



Phylogenetics and taxonomy of the New World leafy spurges, *Euphorbia* section *Tithymalus* (Euphorbiaceae)

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The 480 species of leafy spurges, *Euphorbia* subgenus *Esula*, represent the main temperate radiation in the large genus *Euphorbia*. This group is distributed primarily in temperate Eurasia, but with smaller, disjunct centres of diversity in the mountains of the Old World tropics, in temperate southern Africa and in the New World. The majority of New World diversity (32 species) occurs in a single section, section *Tithymalus*. We analysed sequences of the nrITS and plastid *ndhF*, *trnH-psbA*, *trnS-trnG* and *trnD-trnT* regions to reconstruct the phylogeny of section *Tithymalus* and to examine the origins and diversification of the species native to the New World. Our results indicate that the New World species of section *Tithymalus* form a clade that is sister to the widespread, weedy *E. peplus*. The New World species fall into two primary groups: a ‘northern annual clade’ from eastern North America and a diverse clade of both annual and perennial species that is divided into three subgroups. Within the second group, there is a small ‘southern annual clade’ from Texas and northern Mexico, a perennial ‘*Brachycera* clade’ from the western United States and northern Mexico, and a perennial ‘*Esuliformis* clade’ from montane areas of Mexico, Guatemala, Honduras and the Caribbean island of Hispaniola. Ancestral state reconstructions indicate that the annual habit probably evolved in the ancestor of *E. peplus* and the New World clade, with a subsequent reversal to the perennial habit. In conjunction with this phylogenetic framework, the New World species of section *Tithymalus* are comprehensively reviewed. © 2014 The Linnean Society of London, *Botanical Journal of the Linnean Society*, 2014, 175, 191–228.

ADDITIONAL KEYWORDS: ancestral character reconstruction – Hispaniola – ITS – life history – Mexico – North America – phylogenetics – plastid DNA – taxonomic revision.

INTRODUCTION

Recent molecular phylogenetic studies of *Euphorbia* L. (Euphorbiaceae) have greatly refined and improved our understanding of infrageneric relationships within this worldwide genus of c. 2000 species (Yang *et al.*, 2012; Dorsey *et al.*, 2013; Peirson *et al.*, 2013; Riina *et al.*, 2013). A recent phylogenetic study using markers from all three plant genomes and with broad sampling across the genus (Horn *et al.*, 2012) pro-

duced a well-supported backbone topology confirming that *E.* subgenus *Esula* Pers. is sister to the other three subgenera, with *E.* subgenus *Athymalus* Neck. ex Rchb. [the former *E.* subgenus *Rhizanthium* (Boiss.) Wheeler; see Peirson *et al.*, 2013] sister in turn to *E.* subgenus *Euphorbia* and *E.* subgenus *Chamaesyce* Raf. The leafy spurges (subgenus *Esula*) comprise about 480 species in 21 sections and represent the largest radiation of the genus in temperate areas of the Old World (Riina *et al.*, 2013). This major clade has a nearly worldwide distribution (although absent from Australia and Antarctica) and is most

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diverse in temperate Eurasia, particularly in the Mediterranean and the Irano-Turanian regions. The subgenus also occurs in Macaronesia, temperate southern Africa, the Arabian Peninsula, South-East Asia, Madagascar, Reunion, New Zealand and Samoa, and the New World. Species of leafy spurge native to the New World are distributed from Canada and the United States south to Honduras and on Hispaniola. There is also a single, native species of leafy spurge that occurs disjunctly in South America in central Chile.

