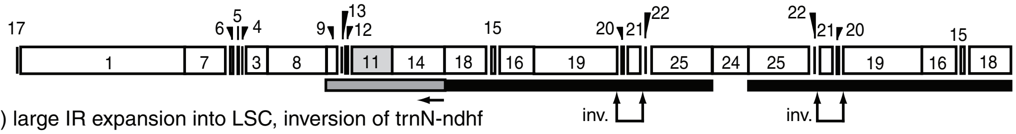


d) large IR expansions into both SC regions

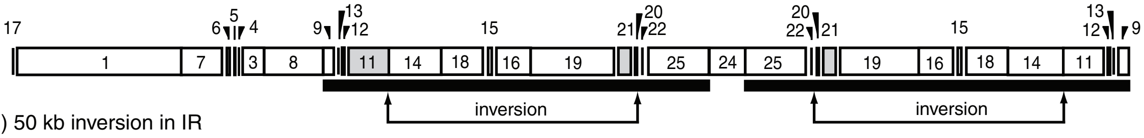


move depiction of trnI (17) to beginning of LSC

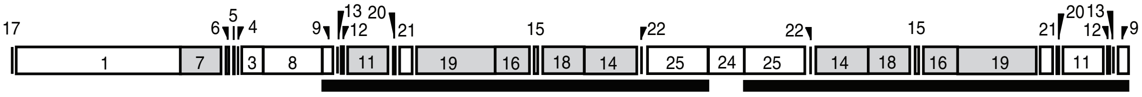
e) large IR expansion into ycf2 region



f) large IR expansion into LSC, inversion of trnN-ndhf



g) 50 kb inversion in IR



h) rearranged genome without high complexity repeat associations

Fig 5. A simple evolutionary model for the major expansions and contractions of the IR and some of the inversions present in the chloroplast genome of *Pelargonium*. a) The presumed tobacco-like ancestral state. b) Small contractions of the IR remove *rpl2, rpl23*, and *ycf1* from the IR, leaving *trnI* at the IRa/LSC junction (JLA); inversions flip the order and orientation of *psbD-rps14* and *psaI-rps18*. c) A major contraction removes *trnL-trnI* (including ycf2) from the IR (leaving them only on the JLA side of the LSC) and an expansion into the SSC moves *ndhF* and *rpl32* into the IR; an inversion flips *psbD-psbZ* back into their original orientation, though appearing translocated, and another flips *rpl33-rps18* . d) Expansion of the IR into both the LSC and SSC including the S10 operon (*rpl23-rpoA*, possibly to *petD*) and *ycf1-ndhA*, respectively. e) Expansion of the IR to include *ycf2*, leaving *trnI* stranded at the beginning of the IR. f) Large expansion of the IR to include *rbcL*; inversion of trnN-ndhF. g) 50 kb inversion of most of the IR. h) Current structure of the genome showing without locations of the high complexity major repeat associations 1 and 2 (see fig. 6 and 7).

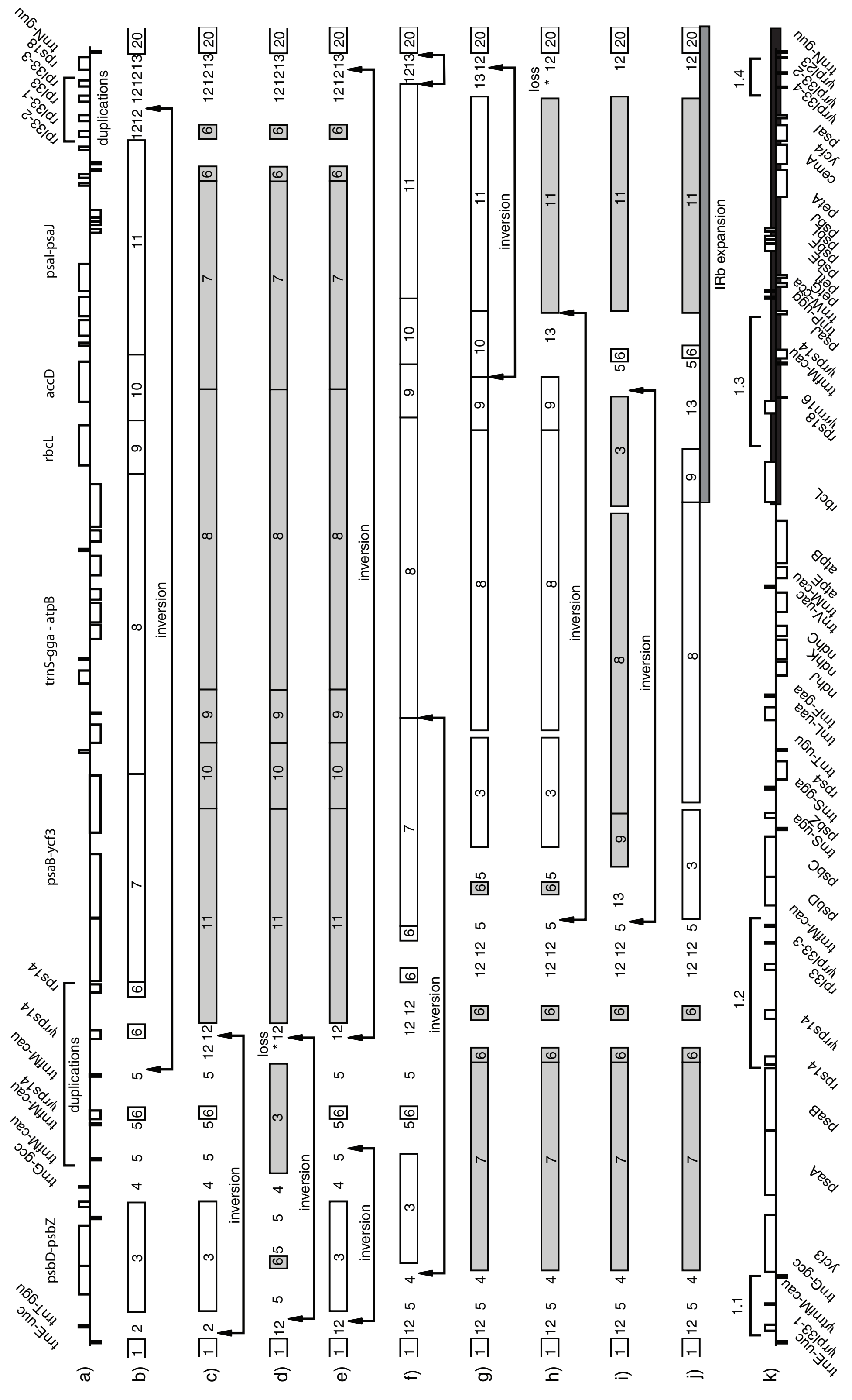
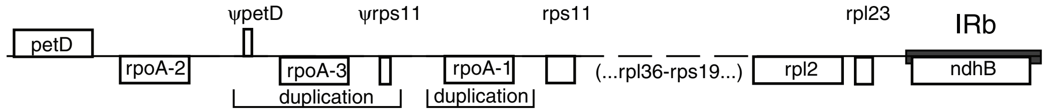
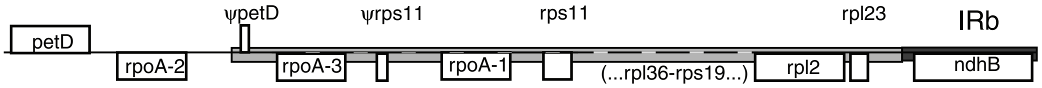

a)
b)
c)
d)
e)
f)
g)
h)
i)
j)
k)
trnE-uuc
trnT-ggu
psbD-psbZ
trnG-gcc
trnM-cau
ycrps14
rps14
duplications
psaB-ycf3
trnS-gga - atpB
rbcL
accD
psaI-psaJ
rpl33-2
rpl33-1
rpl33
rpl33-3
rps18
trnN-guu
inversion
loss
IRb expansion
1.1
1.2
1.3
1.4
ycrpl33-1
ycrtrnM-cau
ycf3
psaA
psaB
ycrpl33-3
psbD
psbC
trnS-uga
psbZ
rps4
trnT-ugu
trnL-uaa
trnF-gaa
ndhJ
ndhK
ndhC
trnV-uac
atpE
atpB
ycrrn16
petA
cemA
ycf4
psaI

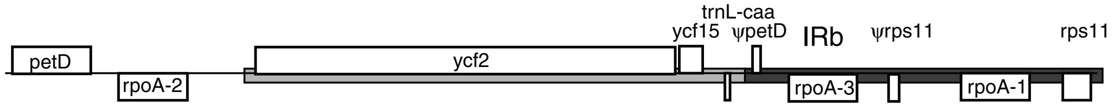
Fig. 6. An evolutionary model for major repeat association 1. a) Putative ancestral arrangement of genes in this region, including duplications of *rpl33*, *trnfM* and *rps14*. b) A schematic diagram of the above, showing blocks of conserved gene order as found in the modern *Pelargonium* genome relative to tobacco. c-i) Inversion series required to transform putative ancestral genome into the modern. j) Schematic for the current *Pelargonium* chloroplast genome. k) The current arrangement of genes for this region as determined in this study.



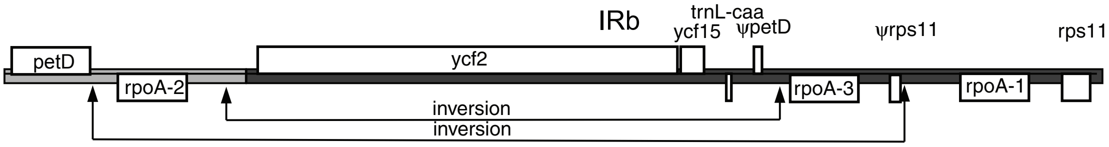
a) ancestral condition after IR contractions orphan trnI and the trnL-ycf15-ycf2 cluster on IRa side of genome



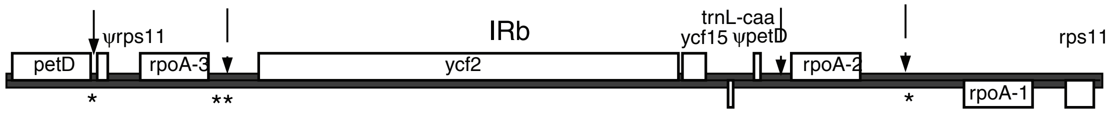
b) IR expands on IRb side to include the S10 operon including two of the rpoA duplicates



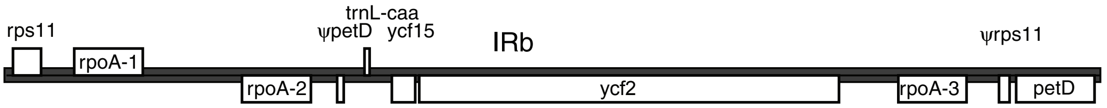
c) IR expands on IRa side to include the trnL-ycf15-ycf2 cluster



d) IR expands beyond petD, and two nested inversions occur



e) inversions result in modern arrangement of genes and gene fragments; * marks locations of fragments of 4.5S-5S spacer



f) large inversion within the IR results in modern orientation

Fig. 7. An evolutionary model for major repeat association 2.

Appendix 1: Index to Collectors and Collections

[Without collector] *africana* ssp. *africana* s.n. (SAM), *heterophylla* 6438 (MEXU), s.n. (MEXU), *longiflora* s.n. (GH), *scabra* var. *sonorensis* 44 (US), *scabra* var. *scabra* s.n. (NY)

Abrams, L. R. (LeRoy) *spinescens* var. *spinescens* 14101 (GH); *scabra* var. *glabrescens* 3641 (A, GH, MO, NY, UC, US)

Ackerman, T. L. *spinescens* 83-445 (NY)

Acocks, J. P. H. *africana* ssp. *australis* 12415 (PRE), *juncea* 14996 (K, PRE), 15885 (PRE), 18643 (PRE), 19008 (K, PRE), 19080 (PRE), 20559 (PRE), 20633 (PRE)

Adole L., Sr. *coulteri* 6435 (US)

Adolfo, Bro. *integrifolia* 316 (US)

Aguilar, R. M. *integrifolia* 415 (MO), *integrifolia* 246 (LIL), 310 (NY, UC)

Aguirre *laevis* 35 (NY)

Ahumada, O. *integrifolia* 1315 (CTES), 1471 (CTES)

Albers, C. A. *heterophylla* 243 (NY)

Albers, C. C. *heterophylla* 44039 (TEX), 44058 (TEX), *laevis* 46193 (TEX)

Alexander, Annie M. *scabra* var. *sonorensis* 415 (UC), 1340 (UC), 1399 (GH, UC), *scabra* var. *glabrescens* 823 (JEP, UC), 2208 (GH, UC), *spinescens* var. *spinescens* 2751 (A, NY, UC)

Allen, R. P. *scabra* var. *scabra* 906 (UC)

Alonso *integrifolia* 574 (SI)

Alvarez, Santiago *heterophylla* 7917 (TEX), 8019 (TEX)

Ambrosetti, J. A. *decemfida* s.n. (MERL), 29182 (MERL), 29208 (MERL), 31104 (MERL), 31120 (MERL), *robusta* s.n. (MERL)

Ameghino, Carlos *robusta* 20 (BA), s.n. (LP)

Anderson, William R. *longiflora* 13488 (MICH, MO, NY)

Anderson, David Lee *scabra* var. *scabra* 5096 (TEX)

Andrada *decemfida* 378 (SI)

Andreasen, M. *coulteri* 527 (MICH, MO)

Andrews, J. H. *longiflora* 62 (A)

Andrieux, G. *mexicana* 228 (G-DC, K, P), s.n. (G)

Anisits, J. D. *integrifolia* 2612 (P)

Annable, C. (C. R., Carol R.) *spinescens* var. *spinescens* s.n. (UC), 481 (NY), 2568 (NY)

Antezana, C. *integrifolia* 1015 (BOLV)

Appleyard *africana* ssp. *africana* s.n. (SAM)

Arbo, M. M. *integrifolia* 2488 (CTES), *integrifolia* 536 (CTES)

Archer, W. A. (W. Andrew) *scoparia* 7339 (UC)**,** *spinescens* var. *spinescens* 6808 (A, NY, UC)

Argañaraz *integrifolia* 366 (LIL)

Arguelles, Elizabeth *helianthemoides* 1067 (MEXU), 1671 (MEXU), 2278 (MEXU), 2992 (MEXU)

Arribalzaga, Enrique Lynch *integrifolia* 45 (LIL)

Arséne, Bro. G. *longiflora* 6148 (MO, US) *scabra* var. *scabra* 15819 (UC), 16755 (US)

Atha, Daniel *longiflora* 297 (NY)

Atwood, D. (Duane) *laevis* 22800 (NY), *scabra* var. *glabrescens* 17043 (MO, NY)**,** *scabra* var. *glabrescens* 18105 (NY), *spinescens* var. *spinescens* 7989 (NY), 12015 (NY)**,** 21712 (NY)

Baca, O. *scabra* 432 (UNM)

Bacigalupi, Rimo *spinescens* var. *spinescens* 3646 (JEP), 9166 (JEP)

Bacigalupo, N. M. *integrifolia* s.n. (SI)

Bailetti, Ernesto *integrifolia* 390 (LIL, MO)

Bailey, Vernon *laevis* 748 (US)

Baird, Josephine *heterophylla* s.n. (TEX)

Balansa, B. *integrifolia* 2365 (G, P)

Balegno, B. *integrifolia* 1094 (LIL), 1424 (LIL), 206 (LIL), 322 (NY), 990 (MO), s.n. (LIL)

Balkwill, K. *africana* ssp. *africana* 9868 (K)

Bang, Miguel *integrifolia* 942 (GH, MO, NY, NY, US, US)

Barber, N. P. *africana* ssp. *australis* 443 (PRE)

Barker, Harriette *scabra* var. *sonorensis* 78-38 (LL)

Barkley, F. A. (Fred A.) *coulteri* 16063b (GH, NY, TEX), *decemfida* 19Ar892 (NY), 19Ar940 (NY), *heterophylla* 13819 (TEX) *laevis* 14539A (UC), 14539c (TEX)

Barlow, Bronson *laevis* s.n. (UC, US)

Barlow-Irick, P. *scabra* 93-103 (UNM)

Barneby, R. C. *scabra* var. *scabra* 17990 (NY, US), *spinescens* var. *spinescens* 18109 (NY)

Barnett, L. C. *heterophylla* 45 (MO, TEX)

Bartlett, H. H. *decemfida* 19183 (MICH, SI, US), 19321 (GH, MICH, SI, US), 19391 (MICH, SI, US), *integrifolia* 21081 (TEX), *integrifolia* 21081 (GH, MICH, NY, US), *integrifolia* 19945 (MICH, US), *integrifolia* 19729 (MICH, US), 19789 (MICH), 20420 (GH, MICH, NY, UC, US), 20488 (MICH), *longiflora* 10541 (GH, MO, US)

Bastión, E. *integrifolia* 1279 (TEX), 821 (TEX), 88 (TEX)

Batista *integrifolia* 2327 (CTES)

Bayliss, R. D. A. *juncea* 5020 (A, MO, NY, PRE, UC, US)

Beal, Mary *scabra* var. *glabrescens* (JEP), 293 (JEP), 313 (JEP), 561 (JEP), 938 (JEP), s.n. (GH)

Beals, Ida N. *laevis* s.n. (A)

Beard, A. *scabra* var. *scabra* s.n. (MO)

Bebr, C. M. *africana* ssp. *africana* 788 (PRE)

Beck, St. G. *integrifolia* 906 (LPB), 11003 (TEX), 14596 (LPB), 27208A (TEX)

Bedker, E. J. *scabra* 260 (UNM)

Benedict, Bro. *laevis* 80 (US)

Benke, H. C. *heterophylla* 5431 (MO)

Benson, Lyman *spinescens* var. *spinescens* 10153 (UC)

Berlandier *heterophylla* 1499 (G, G-DC), 201=1461 (MO), 516 (GH)

Bertoni, M. *integrifolia* 2592 (LIL)

Bethel, E. (Ellsworth) *scabra* var. *scabra* s.n. (GH, RM)

Bezuidenhout, H. *africana* ssp. *australis* 127 (PRE)

Biurrun, F. *decemfida* 5327 (CTES), 5489 (CTES), 6749 (CTES), *integrifolia* 639 (CTES), 865 (CTES), 5435 (CTES), 6112 (CTES)

Blanchou, C. *integrifolia* 2203 (CTES)

Bloomer, R. R. *scoparia* 50-307 (TEX)

Böcher, T. W. *decemfida* 2107 (MO)

Boelcke, O. *integrifolia* 3061 (SI), *integrifolia* 7749 (CTES)

Bogler, David *laevis* 77 (TEX)