Previous phylogenetic studies indicate that species of subgenus *Esula* native to the New World represent three different sections of the subgenus and resulted from four independent introductions from the Old World, most probably from Europe and the Mediterranean region (Riina *et al.*, 2013). One introduction took place in the largely Atlantic maritime section *Paralias* Dumort., represented by *E. trichotoma* Kunth in the Caribbean. There were two separate introductions in section *Helioscopia* Dumort., one involving the Appalachian perennial *E. purpurea* (Raf.) Fernald and another involving the mainly annual *E. alta* Norton, *E. spathulata* Lam., *E. texana* Boiss. and, presumably, the disjunct *E. philippiana* (Klotzsch & Garcke) Boiss. from Chile. The majority of the New World diversity (32 species), however, occurs in a single section, *E. section Tithymalus* (Gaertn.) Roep. (Riina *et al.*, 2013). Boissier (1862) placed most species of leafy spurges in *E. section Tithymalus*, but his concept of that large section also included species or subsections that have now been shown to belong to each of the other three subgenera of *Euphorbia* (Steinmann & Porter, 2002; Horn *et al.*, 2012; Yang *et al.*, 2012; Dorsey *et al.*, 2013; Peirson *et al.*, 2013). Following the recent revision of subgenus *Esula* by Riina *et al.* (2013), section *Tithymalus* has been redefined as the group encompassing its type species, *E. pepus* L. and closely related species from both the New and Old Worlds (Fig. 1). The New World species of section *Tithymalus* possess well-developed leaves that lack stipules, cyathia that are arranged in cymose rays around a terminal cyathium, with the rays further divided into dichasial branches, four involucre glands that are entire, crenate or with horn-like (but never petaloid) appendages, smooth capsules and seeds that are usually pitted, sulcate or shallowly sculptured and always carunculate (Figs 2, 3).

The New World species of section *Tithymalus* have not been treated in their entirety since the worldwide treatment of the genus by Boissier (1862). Norton (1900) treated all species of subgenus *Esula* occurring north of Mexico and Johnston (1975) treated those occurring in the Chihuahuan Desert region of northern Mexico. Turner (2011a) dealt with the four

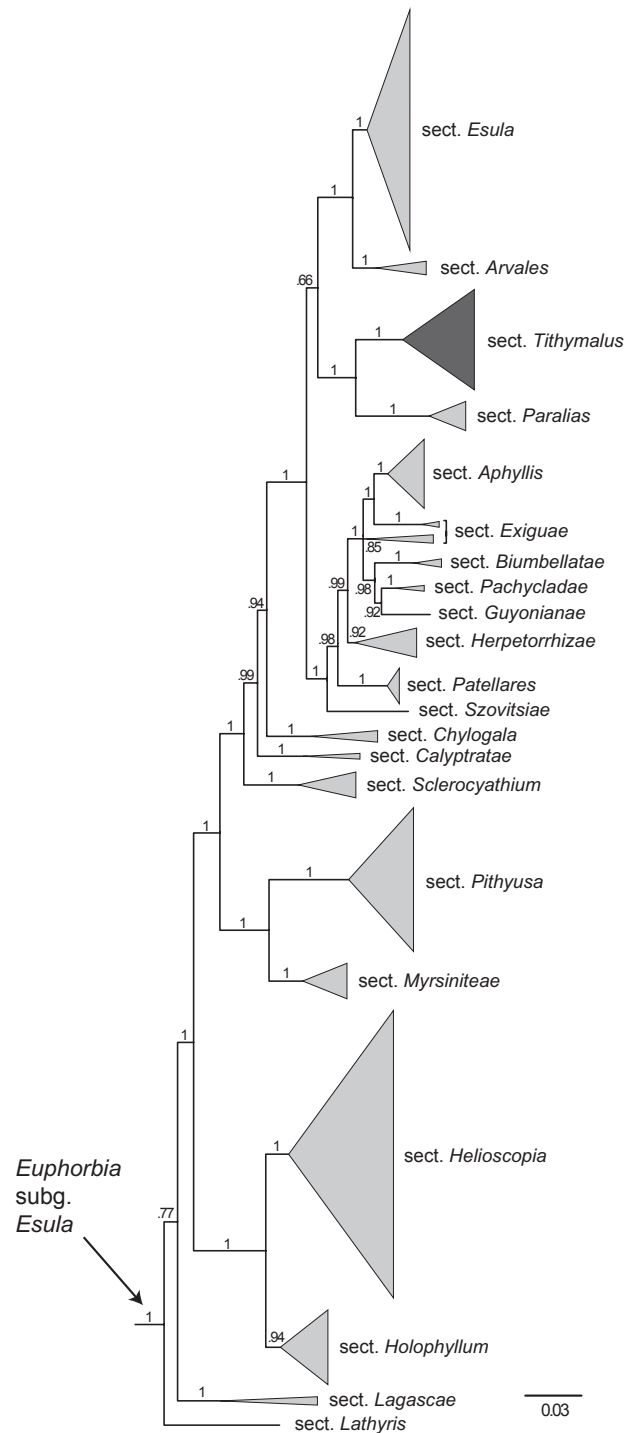


Figure 1. Schematic representation of the Bayesian phylogram from analysis of the combined ITS + *ndhF* dataset of *Euphorbia* subgenus *Esula* and outgroups from Riina *et al.* (2013). Sections recognized in their classification are represented by filled triangles, vertical axes of which are scaled to reflect the number of species in each section. Bayesian posterior probabilities (≥ 0.50) are indicated above the branches.



Figure 2. See caption on next page.

Figure 2. Seeds of *Euphorbia* section *Tithymalus*, showing dorsal surface on left and ventral (adaxial) surface on right: A–L, northern and southern annual clades and Old World members of the section; M–T, *Esuliformis* clade; U–Y, *Brachycera* clade. A, *E. peplus*, a widespread and weedy annual species sister to the New World clade, from Berry in Nov. 2011 (MICH); B, *E. nesomii*, from Mayfield 1905 (MICH); C, *E. austrotexana* var. *carrii*, from Mayfield 3839 (KSC); D, *E. tetrapora*, from Mayfield et al. 1168 (TEX); E, *E. helleri*, from Marx 1945 (NLU); F, *E. longicruris*, from Mayfield 3127 (KSC); G, *E. georgiana*, from Blake & Montgomery 136 (GA); H, *E. ouachitana*, from Mayfield 3108 (KSC); I, *E. crenulata*, from Mayfield 3573 (MICH); J, *E. isaurica*, a perennial species from Turkey, from Davis 16189 (K); K, *E. roemeriana*, from Pilsbry in Apr. 1903 (PH); L, *E. commutata*, from Kral 39081 (GA); M, *E. tuerckheimii*, from Clase 7332 (MICH); N, *E. orizabae*, from Webster 11555 (DAV); O, *E. beamanii*, from Ginzburg 144 (DAV); P, *E. greggii*, from Hinton 25928 (TEX); Q, *E. furcillata*, from Rzedowski 29148 (K); R, *E. esuliformis*, from Rzedowski 30824 (MICH, dorsal face) and Steinmann 5844 (MICH, ventral face); S, *E. longicornuta*, from Pringle 2545 (MICH); T, *E. neilmulleri*, from Mueller & Mueller 1048 (TEX); U, *E. brachycera*, from Mayfield et al. 1439 (TEX); V, *E. lurida*, from Mayfield et al. 3356 (KSC); W, *E. yaquiiana*, from Pringle s.n. (MICH); X, *E. schizoloba*, from Lehto 18110 (MSC); Y, *E. chamaesula*, from White 2512 (MICH). Composition by K. Elliot.

papillose-pubescent species of the *E. longicornuta* complex in northern Mexico and also included notes on two related species. Geltman *et al.* (2011) presented a synopsis of the species of subgenus *Esula* native to the United States and Canada, including typification and new synonymy. More recently, Mayfield (2013) reviewed the annual species of section *Tithymalus* and described four new species from the United States and Mexico. Lastly, Berry *et al.* (in press) treated all native and naturalized species of *Euphorbia* occurring in Canada and the continental United States in the *Flora of North America North of Mexico* Euphorbiaceae treatment.

We focus here on the species of section *Tithymalus* that are native to the New World. Riina *et al.* (2013) included nine species in their molecular phylogenetic analyses (six New World and three Old World), with the remaining species assigned to the section according to morphological and geographical affinities. Given this scenario, our aims in this study were to test the monophyly of section *Tithymalus* more rigorously and reconstruct the evolutionary history of the species through phylogenetic analyses of nuclear ribosomal and plastid DNA regions, review the species-level taxonomy of the New World species in light of the phylogenetic framework and address broader questions concerning the diversification of the section.

MATERIAL AND METHODS

FIELDWORK AND HERBARIUM STUDIES

Fieldwork was conducted by the authors and their colleagues in parts of the Caribbean, the United States and northern Mexico. Specimens from the following herbaria were examined: ARIZ, BM, CIIDIR, DAV, FI, G, IEB, ISC, JBSD, K, MEXU, MICH, MO, MSC, NY, OXF, P, PH, TEX and US. Digital images of specimens and specimen data were accessed using online resources (e.g. Consortium of California Herbaria, Consortium of Pacific Northwest Herbaria, JSTOR

Plant Science, NCU Flora of the South-eastern United States, RM Herbarium Specimen Database, Tropicos and Wisconsin Herbaria Plant Specimen Database). Exsiccatae examined for this study were georeferenced to produce the distribution maps and are all listed in supplementary Appendix S1. Distribution maps were created with ArcMap v. 10.0 (ESRI).