Bogusch, E. R. *longiflora* 4739 (MO)

Bohrer, Vorsila L. *scabra* var. *scabra* 636a (UC)

Boke, Norman *muellerae* 225 (MICH)

Bolaños, Oscar Bravo *laevis* 195 (MEXU)

Bonpland, A. *helianthemoides* 4114 (P), *integrifolia* s.n. (NY), *integrifolia* s.n. (P)

Bordón, A. D. *integrifolia* 61-E10 (CTES)

Botello, Luis *heterophylla* 19 (TEX)

Botha, D. J. *africana* ssp. *africana* 3350 (PRE)

Bottino, Osvaldo *integrifolia* 270 (MERL)

Boufford, D. E. *longiflora* 10578 (MO)

Braack, A. *juncea* 39 (PRE)

Brackett, Eunice *heterophylla* s.n. (GH, TEX)

Braem, Selma *scabra* var. *glabrescens* s.n. (A)

Brandegee, Katharine *scabra* var. *sonorensis* s.n. (UC, UC), *spinescens* var. *spinescens* s.n. (UC, UC)

Brandegee, T. S. *scabra* var. *scabra* 11936 (MO), *scabra* var. *glabrescens* s.n. (GH, UC, UC, UC, UC, US)

Brandt, C. *scabra* var. *scabra* 1014 (UNM)

Brass, L. J. *scabra* var. *sonorensis* 14261 (GH, MO, NY)

Bratz *laevis* s.n. (NY)

Bray, W. L. *heterophylla* 319 (TEX, US)

Bredenkamp, G. J. *africana* ssp. *africana* 45 (K, MO, PRE), 105 (PRE), s.n. (PRE)

Brizuela, A. *integrifolia* 1000 (LL), 466 (LIL), 683 (NY), 876 (TEX, UC)

Brizuela, J. (Julio) *integrifolia*111 (LIL), 142 (LIL), 185 (LIL), 376 (LIL), 685 (LL), 740 (LIL), 1020 (LIL), 1069 (NY, UC), 1157 (LIL), 1231 (LIL), 1278 (LIL), 1333 (LIL)

Brizuela, F. *integrifolia* 12 (CTES)

Broder, R. E. *scabra* var. *glabrescens* 593 (US)

Brown, George William *longiflora* B131 (GH, TEX)

Brown, R. H. *decemfida* 31763 (MERL)

Brueckner, A. *africana* ssp. *africana* 420 (PRE)

Bruzzone, R. Maldonado *integrifolia* 1600 (LP)

Buratovich, F. *integrifolia* 935 (NY)

Burge *heterophylla* 2955 (TEX)

Burgess, T. L. *laevis* 1025 (TEX), 2486 (TEX), 3865 (TEX), *longiflora* 1176 (TEX), 1504 (TEX)

Burkart, A. *integrifolia* 14458 (SI), *integrifolia* 10381 (MO, SI), 20867 (SI), 21332 (CTES), 21858 (CTES), 22262 (CTES, NY, US), 23773 (NY, SI), 23774 (K), 25770 (MICH), 7422 (K), 8494 (MO)

Burke *africana* ssp. *africana* 134 (K, SAM)

Burkhardt, W. *spinescens* var. *spinescens* s.n. (NY)

Burmeister, Carlos *robusta* 121 (LIL)

Burr, R. C. *heterophylla* 446 (TEX)

Burtt-Davy, Joseph *africana* ssp. *africana* 12480 (PRE)

Bush, B. F. *heterophylla* 1181 (GH, US)

Bustos, Martha *coulteri* s.n. (MEXU)

Butterwick, M. *heterophylla* 303 (TEX), 1363 (TEX), *laevis* 686 (TEX), 841 (TEX), 3175 (LL), 3554 (TEX), 3606 (TEX), 3677 (TEX), 3703 (TEX), 3808 (TEX), *longiflora* 643 (TEX), 3616 (TEX), *scabra* var. *sonorensis* 7241 (TEX)

C. S. *integrifolia* s.n. (LP), *integrifolia* s.n. (LP)

Cabral, E. *integrifolia* 318 (CTES)

Cabrera, A. L. *decemfida* 17940 (LP), 24325 (LP), 24511 (LP), *integrifolia* 29169 (SI), 32340 (SI), *integrifolia* 14862 (LP)**,** 15553 (LP), 27627 (SI), 29944 (SI), *pulchella* 17631 (CTES), *pulchella* 7796 (LP), 9457 (BAB), 9461 (LP), *robusta* 18645 (CTES)

Cabrera, Cynthia *heterophylla* 59 (TEX)

Cáceres, S. *integrifolia* 301 (CTES)

Camazine, S. *scabra* 98 (UNM)

Canby, William M. *heterophylla* 112.5 (GH)

Cárceres, Manuel R. *decemfida* 362 (NY)

Cárdenas, M. *integrifolia* 3909 (US), 4791 (US)

Carnevali, R. *integrifolia* 1335 (CTES), 2901 (CTES), 3324 (CTES)

Carr, W. R. *heterophylla* 13317 (TEX), *longiflora* 10869 (TEX), 11174 (TEX), 16298 (TEX)

Carranza, M. A. *longiflora* C744 (MEXU), C802 (MEXU), 2343 (MEXU)

Carsuer *heterophylla* 4348 (TEX)

Carter, J. H. *africana* ssp. *australis* 808 (PRE), 834 (PRE)

Casey, Clifton *heterophylla* s.n. (TEX)

Castellanos, A. (Alberto) *integrifolia* s.n. (BA), *integrifolia* 33816 (LIL), s.n. (LIL), *pulchella* s.n. (BA), *robusta* s.n. (LIL)

Castillón *decemfida* 3739 (LIL), s.n. (GH), *integrifolia* 553 (LIL)

CDRI *laevis* I002 (TEX)

Centurión, T. R. *integrifolia* 559 (NY)

Chambers, Kenton L. *scabra* var. *glabrescens* 632 (UC)

Chandler, J. *spinescens* var. *spinescens* 245 (RM)

Chapline, William R. *longiflora* 485 (GH), 485.5 (NY)

Chauvin, Y. *scabra* 97YC001 (UNM)

Chávez, F. *laevis* 73 (MEXU)

Chiang (C.), F. (Fernando) *coulteri* 7896 (LL, MEXU, NY), 7945 (LL, MEXU), 8204 (LL, MO, NY), *coulteri* 8076 (LL, MEXU), *intricata* F-2256 (TEX), *laevis* (LL), 7832 (LL, MEXU, NY), 8681e (LL, MEXU), 8703 (LL), 9104 (LL, MEXU, TEX, US), 9138 (LL, MEXU, NY), *longiflora* 7514 (LL, MO), 7528 (LL, MO, NY), *mexicana* 8137 (LL), *tehuacana* F-2279 (MEXU), F-2332 (MEXU, TEX), F-330 (MEXU)**,** F-2603 (LL, MEXU, MO)**,** 2239 (TEX)

Chodat, R. *integrifolia* s.n. (G, G)

Chumley, Timothy W. *africana* ssp. *africana* 7338 (TEX), 7339 (TEX), *africana* ssp. *australis* 7340 (TEX), *scoparia* 7404 (TEX), *coulteri* 7402 (TEX), 7406 (TEX), *decemfida* 7371 (TEX), 7375 (TEX), 7377 (TEX), *gypsophila* 7394 (TEX), 7396 (TEX), 7397 (TEX), 7399 (TEX), *heterophylla* 7302 (TEX), 7303 (TEX), 7304 (TEX), 7343 (TEX), 7370 (TEX), *integrifolia* 7420 (TEX), *juncea* 7324 (TEX), *integrifolia* 7424 (TEX), *integrifolia* 7409 (TEX), 7410 (TEX), 7411 (TEX), 7412 (TEX), 7414 (TEX), 7415 (TEX), *integrifolia* 7381 (TEX), 7382 (TEX), 7383 (TEX), 7413 (TEX), *intricata* 7400 (TEX), 7401 (TEX), *laevis* 7306 (TEX), 7313 (TEX), 7314 (TEX), 7341a (TEX), 7342 (TEX), 7391 (TEX), 7392 (TEX), 7405 (TEX), *longiflora* 7299 (TEX), 7300 (TEX), 7301 (TEX), 7305 (TEX), 7357 (TEX), 7356 (TEX), 7358 (TEX), 7393 (TEX), 7395 (TEX), 7403 (TEX), *robusta* 7422 (TEX), 7422a (TEX), 7422b (TEX), *scabra* var. *scabra* 7363 (TEX), 7366 (TEX), 7367 (TEX), 7368 (TEX), 7369 (TEX), *scabra* var. *sonorensis* 7318 (TEX), *scabra* var. *glabrescens* 7361 (TEX), *spinescens* var. *spinescens* 7315 (TEX), 7316 (TEX), 7317 (TEX), 7344 (TEX), 7347 (TEX), 7348 (TEX), 7349a

(TEX), 7349b (TEX), 7350a (TEX), 7351 (TEX), 7352 (TEX), 7353 (TEX), 7354 (TEX), 7355 (TEX), 7435 (TEX), 7436 (TEX)

Ciccarelli, A. *decemfida* s.n. (MERL)

Cisneros, Felipe *heterophylla* 19 (GH, TEX)

Cisneros, R. Cruz *helianthemoides* 1674 (LL, MICH)

Clark, Ora M. *scoparia* 4195 (G, MO), *heterophylla* 3980 (MO), *longiflora* 4133 (MO)

Clarke, B. *africana* ssp. *africana* 1098 (PRE)

Clemens, J. *heterophylla* s.n. (TEX, UC)

Clokey, I. W. *scabra* var. *scabra* 4235 (RM, UC), 4236 (MO, NY, RM, UC, US), *spinescens* var. *spinescens* 5763 (NY, UC), 7233 (NY, UC), 8058 (A, NY, UC), 8059 (A, GH, MO, NY, UC, US)

Clover, Elzada U. *heterophylla* 1063 (NY)

Codd, L. E. *africana* ssp. *australis* 8937 (K, PRE)

Coetzee, B. J. *africana* ssp. *africana* 492 (PRE)

Cole, James E. *scabra* var. *glabrescens* 839 (UC), *spinescens* var. *mohavensis* 517 (UC)

Cole *laevis* 3279 (NY)

Collum, Rose E. *scabra* var. *glabrescens* 68 (GH, MO, US), s.n. (NY)

Columbus, J. Travis *laevis* 568 (UC)

Comins, D. M. *africana* ssp. *africana* 860 (PRE)

Condit, I. J. *scabra* var. *scabra* s.n. (UC)

Cooper, J. G. *scabra* var. *glabrescens* s.n. (GH, US)

Copple, Robert F. *scabra* 20 (RM), E-5 (RM)

Correa, M. N. *robusta* 4839 (CTES, P), 9650 (CTES)

Correll, D. S. *scoparia* 27829 (GH, LL, UC), 29889 (GH, LL), *coulteri* 21329 (LL, NY), 21385 (LL, MEXU, NY), *heterophylla* 15716 (LL, UC), 15987 (LL), 18099 (LL), 19526 (LL), 20757 (LL), 25501 (LL), 27773 (LL), 27899 (LL), *laevis* 19371 (LL, MO, NY), 19973 (LL, NY), 21550 (LL, NY), 21879 (LL, NY), 21888 (LL), 22617 (LL), 23310 (LL), 23695 (LL, NY), 26555 (LL), 26611 (LL), 29837 (LL, MO) 31683 (LL, NY), 33839 (LL), *longiflora* 17301 (GH, LL), 18188 (LL), 19149 (LL), 27757 (GH, LL), 27878 (LL), 31616 (LL), 34058 (LL), 34088 (GH, LL), 34130 (GH, LL, UC)

Cory, V. L. *scoparia* 35193 (GH), *heterophylla* 20670 (GH), 51375 (NY), 54150 (LL), 55213 (US, US), *laevis* 2171 (GH), 31237 (GH), 3716 (GH), 40544 (TEX), 45113 (TEX), *longiflora* 2172 (GH)

Cota G., Olga *helianthemoides* 18 (TEX)

Cottam, W. P. *scabra* var. *scabra* 14004 (GH, US)

Coues, Elliott *scabra* var. *glabrescens* 223 (MO)

Coulter, (J. M) *coulteri* 938 (K)

Covas, G. *decemfida* 1672 (SI), 3068 (SI), 824 (SI), 874 (SI)

Coville, Frederick V. *spinescens* var. *spinescens* 87 (US)

Cowan, Clark C. *longiflora* 3623 (TEX)

Cox, B. J. *heterophylla* 2900 (TEX)

Craig, T. *spinescens* var. *spinescens* 907 (MO)

Crampton, B. *spinescens* var. *spinescens* 2651 (UCD)

Cristóbal, C. L. *integrifolia* 1903 (CTES), *integrifolia* 224 (CTES), *integrifolia* 1655 (CTES, MO)

Crockett, R. L. (Robert L.) *heterophylla* 849 (LL)**,** 8101a (LL)

Croft, Mary B. *heterophylla* 13 (NY)

Cronquist, Arthur *spinescens* var. *spinescens* 9845 (GH, NY)

Crosby, M. *africana* ssp. *africana* 616 (PRE)

Crovetto, R. Martínez *integrifolia* 10173 (CTES)

Crutchfield, J. R. (John) *heterophylla* 1169 (LL, NY)

Cuezzo, A. R. Cuezzo *integrifolia* 778 (LIL), 1012 (LIL), 908 (MO, NY)**,** 2098 (LIL)

Cutler, Hugh C. Cutler *integrifolia* 10008 (GH), *laevis* 1900 (MO)

D'Orbigny *integrifolia* 1220 (G)

Daciuk, Juan *robusta* 798 (LP), 800 (LP)

Dahlstrand, K. Å. *africana* ssp. *africana* 1081 (GB)

Dalmasso, A. *decemfida* 31847 (MERL)

Damrel, D. Z. *scabra* 2504 (FHO)

Daniel, Thomas F. *scoparia* 543 (MICH), *coulteri* 492 (MICH), *longiflora* 883 (MICH)

Darry, J. Burtt *heterophylla* 30 (UC), 41 (UC)

Davidson, A. *scabra* var. *scabra* 444a (GH)

Davis, Earl G. *scabra* var. *occidentalis* s.n. (TEX)

Dawson *decemfida* 1532 (BAB)

de Jesus Solis, Maria *heterophylla* 121 (LL), 69 (TEX)

de la Barra *integrifolia* 155 (BOLV)

de la Garza, Clara *heterophylla* 36 (TEX)

de la Solta, A. V. (Adolfo) *integrifolia* 445 (LIL), 1252 (LIL), 3726 (LIL), 3796 (LIL), 4094 (LIL), 4199 (LIL)

de la Sota, E. *integrifolia* 2979 (LP)

de Varela, F. Juarez *integrifolia* 148 (MCNS)

de Volpoui, Alba S. *integrifolia* 940 (SI)

Degener, Otto *longiflora* 5013 (NY), *scabra* var. *scabra* 4413 (NY)

del Puerto *integrifolia* 3266 (US)

del Vitto-Belgrano *integrifolia* 27666 (MERL)

Demaree, Delzie *scabra* var. *sonorensis* 8012 (MO)

Dempster, Lauramay T. *scabra* var. *glabrescens* 1908 (JEPS)

Dickey, Esther K. *heterophylla* 54 (TEX)

Diem *integrifolia* 1572 (SI)

Dole, N. E., Jr. *longiflora* 4 (UC)

Dominguez, Martha *heterophylla* 8291 (TEX)

Donat, A. *robusta* 182 (K, MO, SI, UC)

Dorr, L. J. *integrifolia* 6990 (CTES, NY)

Douthitt, Fred *scabra* var. *scabra* 170 (RM)

Dressler, Robert L. *laevis* 1124 (GH, MO)

Drushel, J. A. *heterophylla* 6327 (NY), 9556 (US), *scabra* var. *scabra* 8477 (US)

Du Prosser *africana* ssp. *africana* 1650 (PRE)

Dugés, A. *helianthemoides* 18 (GH, NY)

Dunn, D. B. *coulteri* 23178 (MEXU, TEX) *heterophylla* 16160 (UMO), 17013 (MO) *spinescens* var. *spinescens* 818 (UMO)

Duran, Victor *spinescens* var. *spinescens* 1931 (UC), 2527 (UC)

Dwyer, John D. *scabra* var. *sonorensis* 14102 (MEXU, MO)

Earle, F. S. *laevis* 482 (NY), *scabra* var. *scabra* 74 (NY)

Eastwood, Alice *scabra* var. *glabrescens* 17071 (GH, UC), 18187 (US), 8671 (GH, UC, US)**,** *spinescens* var. *spinescens* 7759 (UC), 8917 (GH)

Ecklon *juncea* 5 [94-12] (MO)

Edwards, Mary Taylor *longiflora* 314 (MO, TEX)

Edwards, T. *africana* ssp. *africana* 1636 (NU)

Edwards, Jack *scabra* var. *scabra* 4783 (NY)

Egg, Mamie *heterophylla* s.n. (TEX)

Eggert, H. *heterophylla* s.n. (GH, MO), *longiflora* s.n. (GH, GH, MO)

Eggleston, W. W. *laevis* 19430 (US), *longiflora* 16725 (US), *scabra* var. *scabra* 20354 (NY)

Ehrich, R. *integrifolia* 467 (TEX)

Ehul *africana* ssp. *africana* s.n. (SAM)

Ekman, E. L. *integrifolia* 1949 (NY, US)

Elias, T. S. *scabra* var. *scabra* 12085 (NY)

Ellis, Charlotte C. *scabra* var. *scabra* 372 (MO, NY, US)

Ellison, F. *laevis* 807 (MO)

Engard, R. *scabra* s.n. (UMO)

Engelmann, George *scabra* var. *scabra* s.n. (MO)

Ertter, B. (Barbara) *heterophylla* 4693 (NY, TEX), 5464 (NY), *scabra* var. *scabra* 2935 (NY), 2945 (NY), *spinescens* var. *spinescens* 2792 (NY)

Escalante, Lorenzo *heterophylla* 25 (TEX)

Ewan, Joseph *scabra* var. *scabra* 15324a (NY)

Eyerdam, W. J. *integrifolia* 22438 (GH), *integrifolia* 23553 (GH, MO, SI, UC), 23653 (G), *integrifolia* 22428 (G, UC) 24924 (GH, MO, UC)

Fabris, Humberto A. *decemfida* 1205 (LP, US), *integrifolia* 5642 (LP), 5663 (LP), *robusta* 821 (LP)

Farhat *integrifolia* 109 (LIL), 54 (LIL)

Fasus *integrifolia* 5663 (CTES)

Feddema, Charles *scabra* var. *scabra* 3682 (RM)

Felger, Richard S. *scabra* var. *sonorensis* 3980 (MEXU), *scabra* var. *occidentalis* 88-221 (MEXU), 89-21 (MEXU), 93-289 (TEX)