MOLECULAR SAMPLING

We sampled 31 species (81 accessions) in section *Tithymalus*, including multiple accessions of species in many cases. For outgroups, we included seven species from other sections of subgenus *Esula* (three species from the sister group, section *Paralias*, and four species from more distantly related clades). Voucher information and GenBank accession numbers for all sequences analysed in this study are listed in Appendix 1.

DNA EXTRACTION, AMPLIFICATION AND SEQUENCING

Genomic DNA was extracted from leaf tissue dried in silica-gel or from leaf fragments from herbarium specimens, using either a DNeasy Plant Mini Kit (Qiagen) or a modified CTAB extraction procedure (following Doyle & Doyle, 1987; Loockerman & Jansen, 1996). For amplification of the nuclear ribosomal internal transcribed spacer (nrITS) region and plastid *ndhF* gene, we followed the protocols described in Yang & Berry (2011) and Riina *et al.* (2013), respectively. For amplification of the three plastid DNA spacer regions we followed the protocol used for *ndhF* with the following primers: *trnH-psbA* (*trnH-f* and *psbA-3f*; Kress *et al.*, 2005), *trnS-trnG* [*trnS* (GCU) and *trnG* (UCC); Hamilton, 1999] and *trnD-trnT* [*trnD* [tRNA-ASP (GUC)] and *trnT* [tRNA-Thr (GCU)]; Demesure, Sodji & Petit, 1995). PCR products were purified using ExoSap-IT (USB Corp.) or a QIAquick PCR Purification Kit (Qiagen). Purified PCR products were