Fendler, A. *scabra* var. *scabra* 693 (GH, NY, NY, UC, US)

Fernandez, J. G. *integrifolia* 1075 (CTES)

Fernow, B. E. *scabra* var. *scabra* s.n. (US), *scabra* var. *glabrescens* s.n. (US)

Ferraro, L. *integrifolia* 1009 (CTES, SI)

Ferris, Roxana S. *laevis* 2411 (NY), *longiflora* 2820 (MO), 2821 (NY), *spinescens* var. *spinescens* 8060 (UC), 13520 (TEX), 7325 (NY)

Ferruglio *robusta* s.n. (BA)

Feuerer, T. *integrifolia* 7536 (LPB), 7536a (NY)

Fiebrig, K. *integrifolia* 4368 (GH), *integrifolia* 908 (A, GH, US), *integrifolia* 2531 (GH, MO, NY, US), *pulchella* 2984 (NY)

Filipovich, R. *integrifolia* 422 (LIL)

Fischer, Walter *integrifolia* 221 (GH, MO, NY, SI, US), *robusta* 28 (GH, MO, NY, SI, US)

Fish, R. M. *scabra* var. *scabra* 25 (UC)

Fisher, Geo. L. *laevis* 44231 (GH, MO), 44266 (NY), *laevis* 319 (NY), *scabra* var. *glabrescens* 36 (US)

Flanagan, H. G. *africana* ssp. *africana* 1472 (SAM)

Fleetwood, Raymond J. *heterophylla* 3142 (TEX), 3453 (TEX)

Fletcher, R. *scabra* 4885 (UNM), 5622 (UNM), 721 (UNM), 793 (UNM)

Flyr, David *laevis* 1407 (MO), *longiflora* 773 (TEX)

Fortunado, Renée H. *integrifolia* 4745 (NY, US), *robusta* 4799 (G, NY)

Foster, R. C. *scabra* var. *sonorensis* 163 (GH)

Franklin, B. *scabra* var. *scabra* 4846 (NY, RM)

Frick, Jane *robusta* s.n. (GH)

Fries, Th. C. E. *africana* ssp. *africana* 1855 (MO, PRE)

Fritz, Edward C. *laevis* s.n. (LL)

Fruchard, M. *integrifolia* s.n. (P, P, US)

Galander, C. *integrifolia* s.n. (K)

Gallinal, Rosengurtt *integrifolia* 5853 (MO)

Galpin, E. E. *africana* ssp. *africana* 1071 (K, PRE, SAM, US), *africana* ssp. *australis* 9668 (PRE)

Galvan, R. *helianthemoides* 2745 (TEX), 2750 (MEXU, NY, TEX)

Gamerro, J. C. *integrifolia* 1334 (LP)

Garbers *integrifolia* s.n. (LIL)

Garcia, E. M. *decemfida* s.n. (LIL)

Garcia, Elvira G. *heterophylla* 114 (TEX)

Garcia, J. *helianthemoides* 641 (UMO)

Garcia, Olga A. *heterophylla* 621 (TEX)

Garcia, Pedro *integrifolia* 651 (A, NY)

García, José P. *helianthemoides* 641 (MO)

Gardner, J. L. *scabra* var. *sonorensis* 93 (US)

Gaudichaud, C. *integrifolia* 1015 (P), 3294 (P), 650 (P), 689 (P), 691 (P), 693 (P)

Gaume *scabra* var. *occidentalis* s.n. (GH)

Gentry, Howard Scott *heterophylla* 18435 (LL, US), *laevis* 18122 (LL, US), s.n. (US), *scabra* var. *sonorensis* 14439 (US)

Genz, Ken (Kenneth R.) *spinescens* var. *spinescens* 9130 (NY), 9169 (NY)

Germishuizen, G. *africana* ssp. *africana* 2164 (PRE), *africana* ssp. *australis* 484 (PRE), 612 (PRE)

Gerstner, J. *africana* ssp. *africana* 5527 (PRE)

Giardelli, Maria Luisa *integrifolia* 495 (SI)

Gierisch, R. K. (Ralph K.) *scabra* var. *scabra* 3324 (RM), *scabra* var. *glabrescens* 3766 (RM)

Gillespie, John W. *scabra* var. *occidentalis* 5581 (GH, NY, UC, US)

Gillett, J. B. *africana* ssp. *africana* 2547 (K)

Gillett, Mrs. A. B. *africana* ssp. *africana* M232 (K)

Gillies, L. *decemfida* s.n. (GH), *integrifolia* s.n. (GH)

Gilman, M. F. (M. French) *scabra* var. *sonorensis* 7968 (US)**,** *scabra* var. *occidentalis* 296 (UC)

Glen, H. F. *africana* ssp. *africana* 2518 (MO, PRE), *africana* ssp. *australis* 2493 (MO)

Goddard, David R. *scabra* var. *scabra* 813 (UC)

Gold, D. B. *helianthemoides* 21729 (NY)

Goldblatt, P. (Peter) Goldblatt *juncea* 3045 (MO, NBG, PRE), 8034 (MO, NBG, NY, PRE)

Goldman, E. A. *spinescens* var. *spinescens* 2547 (US)

Gonzalez, Antonio Gomez *coulteri* 1100 (MEXU)

Gonzalez, S. *laevis* 1076 (MO), 1440 (MEXU, NY, TEX)

Gonzalez, E. Javier *heterophylla* 32 (LL)

Goodall, N. *integrifolia* 284 (P)

Goodding, L. N. (Leslie N.) *scabra* var. *scabra* 4394 (RM), *scabra* var. *glabrescens* 720 (GH) s.n. (UC), *spinescens* var. *spinescens* 2340 (MO)

Goodman, G. J. *scabra* var. *scabra* 1302 (GH, MO, NY, RM, UC)

Goodspeed, T. H. *integrifolia* 23236 (GH, UC)

Goossins, A. P. *africana* ssp. *africana* 410 (PRE)

Gordon-Gray, K. D. *africana* ssp. *africana* 3999 (NU)

Gould, F. W. *heterophylla* 5715 (TEX)**,** 8091 (UC), *scabra* var. *glabrescens* 3863 (GH, NY, UC)

Graber, Jean *longiflora* 107 (TEX)

Gray, Asa *spinescens* var. *spinescens* 9 (P)

Gray, C. E. *africana* ssp. *australis* 4131 (PRE)

Green, D. M. *africana* ssp. *africana* 322 (NH)

Greene, Edward L. *scabra* var. *scabra* s.n. (GH)

Greenman, J. More, Jr. *scabra* var. *sonorensis* 4 (MO)

Greenwood, Frances *laevis* 6 (TEX)

Gregg *laevis* 527 (GH)

Gregg, J. *coulteri* 44 (GH), *heterophylla* 883 (MO), *scabra* var. *glabrescens* 527 (K)

Griffiths, David *scabra* var. *sonorensis* 2436 (NY), *scabra* var. *scabra* 4767 (US), 4882 (US), 5389 (US)

Grinnell, Joseph *spinescens* var. *spinescens* s.n. (UC)

Grosse, Herm. *integrifolia* 3729 (GH, NY)

Guaglianone, E. R. *integrifolia* 1795 (SI), 227 (NY, SI)

Guajardo, Francisca *heterophylla* 55 (LL)

Gutierrez, José *integrifolia* 28 (LIL), *integrifolia* 110 (TEX)

H. & W., *heterophylla* s.n. (UC)

Hafstrom, A. (Adolf) *africana* ssp. *africana* H902 (PRE)**,** 972 (A), 992 (A), H992 (PRE)

Hall, Carleton R. *heterophylla* 955 (US)

Hall, Elihu *heterophylla* 293 (MO, NY, US)

Hall, H. *juncea* 782 (NBG)

Hall, H. M. (H. Mears) *heterophylla* 1477 (TEX), *spinescens* var. *spinescens* 7096 (UC), *spinescens* var. *mohavensis* 6780 (UC)

Hammarlund, C. *integrifolia* 410 (NY)

Hammel, Barry *pulchella* 5998 (MO)

Hanekom, W. J. *africana* ssp. *australis* 1514 (PRE)

Hansen, O. J. *africana* ssp. *australis* 3464 (K, PRE)

Hansen, Bruce *heterophylla* 3868 (LL, MEXU), *intricata* 3774 (LL, US)

Hanson, H. C. (Herbert C.) *laevis* 791 (GH, US), s.n. (TEX)

Harbor, W. A. H. *africana* ssp. *australis* 17012 (PRE)

Hardy, D. S. *africana* ssp. *africana* 1243 (K), *juncea* 208 (PRE), 1123 (K, PRE)

Hargrove *scabra* var. *scabra* s.n. (MO)

Harmon, W. E. *heterophylla* 5598 (MO)

Harrington, H. D. *scabra* var. *scabra* 7307 (MO)

Harrison, G. J. *scabra* var. *sonorensis* 8916 (US)

Hartman, Ronald *scabra* var. *scabra* 79222 (RM)

Harvey, Priscilla *scabra* var. *sonorensis* s.n. (LP)

Hassler, E. *integrifolia* 11073 (MICH, MO, NY, P, SI, UC, US), *integrifolia* 1281 (NY, P), 6475 (GH, MICH, MO, NY, P, UC), 7493 (NY)

Havard, V. *scoparia* s.n. (US, US), *longiflora* s.n. (US)

Hawkes, J. G. *decemfida* 3153 (K), *integrifolia* 3307 (MO)

Headley, Frank B. *heterophylla* s.n. (US)

Heald *heterophylla* 900 (TEX), s.n. (TEX)

Heenderly, R. *africana* ssp. *australis* 11325 (PRE)

Heinonen, S. *integrifolia* 266 (CTES)

Heller, A. A. (A. Arthur) *heterophylla* 1390 (GH, MO, NY, P, UC), *longiflora* 1880 (GH, MO, NY, UC, US)**,** *scabra* var. *scabra* 3826 (GH, MO, NY, US)*spinescens* var. *spinescens* 8202 (GH, MO, NY, US)

Helmkamp, G. *scabra* var. *scabra* 234 (TEX)

Henrickson, James *scoparia* 12074 (TEX), 12185 (TEX), 15917 (TEX), 17635 (TEX), 18501b (TEX), 23108 (TEX), 23750a (TEX), 23956b (TEX), 23977 (TEX), 6165 (TEX), 6944 (TEX), *coulteri* 17561 (TEX), 17597 (TEX), 18641 (TEX), 19144 (TEX), 22433 (MEXU, TEX), *intricata* 23734 (TEX), *laevis* 5834d (TEX), 5949 (TEX), 6104 (TEX), 6783 (TEX), 6825a (TEX), 6928b (TEX), 7573 (TEX), B6310 (TEX), 7900 (TEX), 11284 (TEX), 11390 (TEX), 11549 (TEX), 12023 (TEX), 12364 (TEX), 13023a (TEX), 13678 (TEX), 14138 (TEX), 15084 (TEX), 15838 (TEX), 15886 (TEX), 16173 (TEX), 18477 (TEX), 18511 (TEX), 20384 (TEX), 23155 (TEX), *longiflora* 11532 (TEX), 11577 (TEX), 12951b (TEX), 15206 (TEX) 18464 (TEX) 19302 (TEX), 20538 (TEX), 6165a (TEX), *muellerae* 19093 (TEX), *scabra* var. *sonorensis* 10522 (LL, NY), *spinescens* var. *spinescens* 10426 (TEX), 11162 (LL), 9481 (NY, TEX)

Hernández Magaña, Rafael *coulteri* 4607 (MEXU, MO), 6456 (MEXU), *helianthemoides* 10349 (MEXU), 4339 (MEXU) 5714 (MEXU, MO), 6289 (MEXU, MO), 9741 (MEXU), 9907 (MEXU)

Hernández X., E. *laevis* N-1772 (MEXU)

Hernandez, L. *coulteri* 954 (MEXU)

Hernandez, A. *coulteri* 16m539 (TEX), *longiflora* 16m530 (TEX, TEX)

Herre, H. *juncea* 12080 (NBG), 12195 (NBG), 12200 (NBG), 18995 (NBG)

Herrick, C. L. *laevis* 708 (US), *scabra* var. *scabra* s.n. (NY)

Hess, W. *scabra* var. *scabra* 351 (UC)**,** 503 (NY)

Hevron, B. (or W.) *scabra* var. *scabra* 2143 (MEXU)

Hicken, C. M. *integrifolia* 26 (SI)

Higgins, L. (Larry C.) *heterophylla* 5589 (NY), *laevis* 6798 (NY), 6837 (NY), *longiflora* 17908 (NY), 5600 (NY), *scabra* var. *scabra* 7749 (NY), *scabra* var. *occidentalis* 7887 (NY), *scabra* var. *glabrescens* 18074 (UMO)

Hill, Steven R. Hill *heterophylla* 22446 (GH, NY), 4708 (NY), 5298 (NY)**,** *scabra* var. *scabra* 12133 (NY)

Hillary *africana* ssp. *africana* 480 (PRE)

Hinckley, L. C. *laevis* 1046 (NY), 1231 (NY), 1550 (NY, TEX), 1644 (US), 1974 (NY, TEX, US), 2316 (GH, LL, NY), 236 (NY), 3046 (NY), 3716 (NY), 3733 (NY), s.n. (GH, TEX), *longiflora* 1260 (NY), 1698 (GH, TEX), 2253 (NY), 2254 (GH, NY), 3969 (LL, NY), 4886 (US)

Hinton, G. B. Hinton *gypsophila* 25863 (TEX), *longiflora* 16550 (MEXU, US), *muellerae* 18820 (MEXU, MEXU, NY, TEX)

Hinton et al. *scoparia* 23539 (MEXU, TEX), *coulteri* 16518 (NY, US), 19679 (MEXU, TEX), 21959 (TEX), *coulteri* 18447 (MEXU, TEX), 23042 (TEX), 25357 (TEX), 25487 (TEX), 25823 (TEX, TEX), 25897 (TEX), 27198 (TEX), *gypsophila* 24474 (NY, TEX), 25643 (TEX), 25836 (TEX), 25863 (TEX), *henricksonii* 20240 (GH, TEX), 22066 (TEX), *laevis* 23533 (TEX), 23571 (MEXU, TEX), 24734 (TEX), *longiflora* 20770 (GH, TEX), 23851 (TEX), 25648 (MEXU, TEX), 25864 (TEX), 25870 (TEX), *henricksonii* var. *confusa* 21048 (TEX), *muellerae* 18220 (TEX), 25349 (MEXU, TEX), 25810 (TEX)

Hiriart, P. *coulteri* 332 (MEXU), *intricata* 712 (MEXU)

Hitchcock, Albert E. *scabra* var. *scabra* 104 (US)

Hitchcock, C. L. *longiflora* 4255 (RM, UC), 4275 (RM, UC), 6792 (UC), *scabra* var. *scabra* 4218 (RM, UC), *spinescens* var. *spinescens* 6155 (NY, UC), 12335 (A, MO), 22265 (MO), 23319 (MO)

Hodgson, Wendy *scabra* var. *glabrescens* 2837 (NY)

Holmgren, Noel *scabra* var. *scabra* 2033 (GH, NY, TEX), *spinescens* var. *spinescens* 8690 (NY), 9197 (NY)

Holub *africana* ssp. *australis* s.n. (PRE)

Hooker, L. H. *heterophylla* 6000 (US)

Hough, Walter *scabra* var. *scabra* 34 (GH, MO, US)

Howard, Winnie *scabra* var. *scabra* s.n. (MO)

Hoyt, Mrs. R. W. *scabra* var. *sonorensis* s.n. (NY)

Huerta B., Victor M. *mexicana* 1285 (MEXU), 1631 (MEXU)

Huidobro, A. M. R. *integrifolia* 3577 (MO), *integrifolia* 31112 (TEX), 3133 (UC)

Hunziker, A. T. *integrifolia* 586 (LIL), 14866 (MO)

Ibarrola, T. (Tito S.) *integrifolia* 1521 (LIL), 2539 (NY), *integrifolia* 2395 (NY), 2670 (UC), 2701 (A, NY), 3582 (LIL)

Illin, Nicolas *robusta* 102 (BA), 74 (SI, UC)

Innes, R. R. *laevis* 1191 (GH), *longiflora* 1257 (GH)

Insfrán, P. *integrifolia* 873 (CTES)

Irigoyen, J. *integrifolia* 186 (CTES)

Jacobsen, N. *africana* ssp. *africana* 2554 (PRE)

Jaeger, Edmund C. *spinescens* var. *spinescens* 66 (US)

Janse, J. T. *africana* ssp. *africana* 170 (SI)

Janszen, M. H. (or simply Janszen) *laevis* 77 (TEX), *longiflora* 67 (TEX)

Jeffers, L. F. *africana* ssp. *africana* 413 (PRE)

Jepson, W. L. *scabra* var. *glabrescens* 18169 (JEP), *spinescens* var. *spinescens* 15805 (JEPS), 19822 (JEPS), 20430 (JEP), 4120 (JEP), 5467 (JEP), *spinescens* var. *spinescens* var. *mohavensis* 5415 (GH, JEP, US), 6635 (A, GH, JEP, US, US)

Jermy, G. (Gust.) *heterophylla* 164 (GH), 262 (GH), 35 (NY), 447 (US), s.n. (MO, NY, US)

Jermy, Julius *heterophylla* 9 (US), 55 (US),

Jiménez, R. *laevis* 17 (MEXU)

Joaquín, N. *integrifolia* 11302 (CTES)

Job, M. M. *integrifolia* 521 (LP, NY)

Johnson, Frank W. *laevis* 3 (NY)

Johnson, J. C. (Joe C.) *coulteri* 16241m (TEX), *heterophylla* 651 (TEX)**,** 1241 (TEX), *longiflora* 303 (TEX)

Johnston, I. M. *scoparia* 7231 (GH), 8375 (GH), 8794 (GH), *coulteri* 7663 (GH, LP), *laevis* 119 (GH, LL, MEXU), 1433 (GH, LL), 7121 (GH, UC), 7176 (GH), 8059 (GH), 8334a (GH), *longiflora* 375 (GH, LL), 676 (GH, LL), 8373 (GH), 9083 (GH)

Johnston, M. C. (Marshall C.) *scoparia* 57 (GH, LL), 326 (GH, LL), 11847a (LL, MEXU), 11911 (MEXU), 12456 (TEX), *coulteri* 10259 (LL), *heterophylla* 243-1 (TEX), 243-2 (TEX), 243-3 (TEX), 3471 (TEX), 3536 (LL), 5080 (TEX), 7411 (TEX), 53243.1 (TEX), 53243.2 (TEX), 53243.3 (TEX), 541544 (TEX), 542302 (TEX), *laevis* 12872 (TEX), *henricksonii* var. *henricksonii*10501 (LL, MEXU, MO, NY), *laevis* 10903 (LL, MEXU), 11281 (LL, MEXU), 11332a (LL), 11911 (LL, TEX), *longiflora* 4054 (TEX), 11846a (LL, MEXU)

Johnston, Ted *laevis* 46101 (TEX)

Jones, Marcus E. *heterophylla* 26718 (UC), 29400 (MO), *laevis* 4167 (NY, RM, US), *scabra* var. *sonorensis* 26448 (MO), 4330 (A), s.n. (MO, US), *scabra* var. *glabrescens* 3924 (A, NY, US), *spinescens* var. *spinescens* s.n. (NY)

Jones, W. W. (Wyatt W.) *scabra* var. *scabra* 87 (GH)**,** s.n. (MO, UC, UC), *scabra* var. *glabrescens* s.n. (UC, UC, UC)

Joor, J. F. *heterophylla* s.n. (MO)

Jorgensen, Pedro *integrifolia* 4045 (A, NY, US), *integrifolia* 2643 (A, GH, LIL), 4045 (LP, MO)

Jorgensen, P. *integrifolia* s.n. (CTES)

Junod, Henri A. *africana* ssp. *africana* 1737 (G)

Jürgens, N. *juncea* 22466 (PRE), 22525 (PRE)

Kass, R. *spinescens* var. *spinescens* 1578 (NY)

Kearney, T. H. *scabra* var. *glabrescens* 12597 (US)

Keil, David Keil *scabra* var. *occidentalis* 4561 (NY)

Keller, H. *integrifolia* 394-B (CTES)

Kennedy, P. B. *spinescens* var. *spinescens* 134 (NY, UC, US)

Kenoyer, L. A. *coulteri* 1079 (GH), 2396 (GH)**,** *coulteri* 2866 (GH)

Kidder, Nathaniel Thayer *heterophylla* s.n. (GH)

Kiesling, R. *decemfida* 4086 (MERL, K), 8860 (NY), *integrifolia* 3705 (SI), 5908 (SI)

Kirkwood, J. E. *coulteri* 20 (GH)

Krapovickas, A. *integrifolia* 14952 (CTES), 18143 (CTES), 18842 (CTES), 20760 (CTES), 21140 (CTES), 25004 (CTES), 41010 (A, CTES), *integrifolia* 11767 (CTES, UC, US), 27412 (CTES), 27655 (CTES), *integrifolia* 22583 (MO) *integrifolia* 2855 (MO), 4771 (CTES), 6650 (LIL, SI), 17329 (CTES), 17386 (CTES), 35728 (CTES)

Kreibohm, Estela D. M. *robusta* 267 (SI, US)

Kroon, N. V. *africana* ssp. *africana* 11624 (PRE), 12013 (PRE)

Kuntze, Otto *africana* ssp. *africana* s.n. (NY), *integrifolia* s.n. (NY, NY)

Kunze, R. E. *scabra* var. *occidentalis* s.n. (NY)

Kurtz, F. *integrifolia* 8456 (LP, NY)

Landbeck *linoides* 1535 (SGO)

Landrum, L. R. *scabra* var. *occidentalis* 6000 (NY)

Lane, M. (Meredith) *intricata* 2916 (TEX)

Langford, A. N. *laevis* s.n. (LL)

Larke, Julia *heterophylla* 8 (NY, TEX)

Lavin, M. *heterophylla* 4639 (TEX)

Lavranos, J. *africana* ssp. *africana* 11062 (MO)

le Roux, A. *juncea* 2839 (NBG, PRE)

Le Roy, P. V. *heterophylla* s.n. (NY)

Leal, A. Ruiz *decemfida* 475 (NY), 1242 (LIL), 2658 (LIL), 14508 (HRL), 4697 (LIL), 5080 (HRL), 5488 (LIL), 5521 (HRL), 7301 (LIL), 8761 (LIL), 969 (HRL), 9997 (LIL), *integrifolia* 25509 (MERL), 25522 (MERL), 26281 (MERL), 8777 (HRL), *integrifolia* 17236 (MERL), 19965 (MERL), 9040 (HRL), *robusta* 5601 (MERL)

Leal, Ruben Antonio Leal *heterophylla* 35 (LL)

LeDoux, Douglas *scabra* var. *scabra* 1861 (MO, NY)

Lee, A. *laevis* 76 (TEX)

Leeman, A. *africana* ssp. *africana* s.n. (PRE)

Leenderlz, R. *africana* ssp. *africana* 5555 (PRE)

Legaspi, J. *integrifolia* s.n. (CTES)

Legname, V. *integrifolia* 153 (LIL), 461 (LIL), 7575 (MO)

Leguiza *integrifolia* 34 (CTES)

Lehr, J. Harry *scabra* var. *occidentalis* 1185 (NY)

Leiberg, J. B. *scabra* var. *scabra* 5555 (US)

Leistner, O. A. *africana* ssp. *africana* 81 (PRE)

Lemmon, J. G. *scabra* var. *sonorensis* 164 (GH)**,** 164 (UC)

LeSueur, Harde *laevis* 121 (GH, MEXU, US), MEX 121 (TEX), MEX121 (TEX), s.n. (MO, UC)

Lewton, F. L. *heterophylla* 176 (US), *longiflora* s.n. (LL)

Leyher *africana* ssp. *africana* 1132 (SAM)

Lhome, G. *africana* ssp. *africana* s.n. (SAM)

Lieb, C. S. *heterophylla* 448 (NY)

Liebenberg, S. *africana* ssp. *australis* 106 (PRE), 15 (PRE)

Lillo, M. *integrifolia* 6077 (NY), 6078 (GH), 7210 (NY), 7265 (NY, US), 8083 (LIL)

Lindheimer, F. *heterophylla* 383a (GH), 454 (GH, NY, NY, UC, US), 455 (GH, MO, UC), 463 (US), s.n. (GH), *longiflora* 652 (US), 652a (MO), 983 (GH, MO, US), s.n. (GH, NY)

Livingston, R. B. *scabra* var. *scabra* 481 (TEX)

Llaguno, Fernando G. *heterophylla* 70 (LL)

Lloyd, Francis E. *coulteri* 140 (US)

Lloyd, R. M. (Robert M.) *spinescens* var. *spinescens* 2743 (NY, UC)

Lopez, Augustin *laevis* 26 (GH)

Lorentz, (P.S.) *integrifolia* s.n. (K, P)

Lossen, W. *integrifolia* 305 (GH)

Louw, W. J. *africana* ssp. *africana* 1977 (PRE), 355 (PRE), 72 (PRE)

Lucas, Willya D. *heterophylla* 14217 (TEX)

Luckow, Melissa *coulteri* 2698 (TEX), *coulteri* 2664 (TEX)

Luna, F. E. *integrifolia* 1495 (LIL), 18 (LIL)

Lundell, C. L. *coulteri* 5152 (MEXU, TEX), 5358 (MICH), 5751 (MICH, MICH, US), *heterophylla* 13551 (LL), 13596 (LL), *laevis* 13178 (LL, NY), *longiflora* 14198 (LL, NY, UC, US)

Lundell, C. L. *heterophylla* 10762 (GH, LL, MEXU, NY, UC, US), 9971 (LL, UC, US), *laevis* 14294 (LL), *longiflora* 14209 (LL)

Lyonnet, E. *tehuacana* 2254 (US)

MacDougal, D. T. *scabra* var. *scabra* 218 (GH, NY, UC, US)

MacGregor, R. L. *coulteri* 550 (LL, US)

Maddux, T. *scabra* 524 (UNM)

Maguire, Bassett *scabra* var. *sonorensis* 10740 (GH, NY), 11703 (NY), *scabra* var. *scabra* 11965 (NY), 12198 (RM), 18885 (RM), *spinescens* var. *spinescens* 25165 (GH, MO, NY, UC, US)**,** *spinescens* var. *spinescens* 4905 (GH, UC), 4907 (GH, MO), 25266 (GH, NY, UC, US)

Mahler, William F. *heterophylla* 3294 (TEX)

Makepeace, J. *scabra* s.n. (UNM)

Makgakga, M. C. *africana* ssp. *africana* 35 (PRE)

Malcara, P. *heterophylla* 37 (LL)

Manning, Wayne E. *coulteri* 531245b (GH)

Manthey, G. T. *scabra* 1238 (UNM, UNM), 693 (UNM)

Marcks, Brian *laevis* 1312 (TEX)

Marloth, R. *juncea* 12282 (NBG), 12282b (A, NBG, PRE), 8347 (A, PRE)

Marroquín, J. *longiflora* 2231 (MEXU)

Marrs-Smith, G. E. *scabra* var. *glabrescens* BLM-49 (NY)

Marsh, E. G. (Ernest G.) *heterophylla* 1117 (GH, TEX), 1777 (GH, TEX), *laevis* 109 (GH, TEX, UC), 313 (UC), 1812 (GH), *longiflora* 1362 (GH, TEX)

Martinez, Mahinda *intricata* 291 (MEXU, TEX)

Martínez M., I. *helianthemoides* s.n. (MEXU)

Matthews, T. W. *juncea* s.n. (NY, PRE)

Matuda, E. *coulteri* 21172 (MO), *helianthemoides* 21081 (MEXU)

Mauve *juncea* 23 (MO, PRE)

May, Joe *heterophylla* 22 (TEX)

Mayfield, M. H. *laevis* 1090 (TEX), *heterophylla* 1760 (TEX)

McCart, William L. *heterophylla* 8 (LL)

McCullough, A. M. *heterophylla* 48 (NY)

McDonald, D. *juncea* 727 (NBG, PRE)

McDougall, W. B. *laevis* 2024 (US)

McKelvey, Susan Delano *heterophylla* 1705 (GH, US), *scabra* var. *scabra* 4585 (A), *spinescens* var. *spinescens* 2733 (A)

McMinn, H. E. *scabra* var. *glabrescens* 4008 (UC)

McNelty, John C. *scabra* 8 (RM)

McVaugh, Rogers *coulteri* 23778 (MICH), *heterophylla* 7744 (GH, TEX), *laevis* 7790 (GH, TEX)

Mearns, Edgar A. *heterophylla* 1324 (US), 1340 (US), *scabra* var. *sonorensis* 1868 (NY, US), *scabra* var. *scabra* 252 (US)

Mears, J. A. *scabra* var. *scabra* 1822 (TEX)

Medina, Miguel *helianthemoides* 1356 (MEXU)

Medrano, F. G. (Francisco González) *coulteri* 8077 (MEXU)**,** 9048 (MEXU) FGM14615 (MEXU), *intricata* 4394 (MEXU), 6945 (MEXU), 9021 (MEXU, MO)

Meebold *scabra* var. *sonorensis* s.n. (NY)

Meeuse, A. D. J. *africana* ssp. *africana* 9573 (K, PRE), 9733 (K, PRE)

Melis, L. Orlando *decemfida* 19Ar892 (NY)

Merello, Mary *scabra* var. *sonorensis* 207 (MO)

Merwe, F. v. d. *africana* ssp. *africana* 2272 (PRE)

Messer, Ellen *mexicana* 127a (MICH)

Metz, Mary C. (Mary Clare) *heterophylla* 65 (TEX)**,** 121 (NY), s.n. (UC)

Meyer, G. *juncea* 9092 (NBG)

Meyer, T. (Teodoro,Theodor) *decemfida* 5080 (MERL), 5524 (MERL), 9309 (MERL), 22.805 (LL), *integrifolia* 10014 (LIL), 16403 (LIL), 3063 (LIL), 5515 (LIL), 5897 (LIL), 8591 (K), 8609 (LIL), *integrifolia* 12745 (UC), 12890 (LIL), 12987 (GH), 13181 (CTES), 13476 (LIL), 13519 (LIL), 13563 (CTES), 17983 (LIL), *pulchella* 34152 (GH)

Middleton *robusta* s.n. (K)

Millán, A. R. *integrifolia* 343 (BA)

Miller, James S. *scoparia* 5109 (MO)

Miranda, M. F. *scabra* var. *scabra* 5736 (UC)

Mogg, A. O. D. *africana* ssp. *africana* 34403 (K), 8024 (PRE), *africana* ssp. *australis* 37262 (PRE)

Monetti, L. (Leon) *integrifolia* 145 (LIL), 1266 (GH, NY), s.n. (MO, NY)

Montenegro, M. A. *integrifolia* 193 (LIL), 231 (LIL), 280 (LIL), 370 (LIL)

Montes, J. E. *integrifolia* 88 (LIL), 357 (NY, SI), 772 (NY), 7240 (SI), 9457 (LIL), 15222 (SI), 15569 (LIL), *integrifolia* 1242 (GH)

Moore, Micheal J. *scabra* var. *occidentalis* 231 (TEX)

Moore, J. A. *scoparia* 3257 (A, GH, MO, NY, UC, US), *heterophylla* 3006 (MO), *laevis* 3256 (GH, MO, UC), *longiflora* 3242 (A, GH, MO, NY, UC), 3245 (US), 3598 (A, GH, MO, NY, UC, US)

Moran, Reid *coulteri* 13389 (UC, US), *scabra* var. *glabrescens* 11185 (UC, US), 13136 (LL, UC), 13656 (UC), 15556 (UC), 17646 (LL, RSA, UC), 23600 (MEXU), 8096 (UC, US), 9734 (GH, UC, US), *spinescens* var. *spinescens* 15386 (LL, UC, US)

Morefield, James D. *scabra* var. *scabra* 2559 (NY), *spinescens* var. *spinescens* 3439 (GH, MO, NY, TEX, UC)**,** *spinescens* var. *spinescens* 4399 (MO, NY, TEX, UC)

Morris, C. *heterophylla* s.n. (NY)

Morrone, O. *integrifolia* 570 (SI)

Mueller, or Muller, C. H. *laevis* 3001 (GH, LL, MO, UC), 8424 (LL, NY), s.n. (TEX), *longiflora* 3041 (GH, LL, UC), 8112 (GH, NY, TEX, US), *muellerae* 463 (TEX, US)

Muenscher, W. C. *spinescens* var. *spinescens* 14842 (A)

Mulford, A. Isabel *laevis* 1073 (US), 251 (MO, NY), *scabra* var. *scabra* 807 (NY, US)

Múlgara *integrifolia* 328 (US)

Muller, D. B. *africana* ssp. *africana* 400 (PRE)

Munsen *longiflora* s.n. (US)

Munz, P. A. (Philip A.) *scabra* var. *glabrescens* 4264 (NY, RM, US), 17450 (NY), *spinescens* var. *spinescens* 11686 (NY), 12479 (MO, UC), 13747 (UC), 14904 (GH, MO), 17408 (NY)

N. & N. *longiflora* s.n. (TEX, UC)

Nealley, G. C. *heterophylla* 262 (US), 378a (US), *laevis* 159a (US), 471 (US), *longiflora* 471a (US), 683/684 (US), s.n. (US)

Nee, M. (Michael) *heterophylla* 24438 (NY), *integrifolia* 47632 (NY)**,** 50027 (NY)

Neel, Maile *scabra* var. *glabrescens* s.n. (TEX)

Neese, E. *scabra* var. *scabra* 15942 (NY, RM)**,** *spinescens* var. *mohavensis* 12765 (NY)

Neff, J. L. *scabra* var. *scabra* 01-08-15-01 (TEX)

Neffa, V. Solis *integrifolia* 259 (CTES, GH, NY)

Negrete, Señorita *decemfida* s.n. (SI)

Nelson, B. E. *scabra* var. *scabra* 61606 (RM)

Nelson, E. W. *coulteri* 4535 (US), *heterophylla* 6602 (GH, US), *laevis* 6362 (GH)

Nelson, R. *scabra* 10692 (UMO)

Nelson, Aven *scabra* var. *sonorensis* 1549 (GH, MO, NY, RM, UC), 1618 (NY, RM), *scabra* var. *scabra* 1549 (RM), *spinescens* var. *spinescens* 3396 (UC), 3437 (UC)

Nesom, Guy *coulteri* 6611 (TEX)**,** *heterophylla* 7535 (TEX), *laevis* 5266 (TEX), *longiflora* 7386 (TEX), 7641 (TEX)

Ngwenya, A. M. *africana* ssp. *africana* 1100 (NH, PRE)

Nicholson, H. B. *africana* ssp. *africana* 961 (PRE)

Nicolas *helianthemoides* var. *helianthemoides* s.n. (G)

Nicora, E. G. *decemfida* 4329 (K, SI), *integrifolia* 3277 (LIL), *integrifolia* 1570 (SI), 1663 (SI), 3247 (SI), s.n. (SI)

Niederlein, G. *integrifolia* 1024 (BA)

Northington, D. K. *laevis* 642 (TEX)

Novara, Lazaro *integrifolia* 5615 (MCNS), 7244 (MCNS), 8134 (MCNS)**,** 9353 (MCNS), 9569 (MCNS)**,** 10290 (MCNS)

O'Donell, C. A. *decemfida* 1041 (A), 1107 (A, UC), *integrifolia* 1609 (LIL), 1642 (A, LIL, US), 1702 (LIL), 1887 (LIL), *integrifolia* 337 (A), 385 (A), 649 (LIL), 2638

(NY), 4334 (GH, TEX, UC, US), 4368 (LIL), 4936 (LIL), *robusta* 3281 (LIL), 3459 (K, LIL), 3549 (UMO)

Oliver, S. S. *africana* ssp. *africana* s.n. (SAM)

Oliver *juncea* 138 (MO, NBG, PRE, US)

Orcutt, C. R. *scoparia* 1318 (US), *laevis* 3131 (MO), *scabra* var. *glabrescens* 926 (GH, GH, UC), 949 (GH), s.n. (NY, UC, UC, US)

Orozco L., C. *helianthemoides* 10291 (MEXU)

Orozco H., Javier *helianthemoides* 9917 (MEXU)

Orzell, Steve L. *heterophylla* 6056 (TEX, TEX)

Osten, C. (Corn.) *integrifolia* 6625b (GH, US)

Osterhout, George E. *scabra* var. *scabra* 6840 (NY, RM), 6909 (MO, RM)

Ottley, Alice M. *africana* ssp. *africana* 2227 (NY)

Ownbey, Gerald B. *laevis* 1840 (UC, US)

P. B. *africana* ssp. *africana* 22 (NU)

Paci *decemfida* 475 (LIL)

Painter, Joseph T. *heterophylla* 14217 (UC)

Palacios *integrifolia* 1901 (LIL)