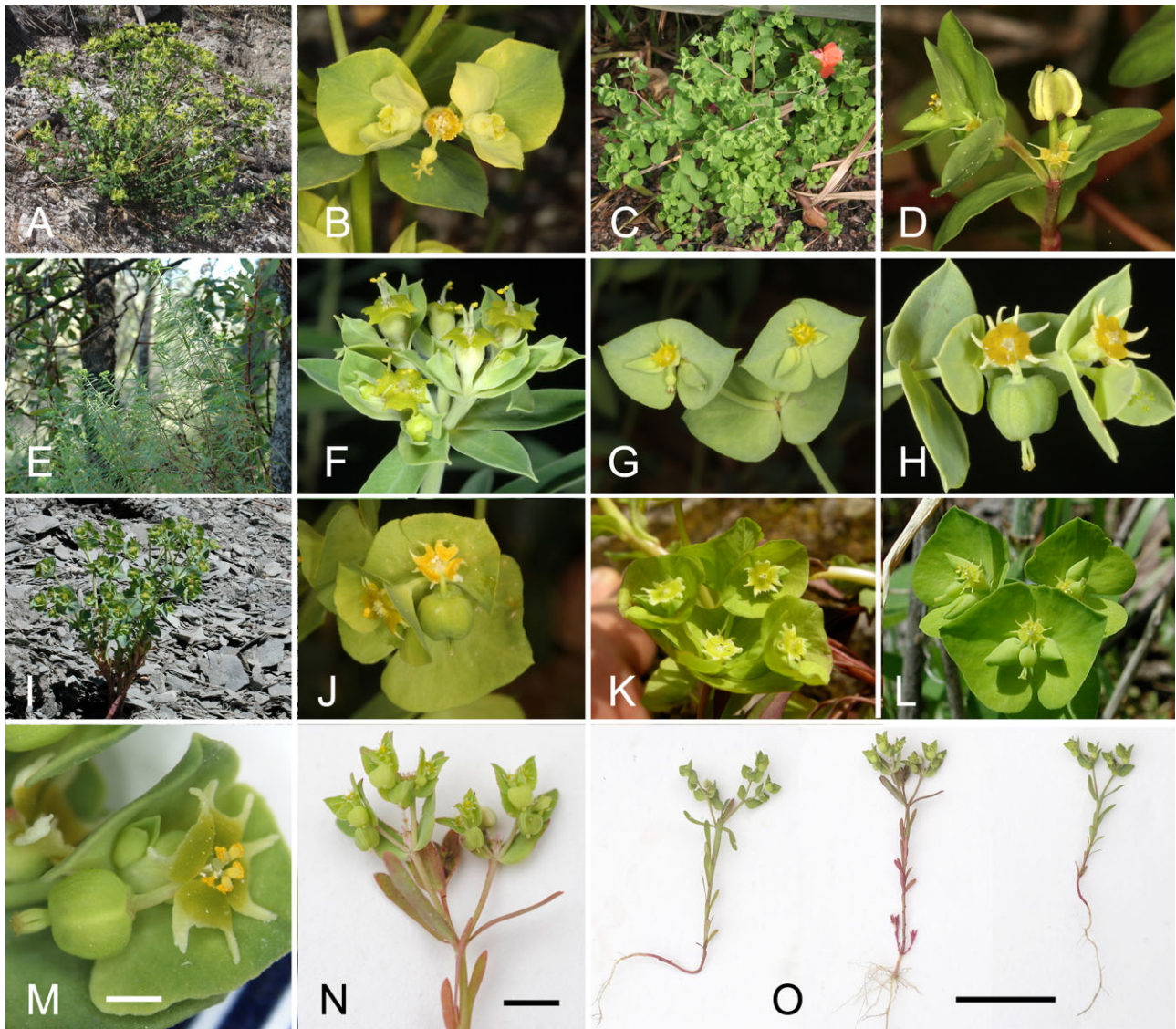


Figure 3. Plants and cyathial features of *Euphorbia* section *Tithymalus*: A and B, *E. yaquiana*, from Pima Co., Arizona; A, habit, B, dichasia and central cyathium showing crenate gland margins and pubescent foliage and cyathia; C and D, *E. peplus*, from Portugal; C, habit, D, cyathia with long-horned glands and capsule with winged ridges; E and F, *E. creberrima*, from Jalisco, Mexico; E, habit showing lax branching and narrow leaves, F, close-up of cyathia and pleiochasium; G, dichasia of *E. brachycera*, from Cochise Co., Arizona; H, cyathia of *E. esuliformis*, from Querétaro, Mexico; I and J, *E. crenulata*; I, habit on loose shale in Archuleta Co., Colorado; J, cyathia and partly fused subcyathial bracts of plant from Lassen Co., California; K, pleiochasium of *E. commutata* from Lewis Co., Tennessee; L, dichasia of *E. ouachitana* from Trousdale Co., Tennessee; M to O, *E. austrotexana*; M, close-up of cyathium of var. *carrii* (scale bar = 1 mm), N, fertile portion of plant of var. *austrotexana* (scale bar = 5 mm); O, entire plants of var. *austrotexana* (scale bar = 5 cm). Photograph credits: A–C, G, J: Paul Berry; D, Ricarda Riina; E–F, H, Victor Steinmann; I, K–O, Mark Mayfield.

sequenced using BigDye chemistry (Applied Biosystems) on an AB 3730xl capillary sequencer.

DATA ASSEMBLY AND PHYLOGENETIC ANALYSES

Chromatogram files were assembled and edited with Sequencher v. 4.10.1 (Gene Codes). Sequence align-

ments were performed with MAFFT v. 5 (Kato *et al.*, 2005) using the default parameters. Final alignments were refined using the Opalescent package in Mesquite v. 2.75 (Wheeler & Kececioglu, 2007; Maddison & Maddison, 2011) and adjusted manually, using a similarity criterion as described in Simmons (2004). The number of parsimony-informative sites was esti-

mated in PAUP* v. 4.0b.10 (Swofford, 2003). Indels in the *ndhF* gene and plastid DNA spacer regions were scored using simple indel coding (SIC *sensu* Simmons & Ochoterena, 2000) with SeqState v. 1.4.1 (Müller, 2005). Four datasets were analysed in the analyses described below: ITS, *ndhF*, plastid DNA spacer (consisting of the concatenated *trnH-psbA*, *trnS-trnG* and *trnD-trnT* spacer regions) and combined ITS + *ndhF* + plastid DNA spacer (with or without scored indels).