Palmer, E. (E. J., Edw., Edward) *scoparia* 795 (NY), 34232 (A), *coulteri* 164 (GH, MO, NY, UC, US), *laevis* 309 (GH, MO, NY, UC, US), *longifolia* 429 (A, UC, US), *gypsophila* X (GH), *heterophylla* 85 (GH, MO, UC, US), 256 (US), 790 (GH, NY, US), 791 (GH, MO, NY, US), 10118 (MO), 11214 (TEX, UC), 13726 (MO, US), 33608 (NY), *henricksonii* var. *henricksonii*34 (GH, MEXU, MO, NY, UC, US), *laevis* 793 (GH), 10937 (MO), 31083 (A, MO), 34191 (MO, NY), *longiflora* 118 (GH, MO, UC, US), 792 (GH, US), 794 (GH, US), 10883 (A, MO, US), 10937 (A, US), 12976 (A, MO, UC, US), 12992 (A, UC), 32115 (A), *scabra* var. *sonorensis* 206 (MO), *scabra* var. *scabra* 65 (GH, MO, NY, US), 69 (US), 795 (GH, MO, US)

Panero, Jose Panero *helianthemoides* 3441 (TEX), *pulchella* 8503 (TEX)

Parada, E. *integrifolia* 164 (MCNS)

Parish, S. B. *scabra* var. *sonorensis* s.n. (A), *scabra* var. *glabrescens* 435 (MO, NY), 10260 (JEP), 10268 (UC), *spinescens* var. *spinescens* 10361 (UC), s.n. (UC), *spinescens* var. *mohavensis* 9795 (UC)

Parodi, L. R. *integrifolia* 6236 (GH)

Parry, C. C. *coulteri* 571 (US), *coulteri* 300-1/2 (GH), *helianthemoides* 570 (F, GH, MO, NY, P), 571 (F, GH, MO, NY), *heterophylla* 1101 (NY), *laevis* s.n. (NY), *longiflora* s.n. (NY)

Pase, C. P. *scabra* var. *scabra* 439 (RM)

Pastore, F. *integrifolia* 43 (SI), *integrifolia* 2063 (SI)

Patterson, T. F. *longiflora* 6595 (TEX)

Payson, Lois B. *longiflora* 56 (RM)

Pearson, H. H. W. *juncea* 5639 (K)

Pederson, Troels Myndel *integrifolia* 15673 (CTES, NY), 16188 (CTES), *integrifolia* 4694 (G, NY, P, UC, US), 6222 (A, US), 8111 (A), 956 (US), *integrifolia* 9917 (K)

Pedrotti *integrifolia* 48 (LPB)

Peebles, R. H. *scabra* var. *sonorensis* 4725 (US), *scabra* var. *glabrescens* 4261 (US), 7945 (US)

Peeters, C. *africana* ssp. *australis* 261 (MO, PRE)

Pegler, A. (Alice) *africana* ssp. *africana* 950 (SAM), *africana* ssp. *australis* 950 (G, K, P, PRE, SAM)

Pennell, Francis *intricata* 18026 (GH, NY, US), *laevis* 18704 (GH, NY, US)

Pérez, E. *mexicana* 4295 (TEX)

Pertosi, Laura A. *integrifolia* 88 (CTES)

Peterson, Keith *heterophylla* 136 (TEX)

Peterson, Paul *spinescens* var. *spinescens* ()

Phalatse, S. D. *africana* ssp. *africana* 47 (PRE)

Philips, J. *africana* ssp. *australis* 53 (PRE)

Pichi Sermolli, R. E. G. *robusta* 7342 (SI)

Pierotti, S. A. *integrifolia* 26 (LIL), 5129 (LIL), s.n. (LIL)

Pillans, N. S. *juncea* 5108 (K)

Pinkava *scabra* var. *occidentalis* 11698 (UNM)

Pinzl, Ann *spinescens* var. *spinescens* 9194 (NY), 9914 (NY), 13252 (NY)

Plank, E. N. *heterophylla* s.n. (NY, NY)

Plowes, D. C. H. *africana* ssp. *africana* 7004 (PRE)

Plowman, T. *scabra* s.n. (UNM)

Pole-Evans, I. B. *africana* ssp. *africana* 452 (PRE)

Port, F. W. *africana* ssp. *africana* 228 (A, A, PRE)

Pott, R. *africana* ssp. *africana* 5593 (G)

Powell, A. M. *laevis* 1971 (TEX), 2328 (TEX), 3331 (TEX)**,** *longiflora* 4064 (MO), 4163 (TEX)

Prather, Alan *longiflora* 1464 (TEX)

Prigge, Barry *spinescens* var. *spinescens* 641 (NY), 798 (TEX), 1360 (TEX)

Pringle, C. G. *helianthemoides* 6918 (MO, P, UC, US), *heterophylla* 13456 (US), 2408 (GH, MEXU, MO, NY, UC, US), *henricksonii* var. *henricksonii*s.n. (MEXU), *laevis* 549 (GH), *longiflora* 539 (GH, US), *scabra* var. *sonorensis* 15602 (MO), s.n. (GH, NY, US, US)

Prosser, L. N. *africana* ssp. *africana* 831 (PRE)

Purpus, C. A. *scoparia* 4497 (MO, UC, US), s.n. (UC), *coulteri* 1447 (GH, MO, NY, UC), 5020 (MEXU, UC), *coulteri* 1447 (GH), *helianthemoides* var. *parviflora* 434 (UC), 437 (MO, UC, US), *intricata* 1318 (UC), 5016 (G, NY, UC, US), 5044 (UC), *longiflora* 5004 (GH, UC), 5022 (MO, US), *scabra* var. *scabra* 6228 (NY, UC, US), 8057 (MO, UC, US), *scabra* var. *occidentalis* s.n. (UC), *spinescens* var. *spinescens* 5903 (NY, UC), *tehuacana* 1319 (G, MO, NY, P, UC), 3392 (GH, MO, NY, UC, US)

Quarín, C. *integrifolia* 3228 (CTES)

Quintero, L. González *coulteri* 3082 (MICH), 3203 (MICH), *helianthemoides* 3572 (MICH)

Ragonese, A. *integrifolia* 7437 (CTES)

Ragonese-Picinini *integrifolia* 6139 (LIL)

Ramaley, Francis *scabra* var. *scabra* 9777 (RM)

Rambo *integrifolia* 10088 (LIL), 25816 (LIL), 26305 (LIL)

Rdrg.-Mendez *decemfida* s.n. (MERL)

Rebman, Jon P. *spinescens* var. *spinescens* 2726 (TEX)

Reddy, R. A. *africana* ssp. *africana* 986 (PRE)

Reed, H. R. *longiflora* s.n. (A)

Reed, Howard S. *spinescens* var. *spinescens* 832 (P)

Reeves, T. *scabra* var. *sonorensis* 6673 (NY)**,** *spinescens* var. *spinescens* 12026 (NY, US)

Rehder, Alfred *scabra* var. *sonorensis* 228 (GH)

Rehn, J. A. G. *laevis* s.n. (A, RM)

Reid, C. *africana* ssp. *africana* 1970 (PRE)

Reif, Brian *scabra* var. *scabra* 9622 (RM), 9684 (RM)

Reina G., A. L. *yecorana* 97-1188 (, NY), 97-752 (TEX)

Repton, J. E. Repton *africana* ssp. *africana* 2765 (PRE)

Retief, E. *africana* ssp. *africana* 1813 (PRE)

Reveal, James L. (or Jack L. or J. L.) *scoparia* 3314 (US), 3315 (MO), *longiflora* 2582 (US), *spinescens* var. *spinescens* 98 (NY), 1669 (NY)

Reverchon, J. *heterophylla* 1328 (MO, NY, UC, US), *longiflora* 1556 (MO, US), s.n. (MO)

Reynos, Judith E. N. *helianthemoides* 103 (MEXU)

Ricketson, Jon *scabra* var. *glabrescens* 4572 (MO)

Riddel *heterophylla* s.n. (NY)

Rios, A. (Alonso) *heterophylla* 93 (LL), 96 (LL)

Ripley, H. D. *heterophylla* 4139 (NY)

Riskind, D. H. *heterophylla* 2065 (TEX)**,** *longiflora* 2291 (TEX)

Rodrigo, A. P. *decemfida* 2988 (LP), *integrifolia* 820 (LP, NY), *integrifolia* 223 (LP), 334 (LP, NY)

Rodriguez, Andres *scoparia* s.n. (TEX)

Rogers, C. M. *heterophylla* 6644 (TEX)

Rogers, F. A. *africana* ssp. *africana* 22393 (NH), *africana* var. *australis* 6225 (K, PRE), 6900 (G, K, NH)

Rogers, C. M. *heterophylla* 6859 (TEX)

Roig, F. *decemfida* 2293 (MERL), 3730 (MERL), s.n. (MERL)**,** *integrifolia* 8645 (MERL)

Rojas, T. *integrifolia* 6292 (MO), *integrifolia* 13246 (LIL), *integrifolia* 9430 (MO)

Rollins, Reed C. *henricksonii* var. *henricksonii*7467 (GH, TEX), *laevis* 74156 (GH, MEXU, TEX), 7464 (GH, MEXU, TEX)

Romanczuk, C. *integrifolia* 32 (SI)

Romero-Rojas *helianthemoides* 353 (MEXU)

Roos, John C. *spinescens* var. *spinescens* 6369 (GH)

Rosario *integrifolia* 4191 (SI)

Rose, J. N. *coulteri* 8311 (US), 9007 (NY, US), *helianthemoides* 8712 (US), *scabra* var. *sonorensis* 13788 (US), *scabra* var. *scabra* 17653 (NY, US), *tehuacana* 5931 (US)

Rose-Innes, Reginald *laevis* 1191 (TEX), *longiflora* 1257 (TEX)

Rosengurtt, Bernardo *integrifolia* B1563 (US), B-2517 (NY)

Ross, Richard *laevis* 52 (TEX)

Rossi *integrifolia* 947 (LIL)

Rothrock, J. T. *scabra* var. *sonorensis* 561 (GH, US)

Rowntree, Lester *spinescens* var. *spinescens* s.n. (A)

Ruiz, Sandra Aguilar*longiflora* 163 (TEX)

Ruiz de Huidobro, M. *integrifolia* 140 (LIL), 258 (UC), 289 (LIL), 3133 (NY), 410 (NY, UC), s.n. (A)

Runyon, R. (Robert) *heterophylla* 548 (GH, TEX, US), 3136 (TEX), 3137 (TEX), 5116 (TEX), 5117 (TEX), 5993 (TEX), 6061 (GH, TEX)

Rusby, H. H. (Henry H.) *scabra* var. *scabra* s.n. (A, NY)**,** 255 (MO, NY, UC, US), 718 (MO, UC), *scabra* var. *glabrescens* 5292 (US), 718 (NY, UC)

Rutisell *laevis* s.n. (NY)

Rzedowski, J. *coulteri* 25565 (MEXU), 28225 (MICH, TEX), 41653 (TEX), 43474 (TEX), 48714 (TEX), 49621 (TEX), 52588 (MEXU), *coulteri* 4223 (LL, MICH, US), 43498 (TEX), 47054 (TEX), 50810 (TEX), *helianthemoides* 18316 (MEXU, MICH, TEX, US, US), 22204 (MICH), 28225 (UMO), 50957 (TEX), *intricata* 46440 (TEX), *jaliscana* 17503 (MICH), *mexicana* 10787 (MICH, TEX), 53625 (TEX)

Saenz, Evangelina *heterophylla* 70 (TEX)

SAGP/SAAB *africana* ssp. *africana* 1/87 (PRE), 2/59 (PRE), 3/66 (PRE), 4/77 (PRE)

Saint-Hilaire, Auguste de *integrifolia* 2410 (P), 2588 (P)

Salinas T., Antonio *coulteri* F-3778 (TEX), *tehuacana* 5487 (MEXU), 6957 (MO)

Sanchez, Anita *heterophylla* 103 (TEX, TEX)

Sánchez V., Isidoro *helianthemoides* 2161 (MEXU, MO)

Sanders, A. C. *laevis* 4147 (TEX)**,** *scabra* var. *occidentalis* 3493 (MEXU)

Sandoval, A. *laevis* 110 (UNM), 168 (UNM), 306 (UNM)

Sanzín, Renato *decemfida* 16 (SI), 195 (SI), 29 (SI)

Scala, A. C. *integrifolia* 56 (SI), s.n. (LP)

Scala, I. C. *integrifolia* s.n. (NY)

Schaffner, J. G. *coulteri* 67 (GH, MEXU, NY), *helianthemoides* 503 (NY, NY), 68 (GH, MEXU), *mexicana* 506 (MICH, MO, NY, US), s.n. (NY)

Scheepers, J. C. *africana* ssp. *africana* 1715 (K)

Schery, R. W. *scoparia* 47 (MO)

Schickendanz *integrifolia* s.n. (LIL)

Schinini, A. *integrifolia* 3902 (CTES), *integrifolia* 7561 (CTES)**,** *integrifolia* 29211 (CTES)

Schlechter, R. *africana* ssp. *africana* 3369 (G)

Schlieben, H. J. *africana* ssp. *africana* 9192 (PRE)

Schnooberger, Irma *helianthemoides* 7859 (MICH)

School *heterophylla* 6000 (LL)

Schramm, D. R. *spinescens* var. *spinescens* ()

Schreiter, R. *decemfida* 6247 (LIL), *integrifolia* 1866 (TEX), 4024 (LIL), 7766 (GH, NY), 56530 (NY), 68614 (UC), s.n. (A)

Schrire, B. *africana* ssp. *africana* 1156 (NH)

Schroeder, Albert H. *laevis* 126 (GH)

Schultz, Ellen D. *laevis* 221 (NY)

Schulz, A. G. *integrifolia* (), 10942 (CTES), 1867 (CTES), 214 (SI), 8382 (CTES), 860 (CTES, NY), *integrifolia* 11267 (CTES), 16371 (CTES), 18093 (CTES), 6553 (CTES), 8934 (CTES)

Schulz, C. L. *integrifolia* 806 (NY), 977 (LIL)

Schwartz, G. *integrifolia* 5187 (LIL)

Schwartz *integrifolia* 2212 (LIL)

Schwarz, G. J. Schwarz *integrifolia* 3526 (GH, UC)

Schwarz, J. G. Schwarz *integrifolia* 784 (NY, UC)

Schwarz, J. *integrifolia* 5458 (GH), *integrifolia* 2060 (LIL), 5191 (LIL), 5701 (LIL)

Schwindt, Elena Schwindt *integrifolia* 1060 (LIL), 2248 (LIL), 3120 (LIL), 3313 (LIL), 4045 (LIL), 4414 (LIL)

Sciavone, Maria *integrifolia* 11749 (CTES)

Scudday, James *heterophylla* s.n. (LL, NY), *longiflora* 512 (UC)

Scully, W. *juncea* s.n. (SAM)

Seijo, G. *integrifolia* 1402 (CTES, GH)

Selander, R. B. *laevis* 12 (TEX)

Sellow *integrifolia* s.n. (G, G-DC, UC, K)

Semper, J. *decemfida* 101398 (NY)

Semple *laevis* 359 (MO, US), 380 (MO, US), *longiflora* 383 (MO)

Serra, Lidia *decemfida* 82 (LP)

Sesmero, E. *integrifolia* 265 (LIL)

Sharsmith, C. W. *spinescens* var. *spinescens* 6128 (SJS), 7554 (SJS)

Shearing, D. *juncea* 132 (K, PRE), 235 (PRE), A160 (NBG, PRE)

Shepherd, Elizabeth *africana* ssp. *africana* 60 (NH)

Shiffler, W. J. *scabra* s.n. (UNM)

Shiller, Ivan *heterophylla* 142 (US), 275 (US)

Shirley, M. E. *africana* ssp. *africana* s.n. (NU)

Shockley, W. H. *spinescens* var. *spinescens* 105 (JEPS), 106 (UC), 17 (UC), s.n. (GH)

Shreve, Forrest *coulteri* 8735 (MICH, US), 9364 (GH, MICH, UC), 9394 (GH, MICH, UC), *heterophylla* 8378 (GH, NY), *laevis* 8740 (US), 8782 (US), 9134 (GH), *scabra* var. *sonorensis* 4988 (UC)

Shute, Harry *heterophylla* 51-1713 (TEX)

Sigle, M. *integrifolia* 172 (TEX)

Sikes, Sam *laevis* 627 (LL, NY), 679 (LL, NY), *longiflora* 575 (LL)

Silva, Ruben Sánchez *coulteri* 29 (MEXU)

Simpson, B. B. *coulteri* 91-VII-17-2 (TEX), *integrifolia* 13-XII-04-2 (TEX), *pulchella* 1-II-00-7 (TEX)

Sinclair, J. F. *heterophylla* M-22 (TEX)

Slater, Mrs. H. D. *laevis* s.n. (US)

Sleumer, H. *decemfida* 347 (LIL)

Small, John K. *heterophylla* 11856 (NY, NY)

Smart *scabra* var. *glabrescens* 213 (GH)

Smith, C. E., Jr. *tehuacana* 4123 (G, GH, MEXU, NY, TEX)

Smuts, J. C. *africana* ssp. *africana* 397 (PRE)**,** 3371 (PRE)

Snow, Neil *coulteri* 6708 (MEXU)

Solbrig, O. T. *scabra* var. *sonorensis* 4367 (GH)

Solomon, J. C. *heterophylla* 2736 (MO)

Sopaga, José *integrifolia* 18 (LIL)

Soriam *robusta* 2770 (SI)

Sparre *integrifolia* 565 (LIL)

Speedy, J. G. *africana* ssp. *africana* 231 (PRE)

Spegazzini, Rutile A. *decemfida* s.n. (BAB)**,** *integrifolia* 1881 (SI)

Spellenberg, R. (Richard) *scoparia* 5418 (NY)**,** *scabra* var. *sonorensis* 3602 (NY)

Spencer, Mary F. *spinescens* var. *mohavensis* 1776 (GH)

Sperry, O. E. (Omer E.) *scoparia* 264 (US), *laevis* 154 (US), 673 (US), 1550 (GH, UC),*laevis* 1550, *longiflora* s.n. (TEX), T147 (US)

Standley, Paul C. *scoparia* 40689 (US), 40729 (US), *laevis* 545 (MO), *longiflora* 40400 (US), 40455 (US), *scabra* var. *scabra* 4967 (GH, MO, NY, US)

Stanfield, S. W. *heterophylla* s.n. (NY)

Stanford, L. R. *coulteri* 46 (GH, MO, NY, UC), *henricksonii* var. *confusa* 200 (GH, MO, NY), *henricksonii* var. *henricksonii* 334 (GH, MEXU, MO, NY, UC)

Stearns, Elmer *laevis* 66 (GH, US), s.n. (NY, US)

Steiger, T. L. *laevis* 1352 (NY), 2036 (NY), *longiflora* 1206 (NY)

Steinbach, J. (José) *integrifolia* 3888 (GH), 8761 (GH, MO, NY, UC, US), s.n. (LIL)

Steinbach, Roy F. *integrifolia* 142 (GH, MICH, MO, NY, TEX, UC, US), *integrifolia* 670 (GH, MO, UC, US)

Steussy, Tod *laevis* 1105 (LL, NY, TEX)

Stewart, Robert M. *scoparia* 1044 (GH), 256 (GH), 939 (GH, LL), *laevis* 251 (GH), 588 (GH, LL, MEXU), 652 (GH), 724 (GH, LL), 1178 (GH, LL), 1760 (GH, LL), 2005 (GH), 2300 (GH), 2416 (GH), 2428 (GH), 2642 (GH), 2995 (GH), 3020 (GH), *longiflora* 442 (GH, LL, MEXU, MO), 1378 (GH, LL), 1609 (GH), 1858 (GH, LL), 2512 (GH)

Story, R. *africana* ssp. *africana* 760 (PRE)

Straw, Richard M. *coulteri* 1160 (GH, MEXU, MICH, UC), *laevis* 1611 (MEXU, UC)

Strey, R. G. *africana* ssp. *africana* 9960 (NU, PRE)

Stuckert, Teodoro *integrifolia* 15235 (LIL), 609 (LIL)

Sundberg, Scott *coulteri* 1804 (MEXU, NY, TEX)

Surratt, H. L. *laevis* 111 (TEX)

Sutton, J. D. *africana* ssp. *australis* 1113 (PRE), 852 (PRE)

Tate, Harry *scabra* var. *sonorensis* 562 (NY)

Taylor, Mary *muellerae* 87 (MO, TEX, UC)

Taylor, John *laevis* 6282 (NY, US), *scabra* var. *glabrescens* 29431 (NY)

Tedone *integrifolia* 4940 (LP)

Templeton, Bonnie C. *spinescens* var. *spinescens* 5763 (NY)

Tenorio L., P. *helianthemoides* 6768 (MEXU, TEX)**,** *laevis* 4238 (MEXU, TEX)

Teran, J. *integrifolia* 188 (TEX)

Terribile, M. *integrifolia* 650 (LIL), 691 (LIL)

Tharp, B. C. *scoparia* 43-747 (TEX, UC), *heterophylla* 49341 (NY, TEX), 52-562 (TEX), s.n. (GH, MO, NY, NY, TEX, TEX, TEX, TEX), *laevis* 3642 (TEX), 43-744 (TEX), 43-745 (TEX, UC), 43-746 (TEX), s.n. (TEX), *longiflora* 3637

(TEX), 3639 (TEX), 43-743 (TEX, UC), 4367 (TEX), 43T243 (MO, TEX), s.n. (GH, LL, MO, MO, NY, TEX, UC, UC)

Thode, J. *africana* ssp. *australis* A1442 (GH, NH, PRE)

Thompson, B. *heterophylla* 48 (TEX)

Thornber, J. J. *scabra* var. *sonorensis* 448 (MO, NY, UC, US), 2317 (GH, NY, TEX), s.n. (UC)

Thorncroft, G. *africana* ssp. *africana* 646 (NH)

Thorne, Robert F. *scabra* var. *sonorensis* 44120 (MO, NY), *scabra* var. *glabrescens* 32083 (GH, UC), 43933 (GH, MO, NY), 44000 (NY), 44154 (NY) *spinescens* var. *mohavensis* 34707 (MO), 57420 (MO), 60538 (MEXU) *spinescens* var. *spinescens* 3165 (NY), 3700 (NY), 43822 (NY)

Thorns, F. W. *juncea* s.n. (NBG)

Thurber, George *laevis* 318 (GH), *scabra* var. *scabra* 232 (GH, NY), 693 (GH), s.n. (NY)

Tidestrom, Ivar *spinescens* var. *spinescens* 10034 (P, US), 8907 (US), 9775 (P, US)

Tiehm, Arnold *spinescens* var. *spinescens* 3049 (NY), 5961 (NY), 9372 (TEX, TEX), 12414 (NY)

Tolaba, Julio *integrifolia* 2693 (MCNS), 78I (CTES, MCNS)

Toledo, Carlos Saravia *integrifolia* 10371 (CTES), 11795 (CTES), 12768 (CTES), 12849 (CTES)

Tolliers *decemfida* 592 (G)

Tolstead, W. L. *heterophylla* 5828 (UC), 7689 (NY, TEX, UC)

Torres, Herminia *heterophylla* 82 (LL)

Torres C., R. *intricata* 14821 (TEX), 15094 (TEX), *longiflora* 994 (MEXU)

Torrico, G. *integrifolia* 265 (LPB)

Tothill, J. C. *spinescens* var. *spinescens* s.n. (UC)

Toumey, J. W. *scabra* var. *sonorensis* 206 (A), 206a (US), *scabra* var. *glabrescens* 206 (NY), s.n. (UC)

Tracy, S. M. *heterophylla* 7653 (MO), 8087 (GH, NY, TEX, US)

Train, P. *spinescens* var. *spinescens* 1456 (NY), 1496 (A, UC), 3972 (NY), s.n. (US)

Trapnell, C. G. *africana* ssp. *africana* 628 (K)

Traverse, Alfred *longiflora* 2153 (LL)

Trécul *heterophylla* 1089 (P)

Trelease *heterophylla* 26 (MO)

Tressens, S. G. *integrifolia* 1653 (CTES), 4392 (CTES, TEX), *integrifolia* 2225 (MCNS), 546 (CTES, GB), *integrifolia* 2292 (MICH), *integrifolia* 2225 (CTES), 2292 (CTES)

Troncoso, N. S. *integrifolia* 1691 (SI), 6042 (SI)

Truscott, D. Gordon *africana* ssp. *africana* 157 (PRE)

Tuck, William *africana* ssp. *africana* s.n. (SAM)

Tucker, J. M. *scabra* var. *glabrescens* 2868 (UC)

Turner, B. L. (Billie L.) *scoparia* 1116 (GH), 1165 (GH), *gypsophila* 93-158 (MEXU, TEX), *heterophylla* 4489 (TEX), 93-168 (TEX), 97-317 (TEX), 98-195 (TEX), 98-499 (TEX), 99-364 (TEX), s.n. (TEX), *laevis* 1032 (LL), 15981 (TEX), 15988 (TEX), 98-437 (TEX), 16029a (TEX), 16029b (TEX), 16029c (TEX), 99-442 (TEX), *longiflora* 15965 (TEX), 15972 (TEX), 15976 (TEX), 93-140 (MEXU, MEXU, TEX), 93-162 (MEXU, TEX), 96-116 (TEX), 96-170 (TEX), 96-30 (TEX), 97-447 (TEX), 97-353 (TEX), 97-472 (TEX), 98-503 (TEX), *scabra* var. *scabra* 93-33 (TEX)**,** *scabra* var. *occidentalis* 95-123 (TEX)

Ulibari, E. A. *integrifolia* 898 (CTES, SI)

Valdes, J. *laevis* VR-731 (UMO)

Valdés R., Jesús *longiflora* 2215 (MEXU)

Valiente B., Alfonso *tehuacana* 741 (MEXU)

Van Devender, T. R. *yecorana* 98-1939 (NY)

Van Jaarsveld *juncea* 12081 (PRE)

van Nouhuys, J. J. *africana* ssp. *australis* 31047 (PRE)

Van Pelt, S. *scabra* s.n. (UNM)

van Rensburg, A. C. *africana* ssp. *africana* 75 (NU)

van Rensburg, S. *africana* ssp. *africana* s.n. (NU)

Van Wyk, A. E. *africana* ssp. *africana* 1741 (PRE)

Van Wyk, S. *africana* ssp. *africana* 262 (PRE)

Varela, Luis A. *integrifolia* 24 (A)**,** *integrifolia* 771 (A), 773 (A, US)

Vasey, G. R. *laevis* s.n. (NY, NY, US), *scabra* var. *glabrescens* 362 (MO, NY, US)

Vasquez, Jose A. *heterophylla* 40 (TEX)

Ventura A., A. *helianthemoides* 1652 (MEXU, MO), *helianthemoides* var. *parviflora* 1504 (CTES, MEXU, US)

Ventura, E. *coulteri* 6219 (MEXU), 7018 (TEX), 8341 (TEX), *coulteri* 6837 (TEX), 7059 (TEX), 7163 (TEX), 7476 (TEX), 8296 (TEX), 8391 (TEX), 9348 (TEX), *helianthemoides* 8505 (TEX), 9291 (TEX), *helianthemoides* 8525 (TEX), 9679 (TEX), *mexicana* 7142 (TEX)

Venturi, S. *decemfida* 10065 (US), 9534 (A, US), *integrifolia* 10574 (US), 1541 (A, GH, US), 5659 (US), 585 (A, SI, US), 7534 (GH, MO, US), 9190 (US)

Verdoorn, I. C. *africana* ssp. *africana* 28544 (MO, PRE)

Vergaro, Gilberto *heterophylla* 8571 (TEX)

Viereck *intricata* 96 (US)

Vignati, M. A. *integrifolia* 216 (LP)

Vilchis, Irene Diaz Vilchis *helianthemoides* 500 (MEXU, TEX), *helianthemoides* var. *helianthemoides* 439 (MEXU, MEXU)

Villafañe, M. *integrifolia* 526 (LIL), 80 (US)

Villarreal, J. A. *coulteri* 5738 (MEXU),**,** *heterophylla* 8502 (MEXU), *laevis* 2254 (TEX), *longiflora* 3880 (TEX)

Villaseñor Ríos, José Luis *jaliscana* 291 (MEXU)

Virdon, Mrs. E. *heterophylla* s.n. (MO)

Viviers, M. 68 (NBG, PRE), *juncea* 2087 (NBG)

Vlok, J. H. J. *juncea* 2081 (MO, PRE)

Von Rozynski, H. W. *intricata* 458 (G)

von Schrenk, Hermann *heterophylla* s.n. (MO)

Wagner, Frank *laevis* 956 (US)

Wagner, Richard H. *scabra* var. *glabrescens* 165 (UC)

Wagner, W. L. *scabra* 3144 (UNM)

Walker, Mrs. E. J. *heterophylla* 40 (GH, TEX)

Walter, Richard G. *scabra* var. *scabra* 11185 (MO)

Ward, Darrell *laevis* 81-160 (MO)

Warnock, B. H. (Barton H.) *scoparia heterophylla* , *laevis* 5711 (LL), *longiflora*

Warnock, Barton H. Warnock *scoparia* 673 (GH, TEX), 675 (US), W114 (GH, TEX), W114A (TEX), *coulteri* 14713m (TEX), 14756m (TEX), 14819 (GH, MO, NY, TEX, UC), *heterophylla* T538 (US), 727 (LL), 6829 (TEX), 11521 (LL), 14960 (LL),15118 (LL), 20790 (TEX), *laevis* 513 (TEX), 1122 (GH, TEX, US), 1123 (TEX), 1165 (LL), 1207 (TEX), 5711 (LL, TEX), 6872 (TEX), 7030 (TEX), 7261 (TEX), 8559 (LL), 8999 (LL), 10125 (LL), 10190 (LL), 10783 (TEX), 10824

(TEX), 11374 (LL), 12825 (LL), 12887 (LL),13454 (LL), 13563 (LL), 13589 (LL), 14494 (LL), 14960 (LL), 14993 (LL), 15169 (LL), 20226 (LL), 20241 (LL), 20911 (TEX), 20971 (LL, UC), 20979 (LL), 21030 (TEX), s.n. (TEX), *longiflora* T538 (GH, LL), W319 (TEX, UC), W510 (GH), 2700 (TEX), 5958 (LL), 8094 (LL) 11865 (LL), 13309 (LL), 13651 (LL), 15114 (LL), 15222 (LL), 20800 (TEX), 20801 (NY, TEX), 20802 (TEX)

Warnock, Michael J. *scabra* var. *scabra* 809 (TEX)

Waterfall, U. T. *laevis* 4236 (GH, NY), 4849 (GH, MO, NY), 5292 (GH, MO, NY), 6124 (GH, MO, NY), 6667 (GH, NY), *longiflora* 4044 (GH, MO), 5053 (GH), 5093 (GH, MO, NY), 5139 (GH), 5224 (GH, TEX)

Watkins *laevis* 581 (LL, UMO)

Weber, W. A. (William A.) *scabra* var. *scabra* 12772 (NY, TEX)

Webster, G. L. (Grady L.) *heterophylla* 14491b (MO, TEX, UC), *intricata* 20545 (MEXU, TEX), *longiflora* 263 (TEX)**,** 472 (TEX)

Wendt, Tom *coulteri* 10013a (LL), *longiflora* 102 (LL, MEXU), 543 (TEX)

Werdermann, E. *africana* ssp. *africana* 1302 (A, A, PRE, US), 1665 (PRE)

Wheeler *scabra* var. *glabrescens* s.n. (GH)

White, Stephen S. *coulteri* 1653 (GH, LP), *laevis* 2186 (GH, MEXU), 2222 (LP, US), 2308 (GH), 2443 (GH, LL), *scabra* var. *sonorensis* 4576 (GH, NY, US)**,** *spinescens* var. *spinescens* 173 (NY)

Whitehead, H. *juncea* s.n. (K)

Whitehead, J. *scabra* var. *glabrescens* 1274 (UC)

Whitehouse, E. (Eula) *heterophylla* s.n. (TEX, TEX), *laevis* s.n. (TEX), *longiflora* s.n. (MO, TEX)

Wiegand, K. M. *heterophylla* 1678 (GH)

Wiggins, Ira L. *scabra* var. *sonorensis* 61 (MO, NY), 6042 (US), 7187 (A, UC, US), *scabra* var. *glabrescens* 9849 (US)

Wild, H. *africana* ssp. *australis* 7273 (K, PRE)

Wilkinson, E. H. *heterophylla* 7 (MO)**,** *laevis* 8 (US), s.n. (UC, US)

Willeges, George G. *heterophylla* 6 (TEX)

Williams, Margaret J. *scabra* var. *scabra* 80-153-9 (NY), *spinescens* var. *spinescens* 78-3-3 (NY), 80-188-1 (NY)

Williams, C. B. *heterophylla* 6 (TEX)

Williamson, E. *laevis* s.n. (US)

Williamson, G. *juncea* 3974 (NBG)

Williges, G. G. *heterophylla* 332 (TEX)

Wilman, M. *africana* ssp. *africana* s.n. (SAM)

Wilms, F. *africana* ssp. *africana* 1068 (G)

Wilson, James S. *coulteri* 10871 (TEX), *laevis* 11364 (TEX), *longiflora* 11379 (TEX), 11456 (TEX)

Wilson, Norman C. *scabra* var. *glabrescens* s.n. (UC, US)

Wislizenus *scabra* var. *scabra* 68 (MO)

Wolf, C. B. (Carl B.) *scabra* var. *glabrescens* (JEP), 2281 (UC), 7593 (UC), 10761 (NY, TEX, UC), *spinescens* var. *spinescens* (UC, UC, UC), 10145 (NY), 10736 (UC), 3302 (UC, US), 6676 (GH, NY), 9616 (NY), 9686 (TEX, UC)

Wolff, Simon E. *longiflora* 932 (US)**,** *scabra* var. *occidentalis* 1882 (US)

Wood, Archie D. *longiflora* 846 (TEX)

Wood, J. Medley *africana* ssp. *africana* 3336 (NH), 5506 (MO), 758 (SAM, US), s.n. (SAM)

Wood, J. R. I. *integrifolia* 7602 (K), 7696 (K)

Woodruff, Lindsay *coulteri* 318 (TEX)

Woodward, R. W. *scabra* var. *scabra* s.n. (GH)

Wooton, E. O. *heterophylla* s.n. (US), *laevis* 154 (GH, NY, RM, UC), s.n. (MO, NY, RM, UC, US, US), *scabra* var. *scabra* s.n. (US, US), *scabra* var. *glabrescens* s.n. (US)

Worthington, R. D. *coulteri* 8369 (TEX), *laevis* 12452 (NY), 12499 (NY), 13483 (NY), 14292 (NY), 14403 (NY), 14497 (NY), 14728 (NY), 14849 (NY), 16914 (NY), 17237 (NY), *scabra* var. *scabra* 13294 (NY), 22438 (NY)

Wright, C. (Charles) *heterophylla* 562 (GH, US), s.n. (GH, NY), *laevis* 504 (US), 564 (GH, NY, UC), 563 (GH, NY, US), *longiflora* 1685 (GH), 1694 (NY), 1695 (GH), 1696 (MO, US), 11935 (MO), *scabra* var. *scabra* 1694 (GH, US)

Wynd, F. Lyle *heterophylla* 297 (GH, MO, NY, US), *laevis* 719 (GH, MO, NY, US), *longiflora* 727 (A, GH, MO, NY, US)

York, C. L. *laevis* 48266 (TEX)

Young, M. S. (Mary S.) *heterophylla* 72 (TEX, UC), s.n. (GH), *laevis* 11 (MO), s.n. (GH, MO, MO, TEX, TEX), *longiflora* s.n. (GH, MO, TEX, TEX, TEX, UC, UC)

Young, R. G. N. *africana* ssp. *africana* A95 (PRE)

Zamudio (R.), S. *coulteri* 2810 (MEXU), 3057 (MEXU), *coulteri* 7872 (TEX)**,** 9967 (MEXU)**,** *helianthemoides* 4021 (MEXU)

Zarate, A. *laevis* A-4 (TEX)

Zelada, Fidel *integrifolia* 9 (LIL)

Zietsman, P. C. *africana* ssp. *africana* 141 (PRE), 436 (PRE)**,** 1361 (PRE),

Zuck, Myrtle *scabra* var. *scabra* s.n. (US), *scabra* var. *glabrescens* s.n. (NY)

Appendix 2: Supplementary Figure and Tables

Table S1. Primer sequences used in completing the sequence of *Pelargonium*. Names indicate placement in the genome and forward/reverse primer usage. Primers designated as a “universal” application were intentionally designed for broader use in other land plants, and angiosperms in particular.