RAxML v. 7.2.6 (Stamatakis, 2006) was used to conduct maximum-likelihood (ML) phylogenetic analyses of the individual datasets (ITS, *ndhF* and plastid DNA spacer regions) and the combined ITS + *ndhF* + plastid DNA spacer dataset (without scored indels). The nucleotide substitution model was set to GTR + γ . We performed 500 ML rapid bootstrap (BS) replicates, followed by a thorough ML search for the best tree. Before concatenation, the trees from the individual analyses were inspected for areas of strongly supported incongruence. As there were no such instances of incongruence, the three individual datasets were concatenated into a single, combined matrix (using a total evidence approach *sensu* Kluge, 1989). The combined dataset was partitioned into the ITS, *ndhF* and plastid DNA spacer regions. The ITS region was not further partitioned.

MrBayes v. 3.1.2 (Huelsenbeck & Ronquist, 2001; Ronquist & Huelsenbeck, 2003) was used to conduct a Bayesian (BI) analysis of a combined ITS + *ndhF* + plastid DNA spacer dataset (with scored indels included), partitioning the dataset as above but with an additional partition for the SIC-scored indels. The nucleotide substitution model GTR + I + γ was applied to each of the three DNA partitions, as selected by Akaike's information criterion (AIC) in jModelTest v. 0.1.1 (Posada, 2008), whereas a binary model was applied to the SIC-scored indel partition. Two independent runs of four chains each (three heated, one cold) were run for 10 million generations, starting from random trees, using the default temperature of 0.2 and sampling trees every 100 generations. The log likelihoods from the independent runs were inspected with Tracer v. 1.5 (Rambaut & Drummond, 2007) to verify that stationarity had been reached. The first 25 000 trees (25%) were discarded as burn-in, using the remaining 75 001 trees to compute the majority rule consensus tree.

ANCESTRAL STATE RECONSTRUCTION

Species of section *Tithymalus* were scored for life-history characteristics and were coded as either annual/biennial or perennial. Mesquite v. 2.75 (Maddison & Maddison, 2011) was used to perform a ML reconstruction of life-history evolution, imple-

menting the Mk1 model of evolution (Lewis, 2001) and using default parameters. The Mk1 model of evolution is a *k*-state, one-parameter model that assumes equal rates of change between states. Life-history reconstructions were traced onto the Bayesian consensus tree, with outgroups beyond section *Paralias* pruned from the tree.

RESULTS

Our sampling within section *Tithymalus* included 31 species (*c.* 75% of the section) and 81 accessions (Appendix 1), which comprised all but four (*E. correllii* M.C.Johnst., *E. eggersii* Urb., *E. georgiana* Mayfield and *E. longicornuta* S.Watson, all very rare) of the New World species in the section. Ingroup sampling for each dataset was as follows: 22 species (59 accessions) for the nrITS, 29 species (78 accessions) for the plastid *ndhF* gene and 29 species (65 accessions) for the plastid spacer regions (note that the *trnS-trnG* and *trnD-trnT* regions were sequenced for only a subset of samples); 29 species (78 accessions) were sampled in the combined dataset (Table 1). *Euphorbia chiribensis* V.W.Steinm. & Felger and *E. furcillata* Kunth were represented only by sequences from the *trnH-psbA* spacer region and were therefore not included in the combined dataset. Of the sequences analysed, 45 ITS, 58 *ndhF*, 65 *trnH-psbA*, 25 *trnS-trnG* and 25 *trnD-trnT* sequences were newly generated.

INDIVIDUAL AND COMBINED DATASETS

Summary statistics for the sequence data are provided in Table 1. The ITS dataset contained the highest proportion of variable sites in this study (31.9%), followed by *ndhF* (12.1%) and the plastid DNA spacer regions (5.6%; note that this latter value is not directly comparable because sampling for the plastid DNA spacers did not include outgroups). Alignments of all three datasets were straightforward with no alignment-ambiguous sites. There were 57 indels scored for the plastid DNA regions (indels were not scored for the ITS dataset). Results of the ML phylogenetic analyses of the individual ITS, *ndhF* and plastid DNA spacer datasets (with all available accessions included for each region) are shown in the online supplement (Figs S1–S3). The monophyly of section *Tithymalus* is strongly supported by ML analyses of the ITS (BS = 100%; Fig. S1) and *ndhF* (BS = 100%; Fig. S2) datasets (the monophyly of the section could not be assessed based on the plastid DNA spacer dataset alone, as those regions were sequenced for ingroup samples only; Appendix 1; Fig. S3).