Name	Length	Sequence (5'-3')	Description	Application
Phort687R	20	GTTCAATTCCCGTCGTTCGC	trnH	Pelargonium
Phort30145F	21	CTCCTTGAAAGAGAGATGTCC	trnE	Pelargonium
Phort30589F	22	TTACTTTGGAATGTACCGGCTG	rpl33 pseudogene	Pelargonium
Phort31058F	22	ACGGACAGTCTTGTGAATTTCC	IGS rpl33/trnfM pseudogenes	Pelargonium
Phort31414F	22	CTATTGGTTGTACAGATGACCC	IGS rpl33/trnfM pseudogenes	Pelargonium
Phort31432F1	20	ACGCATTCAACCCTTCTGTG	IGS rpl33/trnfM pseudogenes	Pelargonium
Phort31432F2	20	ACCCATTCAACCCTTCTGTG	IGS rpl33/trnfM pseudogenes	Pelargonium
Phort32111R	22	CCATAGAGCTCATAGAGATGTT	IGS trnfM-trnG	Pelargonium
Phort32182R	21	GTAACGGTATGGAGTCTAAGG	IGS trnfM-trnG	Pelargonium
Phort32239R	20	ATAGTGCGGTCCTTTGAATG	IGS trnfM-trnG	Pelargonium
Phort32662R	21	TCCATTTATCCGTGATCTAGG	ycf3	Pelargonium
Phort37155F	21	CTATTTCGGTAGTAATCTTCC	psaA	Pelargonium
Phort37817R	21	AGTCCACAGAAAGATTATTGC	psaB	Pelargonium
Phort38213R	20	CTTTGGCTTGGACAGGACAT	psaB	Pelargonium
Phort39804F	21	TTCTTGATTGCTTCTACATCG	psaB	Pelargonium
Phort40163F	21	AAGACCGAGAGCTACCTATCG	rps14	Pelargonium
Phort40851R	21	CGGCATCTTCACATTCTTATC	IGS rps14-rps14 pseudogene	Pelargonium
Phort42493R	21	ATCGTGGATAAGAAGGTTCCG	IGS rps14 pseudogene-rpl33	Pelargonium
Phort43549R	21	GTATTGGGTTCGATCTACTCC	IGS rpl33-rpl33 pseudogene	Pelargonium
Phort43762R	20	TTCCTATGTTTCCGGAGGTG	IGS rpl33-rpl33 pseudogene	Pelargonium
Phort43779R	21	AGCCATTCCGCAAGAGATTCC	IGS rpl33-rpl33 pseudogene	Pelargonium
Phort44080R	20	ACCCCGACTGTAGCATTCCC	IGS rpl33-rpl33 pseudogene	Pelargonium
Phort44081F	21	ACATTCTCTTTCTTTACTTCC	IGS rpl33-rpl33 pseudogene	Pelargonium
Phort44202R	21	CAGTTTCTGGGTTAATATAGC	IGS rpl33-rpl33 pseudogene	Pelargonium
Phort44776R	21	ATGAATACATAATAAGTATGG	IGS rpl33 pseudogene-trnFM	Pelargonium
Phort45456F	21	GAAACCCATTAGATTACAAGG	IGS trnfM-psbD	Pelargonium
Phort45672R	20	CCCTCCGCAACCAGTCATCC	psbD	Pelargonium
Phort45860R	21	ATGCGCTAAACTATTAGCAGG	psbD	Pelargonium

Table S1. (continued)

Name	Length	Sequence (5'-3')	Description	Application
Phort48833F	21	TAGTCTTTCTTGTGGGTATCC	ycf9 (psbZ)	Pelargonium
Phort49733R	20	GCTACGCCTTGAACCACTCG	trnS	Pelargonium
Phort53203F	21	TTCATACTGTGTTTACTTTCG	IGS trnF-ndhJ	Pelargonium
Phort53557R	22	AGAGACTTGTTTCGGATGAGTC	IGS trnF-ndhJ	Pelargonium
Phort54641F	21	ATCTGTACTGAACATTCCTCC	ndhK	Pelargonium
Phort55341R	21	TCTAATTTCCGGCGTTTTAGC	ndhC	Pelargonium
Phort55719F	22	AGTAATTCAAAATAGAATTCGC	IGS ndhC-trnV	Pelargonium
Phort56100R	21	GCTAATGAAAGAGCCCAATGC	trnV intron	Pelargonium
Phort61259F	21	GAGTTTGAAGCAATGGATACC	rbcL	Pelargonium
Phort61915R	21	TGGACTTCAGTCCGATTATCC	IGS rbcL-rps18	Pelargonium
Phort62304F	21	TATTGCTTATGTATTCATTGG	IGS rbcL-rps18	Pelargonium
Phort62504R	20	TCCACCCATCTCGTGTATGG	IGS rbcL-rps18	Pelargonium
Phort62878R	21	CAAGAGATTACTCTGTTTCCG	IGS rbcL-rps18	Pelargonium
Phort63220F	21	CTTATCTAGACGGGTGAATAG	rps18	Pelargonium
Phort63240R	21	CTATTCACCCGTCTAGATAAG	rps18	Pelargonium
Phort63594F	20	ATGATGATGAGCCCCTTTTC	IGS rps18-16S pseudogene	Pelargonium
Phort63858F	21	CTACCTACTATCCAAACGAGG	IGS 16S pseudogene-trnfM	Pelargonium
Phort63873R	20	TTTGGATAGTAGGTAGCTCC	IGS 16S pseudogene-trnfM	Pelargonium
Phort64130F	21	TAGACAATGGCACCCTGTGAT	IGS 16S pseudogene-trnfM	Pelargonium
Phort64327R	21	ACAATAAGGAATCTAGTTCGG	IGS 16S pseudogene-trnfM	Pelargonium
Phort64339R	21	GTATCCCTTATGACAATAAGG	IGS 16S pseudogene-trnfM	Pelargonium
Phort64584R	21	TGAATAGGGATCCTGGCCTGG	IGS 16S pseudogene-trnfM	Pelargonium
Phort64592R	21	TAAGGTAAGGGGTCGATATGC	IGS 16S pseudogene-trnfM	Pelargonium
Phort64889F	20	CGTTATCTGATCAATGATCG	IGS trnfM-rps14 pseudogene	Pelargonium
Phort64961R	23	GCAACAAGATCGAGTTGGTAAGG	rps14 pseudogene	Pelargonium
Phort65295R	21	CGCATCTAGGATCCGACTTCT	IGS rps14 pseudogene-psaJ	Pelargonium
Phort65302R	21	ATCGTTCCGCATCTAGGATCC	IGS rps14 pseudogene-psaJ	Pelargonium
Phort65509F	20	CCAAGGAATCTATCCTTAGG	IGS rps14 pseudogene-psaJ	Pelargonium
Phort65576F	20	CCACAGCCAGAAGAAGAAGC	IGS rps14 pseudogene-psaJ	Pelargonium
Phort65614R	21	CTCGTATGGATAGTTGGGAGC	IGS rps14 pseudogene-psaJ	Pelargonium
Phort66024F	21	GAGTTGAAGAACGTGGTCCG	IGS rps14 pseudogene-psaJ	Pelargonium
Phort66539R	21	AATCGTTTCTTTCCGGATGCG	psaJ	Pelargonium
Phort74618R	22	TGAGCCTTGCGAGCTACCAAGC	IGS rpl33 pseudogenes	Pelargonium
Phort74648F	21	GAAGGTTGTCTTTGAACTCGG	IGS rpl33 pseudogenes	Pelargonium
Phort75182R	21	AGAACTTGTCTTCAGGTTACC	IGS rpl33-rpl23 pseudogenes	Pelargonium
Phort75236R	21	CAAGGGATGAAGTCTATGTGG	IGS rpl33-rpl23 pseudogenes	Pelargonium
Phort123434F	21	TCGTCGTTTGTGGATCACTCG	rpl20	Pelargonium

Table S1. (continued)

Name	Length	Sequence (5'-3')	Description	Application
Phort123454R	21	CGAGTGATCCACAAACGACGA	rpl20	Pelargonium
Phort132591F	19	TTGTATCCCGAGCCGAATC	IGS ycf1-rps15	Pelargonium
Phort132609R	19	GATTCGGCTCGGGATACAA	IGS ycf1-rps15	Pelargonium
Phort132970F	20	CGTCTGCTGTCTTATTTGTC	rps15	Pelargonium
Phort132989R	20	GACAAATAAGACAGCAGACG	rps15	Pelargonium
Phort134652F		TCGTTTATTCAGTATCGGACC	ndhA exon 1	Universal
Phort134661R	20	GCCATGGATGGGCCAATACT	ndhA exon 1	Universal
Phort135406F	21	AATCACTATCAGGAACGAAAG	IGS ndhA-trnL	Pelargonium
Phort135641R	21	CTCGTTTAGAAAATATTATGC	IGS trnL-ccsA	Pelargonium
Phort136074F	21	AYCCAAGGCTTTGCTACTTCG	ccsA	Pelargonium
Phort136157F		AATGATGCATGTMAGTATGATG	ccsA	Universal
Phort136225R	20	GCTATTGATAATAATGATCC	ccsA	Universal
Phort136462F	21	GAGCAGTATGGGCTAATGAGG	ccsA	Pelargonium
Phort136539R		TCCAAGTAATAAATGCCCAAG	ccsA	Universal
Phort136627R	21	ATAAGAAAGCCAATAGAAGCC	ccsA	Pelargonium
Phort136664F	21	AATAGGGTTACATAGTTATGG	ccsA	Universal
Phort136985F	21	TGAGATACAATCAATTCAACC	ndhD	Pelargonium
Phort137141F	20	TATCCRTAGAACATYTGVCCG	ndhD	Universal
Phort137206R	21	AATTGGAATGATATTAACTCC	ndhD	Universal
Phort137513F	20	ATTCCTATAATTATGAAACC	ndhD	Universal
Phort137536R		TATGGGTTTCATAATTATAGG	ndhD	Universal
Phort137806F	20	AGCAAAAGCAATAARAAATC	ndhD	Universal
Phort138000R	20	AAGAAACGTCTSTACTCAGC	ndhD	Universal
Phort138218F	22	AGTCCATCKATTCCYAATCTCC	ndhD	Universal
Phort138625F	21	ATAAGCTAGACCCATACTTCG	psaC	Pelargonium
Phort138731F	20	TCTGTTCKCGGAGCWGAAGC	psaC	Universal
Phort138837R		TGTATAGGATGYACTCAATGTG	psaC	Universal
Phort139073F	21	CATACATACCAACTTCAATGG	IGS psaC-ndhE	Pelargonium
Phort139205F	21	AATGGCTGCTTCAGCGGCTGC	ndhE	Universal
Phort139378R	20	TATGGATTGATCACAAGTCG	ndhE	Universal
Phort139700F		GCACCTATCAAAGMAACTAAA	ndhG	Universal
Phort139795R	21	AGGTAATAGTCAACAAMTTGG	ndhG	Universal
Phort140007R		GGAGCTATAAATGTTTTAATC	ndhG	Universal
Phort140117F	20	TTGGKAAGTAATTCSACCCC	ndhG	Universal
Phort140202R	20	TTRCCTGGACCAATACATGA	ndhG	Universal
Phort140644F		TCATTGATAAACARTTTGTTGG	ndhI	Universal
Phort140734R	20	AAACGMTTGCTTAATTACAG	ndhI	Universal
Phort140907R		ATCGTTTACCTGTAACTATTC	ndhI	Universal
Phort140939F	21	ACCAATGTACCTTGCGGCTCG	ndhI	Universal
Phort141186R	21	CAACTMTTAAATCTTGGGTGG	ndhA exon 2	Universal
Phort141593F	21	GATTGTGCCTCAATTATATCG	ndhA exon 2	Universal
Phort141612F		CAACTGTACTTAAACTGTTAG	ndhA exon 2	Universal
Phort141682R	20	GGTTCTGTAATAGCGGTKGG	ndhA intron	Universal
Phort141825R		ATTCCATTGGTTTAATTCRGG	ndhA intron	Universal
Phort141916F	20	TTTGTTGAGTAATAACTWAA	ndhA intron	Universal
Phort142040F	21	AATGGGACGAGTTCTATCTCC	ndhA intron	Pelargonium
Phort142227F	21	CTTTCGTTCCTGATAGTGATT	ndhA intron	Pelargonium

Table S1. (continued)

Name	Length	Sequence (5'-3')	Description	Application
Phort142477F	21	ATGAGGGAATAGGCAGAAAGG	ndhA intron	Pelargonium
Phort142497R	21	CCTTTCTGCCTATTCCCTCAT	ndhA intron	Pelargonium
Phort142885F		CAATACTTGAAATGGCAATCC	ndhA exon 1	Universal
Phort217735F	20	TTATAATCTTTAACACCTGC	rbcL	Pelargonium

Table S2. Percentage nucleotide composition comparison of six chloroplast genomes.

Taxon	T(U)	C	A	G
Total				
Spinacia	31.9	18.8	31.3	18
Arabidopsis	32.3	18.4	31.4	17.9
Medicago	33.1	17.6	32.9	16.4
Lotus	32.1	17.9	31.9	18.1
Oenothera	30.8	19.5	30.1	19.6
Pelargonium	30.3	19.9	30.1	19.7
Coding (protein only)				
Spinacia	31.8	17.4	30.7	20.1
Arabidopsis	32	17.3	30.8	19.9
Medicago	32.3	16.8	31.1	19.8
Lotus	32	17.1	31.1	19.8
Oenothera	30.3	18.4	30	21.3
Pelargonium	30.6	18.5	29.8	21.1
1st position				
Spinacia	23.7	18.7	30.2	27.4
Arabidopsis	23.9	18.5	30.5	27.1
Medicago	23.7	18.2	30.8	27.3
Lotus	23.8	18.2	31.1	26.9
Oenothera	22.6	19.3	29.9	28.2
Pelargonium	23.1	19.7	29.8	27.4
2nd position				
Spinacia	33	20.4	28.9	17.8
Arabidopsis	33.2	20.2	28.9	17.7
Medicago	33.4	20.1	29.2	17.3
Lotus	33.4	20.1	29.2	17.3
Oenothera	32	20.7	29	18.3
Pelargonium	32.4	20.5	29	18.1
3rd position				
Spinacia	38.7	13	33	15.2
Arabidopsis	39	13	33	14.9
Medicago	39.7	12.2	33.3	14.8
Lotus	39	13	32.9	15.2
Oenothera	36.2	15.3	31.1	17.4
Pelargonium	36.2	15.5	30.6	17.7

Table S3. Comparison of codon usage in six chloroplast genomes. Stop codons shown in red; codon for the lost *trnT*-ggu tRNA in *Pelargonium* shown in blue.

codon		***Spinacia***	***Arabidopsis***	***Medicago***	***Lotus***	***Oenothera***	***Pelargonium***
UUU	(F)	0.041	0.042	0.043	0.042	0.035	0.038
UUC	(F)	0.018	0.019	0.016	0.018	0.020	0.020
UUA	(L)	0.037	0.037	0.036	0.035	0.032	0.031
UUG	(L)	0.020	0.019	0.022	0.021	0.021	0.022
UCU	(S)	0.021	0.021	0.021	0.022	0.020	0.020
UCC	(S)	0.011	0.011	0.011	0.011	0.012	0.012
UCA	(S)	0.015	0.015	0.015	0.015	0.013	0.013
UCG	(S)	0.006	0.007	0.006	0.008	0.008	0.007
UAU	(Y)	0.030	0.030	0.032	0.030	0.027	0.028
UAC	(Y)	0.007	0.006	0.006	0.006	0.008	0.007
UAA	(*)	-	-	-	-	-	0.002
UAG	(*)	-	-	-	-	-	0.001
UGU	(C)	0.008	0.009	0.008	0.009	0.008	0.007
UGC	(C)	0.003	0.003	0.002	0.003	0.003	0.003
UGA	(*)	-	-	-	-	-	0.001
UGG	(W)	0.018	0.018	0.018	0.018	0.018	0.018
CUU	(L)	0.022	0.022	0.022	0.021	0.022	0.027
CUC	(L)	0.006	0.007	0.006	0.006	0.008	0.008
CUA	(L)	0.015	0.014	0.015	0.014	0.014	0.015
CUG	(L)	0.006	0.006	0.006	0.006	0.008	0.008
CCU	(P)	0.018	0.016	0.017	0.015	0.015	0.017
CCC	(P)	0.007	0.007	0.007	0.009	0.010	0.009
CCA	(P)	0.012	0.012	0.013	0.011	0.011	0.011
CCG	(P)	0.005	0.005	0.005	0.005	0.007	0.007
CAU	(H)	0.017	0.017	0.018	0.017	0.016	0.016
CAC	(H)	0.006	0.006	0.005	0.005	0.006	0.007
CAA	(Q)	0.029	0.029	0.027	0.029	0.028	0.026
CAG	(Q)	0.007	0.008	0.007	0.008	0.009	0.009
CGU	(R)	0.014	0.013	0.013	0.013	0.014	0.014
CGC	(R)	0.004	0.005	0.004	0.004	0.005	0.006
CGA	(R)	0.014	0.014	0.014	0.014	0.014	0.013

Table S3. (continued)

codon		***Spinacia***	***Arabidopsis***	***Medicago***	***Lotus***	***Oenothera***	***Pelargonium***
CGG	(R)	0.004	0.004	0.004	0.004	0.005	0.005
AUU	(I)	0.043	0.044	0.045	0.045	0.039	0.037
AUC	(I)	0.015	0.015	0.015	0.016	0.017	0.017
AUA	(I)	0.027	0.027	0.029	0.029	0.024	0.023
AUG	(M)	0.023	0.022	0.022	0.022	0.022	0.022
ACU	(T)	0.021	0.021	0.021	0.020	0.019	0.020
ACC	(T)	0.009	0.009	0.009	0.010	0.010	0.010
ACA	(T)	0.016	0.016	0.016	0.016	0.014	0.014
ACG	(T)	0.005	0.005	0.005	0.005	0.006	0.006
AAU	(N)	0.036	0.036	0.038	0.037	0.033	0.029
AAC	(N)	0.011	0.011	0.010	0.011	0.011	0.011
AAA	(K)	0.042	0.044	0.045	0.045	0.042	0.043
AAG	(K)	0.012	0.011	0.011	0.013	0.014	0.019
AGU	(S)	0.015	0.015	0.015	0.015	0.014	0.013
AGC	(S)	0.005	0.004	0.004	0.004	0.006	0.006
AGA	(R)	0.017	0.017	0.017	0.017	0.018	0.018
AGG	(R)	0.006	0.006	0.006	0.006	0.008	0.008
GUU	(V)	0.021	0.021	0.022	0.021	0.020	0.020
GUC	(V)	0.006	0.006	0.006	0.006	0.008	0.009
GUA	(V)	0.021	0.020	0.022	0.022	0.020	0.019
GUG	(V)	0.007	0.008	0.007	0.007	0.009	0.008
GCU	(A)	0.026	0.027	0.027	0.025	0.025	0.026
GCC	(A)	0.009	0.008	0.008	0.009	0.011	0.010
GCA	(A)	0.016	0.015	0.016	0.015	0.015	0.014
GCG	(A)	0.007	0.006	0.006	0.006	0.009	0.008
GAU	(D)	0.032	0.031	0.032	0.032	0.031	0.028
GAC	(D)	0.008	0.007	0.007	0.007	0.010	0.010
GAA	(E)	0.041	0.041	0.041	0.039	0.039	0.038
GAG	(E)	0.012	0.012	0.012	0.012	0.015	0.016
GGU	(G)	0.023	0.023	0.024	0.023	0.022	0.021
GGC	(G)	0.007	0.007	0.005	0.006	0.009	0.009
GGA	(G)	0.028	0.028	0.028	0.027	0.025	0.024
GGG	(G)	0.012	0.011	0.010	0.011	0.014	0.014

Table S4. Observed nucleotide polymorphisms in the sequence of *Pelargonium*.

Polymorphism type	start	end	location	description
length	4732	4744	trnK intron (LSC)	poly-T, 14 or 15
dinucleotide	6053	6054	IGS rps16-trnQ (LSC)	GA or TC
single nucleotide	7066		IGS psbK-psbI (LSC)	A or T
length	7936	7948	IGS trnS-trnG (LSC)	poly-A, 13 or 12
single nucleotide	8005		IGS trnS-trnG (LSC)	G or T
single nucleotide	16173		rpoC2 (LSC)	T or C; silent, 3rd position
single nucleotide	26397		rpoB (LSC)	A or C; first position, V->G
length	30630	30644	rpl33 pseudogene (LSC)	poly-A, 15 or 16
single nucleotide	40473		IGS rps14-rps14 pseudogene (LSC)	C or T
length	50342	50345	rps4 (LSC)	poly-A, 4 or 5; frameshift mutation
length	51469	51480	IGS trnT-trnL (LSC)	poly-T, 12 or 10
length	53332	53343	IGS trnF-ndhJ (LSC)	poly-G, 12 or undetermined
single nucleotide	58826		atpB (LSC)	C or T; silent, 3rd position, M->I
single nucleotide	59318		IGS atpB-rbcL (LSC)	A or C
length	64349	64362	IGS 16S pseudogene-trnfM (IR)	poly-T, 14 or undetermined
single nucleotide	103722		IGS rpoAa2 fragment - rpoB/C1 fragment (IR)	A or G
single nucleotide	103808		rpoB/C1 fragment (IR)	T or G
length	115570	115584	IGS petD-petB (IR)	poly-A, 15 or 14
length	138542	138554	IGS ndhD-psaC (SSC)	poly-T, 13 or undetermined
length	162071	162085	IGS petD-petB (IR)	poly-T, 15 or 14; reverse complement of 115570
single nucleotide	173847		rpoB/C1 fragment (IR)	A or C; reverse complement of 103808
single nucleotide	173933		IGS rpoAa2 fragment - rpoB/C1 fragment (IR)	T or C; reverse complement of 103722
length	213293	213306	IGS rbcL-LSC (trnI) (IR)	poly-A, 14 or undetermined; reverse complement of 64349

Table S5. Repeat associations and larger repeats in the genome of *Pelargonium*. Number of repeats is the total number including those that are duplicated in the IR. For repeat associations, contents are summarized by gene or repeat fragment as detailed here; for association 1, repeats a-f are not well characterized (see Fig. 3). For direct repeats, the consensus sequence is shown. For tandem repeats, a simple alignment of the repeating units is shown, and the length of the repeating unit is indicated in parentheses following the total length. Underlined sequence indicates a coding region.

Repeat	**Description**	**# repeats incl. IR**	**Range**	**Length**	**Unit/consensus/components**
1.1	Repeat association I member 1	1	30188-32638	2451	Ψrpl33 ,ψtrnfM Repeat a: Ψrpl33-ψtrnfM upstream spacer region Repeat b: Ψrpl33-ψtrnfM downstream spacer from repeat a; a subassociation of small dispersed repeats Repeat c: ψtrnfM-trnG upstream spacer
1.2	Repeat association I member 2	1	39840-45596	5757	rps14-ψrps14-rpl33-ψrpl33-trnfM Repeat d: rps14 or ψrps14 and flanking spacers Repeat e: spacer region between repeat d-b copies Repeat f: rpl33 and part of preceding spacer Repeats a, b, and c
1.3	Repeat association I member 3	2	61286-66491; 211162-216367	5206	rps18 - ψ16S- trnfM- ψrps14 Repeats b, d and e, see above
1.4	Repeat association I member 4	2	74503-75735; 201918-204111	1233	ψrpl33- ψrpl33- ψrpl23- IGS trnV-16S fragment- IGS rpl20-rpl32 fragment Repeat a, c, f (see above), and g-j below
Repeat *g*	16S: ψ16S Repeat association I member 1.3 associate	4	16S: 86487-86517 191136-191166 ψ16S: 63550-63580 214073-214103	31	`cccctaccgtactccagcttggtagtttcca`
Repeat *h*	rpl23: ψrpl23 Repeat association I member 1.4 associate	4	rpl23: 93635-93662 183991-184018 ψrpl23: 75557-75584 202069-202096	28	`gRgttattctattcMatctcttMYaaat`
Repeat *i*	IGS trnV-16S Repeat association I member 1.4 associate	4	87247-87309 75614-75676 190344-190406 201977-202039	63	`gtcaaKacSacKagcctcttMtccattctcaatagaaaaactcccaYcggctttagKgaKaat`
Repeat *j*	IGS rpl20-rpl32 Repeat association I member 1.4 associate	4	124009-124042 75682-75715 153610-153643 201937-201970	34	`tttaYatYtaKMtatttgatttctcgggagaatc`

Table S5. (continued)

Repeat	Description	# repeats incl. IR	Range	Length	Unit/consensus/components
2.1	Repeat association 2 member 1	2	99364-10184; 175813-178289	2531	3’ rps11- rpoB/C1 fragment- petB intron fragment-rpoAα_1 fragment -rpoAβ_1 fragment -IGS 5S-4.5S fragment
2.2	Repeat association 2 member 2	2	102557-103915 173738-175096	1359	rpoB/C1 fragment-rpoAα_2- fragment-rpoAβ_2-; rpoAγ follows; inverted relative to 2.1
2.3	Repeat association 2 member 3	2	111687-114134 163519-165966	2448	ψrps11-rpoB/C1 fragment-petB intron fragment-rpoAα_3, -rpoA$\beta_{3,}$-IGS 5S-4.5S fragment, IGS 5S-4.5S’ fragment follows; inverted relative to 2.1
Repeat *k*	5’ rpoB-IGS-3’ rpoC1 Repeat association II member component; ψrpoB/C1	7	23315-23372 23384-23458 99726-99849 103723-103827 113662-113784 163869-163991 173816-173930 177804-177927	124	atcgatcatagaaatacaattccgattcgttccgattaaacttccaYcctattcatct—----------aagttcttcttattcttagatacaaggaaaKaattcagttctagggacaaagMtcgtagtt
Repeat *l*	IGS 5S-4.5S Repeat association II member 2.1 & 2.3 component (inversion endpoint)	8	79678-79765; 101757-101844 111681-111768 114124-114169 197888-197975 163484-163523 165885-165972 175809-175896	88, 46	RaRaSaccaaaggcctctgcccttgcatcccttgggtagttggttgggtaaatagaRagRRagggcagaacttttggtttttttcatga
Repeat *m*	IGS 5S-4.5S’ Repeat association II member 2.3 associate	4	79941-79977 197674-197710 111652-111688 165963-165999	37	tggtttttttcctgttgtMaaagagttSaacaatgaaa
Repeat *n*	petD: ψpetD Repeat association II member 2.2 associate	4	114483-114516 104026-104059 163136-163169 173593-173626	34	aaaKaccMttcRggtaaKatttccaaaggagttg
Repeat *o*	petB intron Repeat association II member component	4	116588-116621 99890-99923 113587-113620 161032-161065 164033-164066 177730-177763	34	cttattttcttKMttcttttttttYgatKctattt
Repeat p	IGS into trnQ: IGS trnQ-psbK direct repeat	2	6160-6198 6288-6326	39	ctctMtatKtgtatgttcTGRGACGAAAGGATTCSAACC
Repeat q	IGS psbI-trnS : IGS psbZ-trnS direct repeat	2	7343-7373 48981-49011	31	aaagaaaRcaaaaRaaaaaaaggggRgRgggg

Table S5. (continued)

Repeat	Description	# repeats incl. IR	Range	Length	Unit/consensus/components
Repeat r	trnS: trnS direct repeat	2	7414-7444 48253-48283	31	aaMggaRagagagggattcgaaccctcgRta
Repeat s	IGS trnS-trnG: trnI intron direct repeat	3	7741-7780 84738-84777 192876-192915	40	ccctttYYYgaaaggaagaMcgtgaaattct ttKtccYttt
Repeat t	IGS rps2-rpoC2: IGS rps3-rpl16 direct repeat	3	15898-15930 97019-97051 180602-180634	33	tctttcKttcttttttttKttcaaMSaaaaaaag
Repeat u	psaA: psaB direct repeat	2	36215-36264 8439-38488	50	tggctgacYgatattgcWcaYcatcattta gctattgcWWttctttttct
Repeat v	IGS 5S-4.5S tandem repeat	4	79831-79903 197750-197822	73 (18-19 ea.)	ctattgatttcgtcttttc 79831-79849 ct-ttgatttcgttttttc 79850-79867 ct-ttgatttcgtcgtttc 79868-79885 ct-ttccttcttttccctc 79886-79903
Repeat w	16S into IGS trnV: IGS rpl32-ycf1 direct repeat	4	87093-87196 124514-124632 190502-190558 153019-153137	104	catgagattcatagttgcattacttatagc ttccttgttcgtagacaaagctcattcgga attgtctttcattccaaggcatacctcgta tccatgcgcttcat
Repeat x	ycf3 intron 1: IGS trnV-3'rps12 direct repeat	3	33423-33459 89044-89080 188573-188609	37	ggagccgtatgagRtgaaaatMtcaYgtacg gttYtg
Repeat y	3' rps19 & IGS tandem repeat	8	95553-95748 181905-182100	196 (21-28 ea.)	TAAAAAAAAAAGTGATACTAAATCT-GT 95553-95579 TAAAAGCAAAAGTGATACTAAATCT-GT 95580-95606 TAAAAGCAAAAGGGATACTCAATCTCGT 95607-95634 -------CGTTAAtcaaatgaattctgt 95635-95655 taaaagcaaaagggatactcaatctctt 95656-95683 -------cgttaatcaaatgaattctgt 95683-95704 taaaagcaaaagggatactcaatctctt 95705-95732 -------cgttaatcaaatgaat----- 95733-95748
Repeat z	ycf2 tandem repeat 1	12	105753-105985 171668-171901	233 (15-21 ea.)	aagaggaagaggctgagcttc 171668-171688 aagatgaagaggctgagcttc 171689-171709 aggatgaaggggctgggcgta 171710-171730 aagatgaagaggctgagcttc 171731-171751 aagagtttcaa---gatcttg 171752-171769 aagatcctcaa---gatc--- 171770-171784 aagagggtg-gg-----cttc 171785-171799 aagagcttcaa---ggtcttc 171800-171817 aaaaggaagaggcctatcttt 171818-171838 atcaaaaggctcttgagcttc 171839-171859 aagctcaagaggatgagcttc 171860-171880 aaaagtatggtccgggg-ttc 171881-171900

Table S5. (continued)

Repeat	Description	# repeats incl. IR	Range	Length	Unit/consensus/components

Repeat	Description	# repeats incl. IR	Range	Length	Unit/consensus/components
Repeat a1	ycf2 tandem repeat 2	7	109704-109862 167791-167931	141	aaggcacgtcttttctttttgttcg 167791-167815 -tattagttcgttcctttttg-tac 167816-167838 aagtcacttcctttcttgttg-tcg 167839-167862 aagttacctctcttgttg----tcg 167863-167883 aagttacctctcttggtg----tcg 167884-167904 aaggtacttcccttgttg----tcc 167905-167925 aagttactgccttttttcttt-gtg 167926-167949
Repeat a2	ycf1 tandem repeat 1	4	125699-125821 151832-151954	123 (25-33 ea.)	a-gaggaagagaatcaagaaattttggatctcg aagaggaagagaatcaagaaattttggatctcg aagaggaagagaatcaagaaattttggatatgg atgaagaa--------aaaggatttgaaaatac
Repeat a3	ycf1 tandem repeat 2	4	125862-125986 151667-151791	125 (25-34 ea)	tcattttatgctttccttttcaaccggttgaaat tc-tattctggttaccttttcaaccggttgaaat tc-tgttatggttaccttttcgacttgttttcgt ct-tctagtcg--------ctttttgaaccgaat
Repeat a4	ycf1 direct repeat	4	131654-131705 131732-131783 145869-145920 145947-145998	52	aaagaRaaagcRgWctccttggtcttatga gagagtctttggtcWattccac
Repeat a5	trnN-ndhF direct repeat (inversion endpoint)	4	78692-78717 124057-124082 153571-153596 198936-198961	26	atMtaRatgtSWttgacatttcacta
Repeat a6	psbD-psbZ inverted repeat (inversion endpoint)	2	45666-45686 48892-48912	21	ggRgggRYcgtttcgtttttg

Table S6. Comparison of simple sequence repeats (SSRs) in six chloroplast genomes.

motif	**Spinacia**	**Arabidopsis**	**Medicago**	**Lotus**	**Oenothera**	**Pelargonium**
a	150	204	161	208	135	199
c	9	17	7	13	18	22
g	4	13	1	11	17	24
t	153	253	186	208	144	188
ac	1	0	0	0	0	0
ag	0	0	0	0	0	1
at	8	18	26	27	6	4
ct	0	0	2	0	0	1
aat	0	1	0	1	0	0
act	0	0	1	0	0	0
att	0	1	0	1	0	0
SUMMARY						
mononucleotide	316	487	355	440	314	434
dinucleotide	9	18	28	27	6	6
trinucleotide	0	2	1	2	0	0
Total	325	507	384	469	320	440

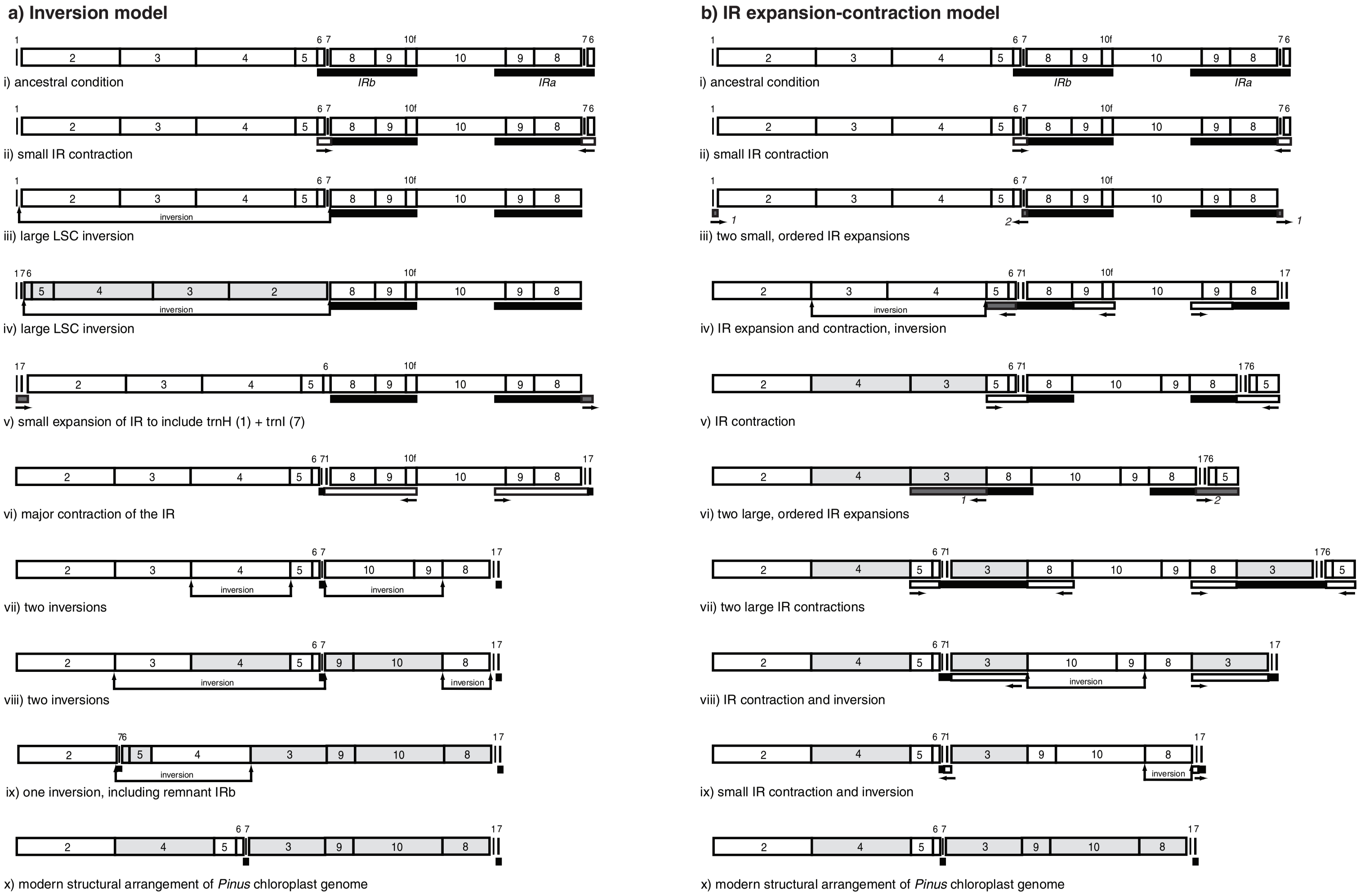


Fig. S1. Two models for organizational evolution in the chloroplast genome of *Pinus*. Blocks of contiguous genes are numbered in the order in which they appear in tobacco; shaded blocks are inverted relative to tobacco. Position of the IR and changes of extent are indicated by the black bar, open boxes (contractions) and shaded boxes (expansions) beneath the blocks. Inversions are indicated by bracketed arrows. a) The inversion model adapted from Strauss et al. (1988) to reflect the sequenced genome of *P. thunbergii* (Wakasugi et al. 1994) requires 3 IR shifts (one involving the near total loss of the IR) and 7 inversions to change from a presumably tobacco-like ancestral configuration. b) The IR expansion-contraction model presented here requires 12 IR shifts and only 3 inversions; the IR is lost through a series of events rather than a single large change.

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Vita

Timothy Wayne Chumley was born in Lubbock, Texas on 13 December, 1961, the son of Donald and Marilyn Chumley. His early years were spent growing up in a short succession of North Texas small towns, and from 1971 on, in San Marcos, Texas, where he graduated from San Marcos High School in 1980. After several years of study at Southwest Texas State University and the University of Texas at Austin, he began working a series of civil engineering-related jobs that eventually led him to Maryland where he worked in subdivision design and commercial development. A growing interest in the natural world led him to study botany at the University of Wyoming, where he received a B.S. in 1995 and an M.S. in 1998. He returned to the University of Texas at Austin in 1998 to pursue a Ph.D. in systematic botany.

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