Table 1. Summary statistics from ITS, *ndhF*, concatenated plastid DNA spacer regions and combined ITS + *ndhF* + plastid DNA spacer datasets for *Euphorbia* section *Tithymalus* and outgroup species analysed in this study

	ITS	<i>ndhF</i>	Plastid DNA spacers	Combined
Total no. of accessions	59	78	65	78
No. of ingroup species	22	29	29	29
No. of outgroup species	7	7	0	7
Unaligned length* (bp)	256–642	946–1484	327–2007	1317–4030
Aligned length (bp)	698	1490	2279	4467
Variable characters [%]	223 [31.9]	180 [12.1]	128 [5.6]	528 [11.8]
Missing data (%)	29.3	7.4	52.9	42.7
Potentially parsimony-informative sites				
Section <i>Tithymalus</i>	64	62	57	176
Section <i>Tithymalus</i> + outgroup	136	96	–	282
ML score (lnL)	–3043.52	–3721.02	–4089.29	–11 050.29

The plastid DNA spacer dataset was a concatenated matrix of the *trnH-psbA*, *trnS-trnG* and *trnD-trnT* spacer regions and did not include outgroup sampling. Likelihood scores for the maximum-likelihood trees from RAxML are provided (see Figs S1–S4 -for the ML trees). Full sampling details can be found in Appendix 1.

*Lower boundaries for unaligned lengths correspond to partial sequences where the full-length sequences failed to amplify or to samples for which only a single region was sequenced (e.g. many samples in the plastid DNA spacers dataset are represented by only the *trnH-psbA* spacer).

The ML tree for the combined ITS + *ndhF* + plastid DNA spacer dataset (without scored indels) and the BI tree for the combined ITS + *ndhF* + plastid DNA spacer dataset (with scored indels included) are both congruent for most moderately or strongly supported nodes [BS \geq 50; posterior probability (PP) \geq 0.80] and are well-resolved overall (Figs 4, S4). Section *Tithymalus* is strongly supported as monophyletic in both the ML and the BI analyses (BS = 100%; PP = 1). The major clades circumscribed from the analyses of the combined datasets (Figs 4, S4) were moderately to strongly supported in the *ndhF* tree (Fig. S2) but were unsupported or only weakly supported in the individual ITS (Fig. S1) and plastid DNA spacer (Fig. S3) gene trees.

PHYLOGENETIC STRUCTURE

In both the ML and the BI combined analyses, section *Tithymalus* was strongly supported as sister to section *Paralias* in subgenus *Esula* (BS = 100%; PP = 1; Figs 4, S4). The BI analysis recovered an early diverging grade of Old World species within section *Tithymalus*. This consisted of a clade of the perennial species, *E. herniariifolia* Willd. and *E. isaurica* M.S.Khan, which is sister to the rest of the section, with the widespread and weedy annual *E. peplus* sister to all of the New World species (PP = 1; Fig. 5). The ML analysis likewise recovered the Old World *E. herniariifolia* and *E. isaurica* clade as sister to the remainder of the section with strong support (BS = 100%; Fig. S4), but *E. peplus* was

weakly supported as embedded in the New World clade (BS = 59%; Fig. S4).

Our results show that the New World clade is composed of two strongly supported main clades (Figs 4, S4). The ‘northern annual clade’ (BS = 82%; PP = 1) contains eight annual species occurring throughout temperate forested regions of the United States and Canada and in prairie or rock-substrate habitats in the southern United States and northern-most Mexico. It is sister to a strongly supported (BS = 92%; PP = 1), diverse clade of both annual and perennial species that is in turn divided into three subgroups. Within this latter clade, the small ‘southern annual clade’ (BS = 100%; PP = 1) is composed of three annual species from prairies and chaparral in Texas and northern Mexico. The remaining species form two entirely perennial and mainly montane groups. The first of the perennial groups is the ‘*Brachycera* clade’ (BS = 74%; PP = 0.99) that consists of seven species from the southwestern United States and adjacent northern Mexico. The second group, here referred to as the ‘*Esuliformis* clade’, includes 14 species distributed primarily in Mexico and extending into Guatemala and Honduras, as well as on Hispaniola. In our phylogenetic analyses, this group consists of a strongly supported core clade (BS = 77%; PP = 0.99), with *E. tuerckheimii* Urb. weakly supported as sister to the core clade (BS < 50%; PP = 0.51) and one accession of *E. orizabae* Boiss. from Jalisco (Mexico) unresolved, forming a polytomy with the *Esuliformis*, *Brachycera* and southern annual clades.

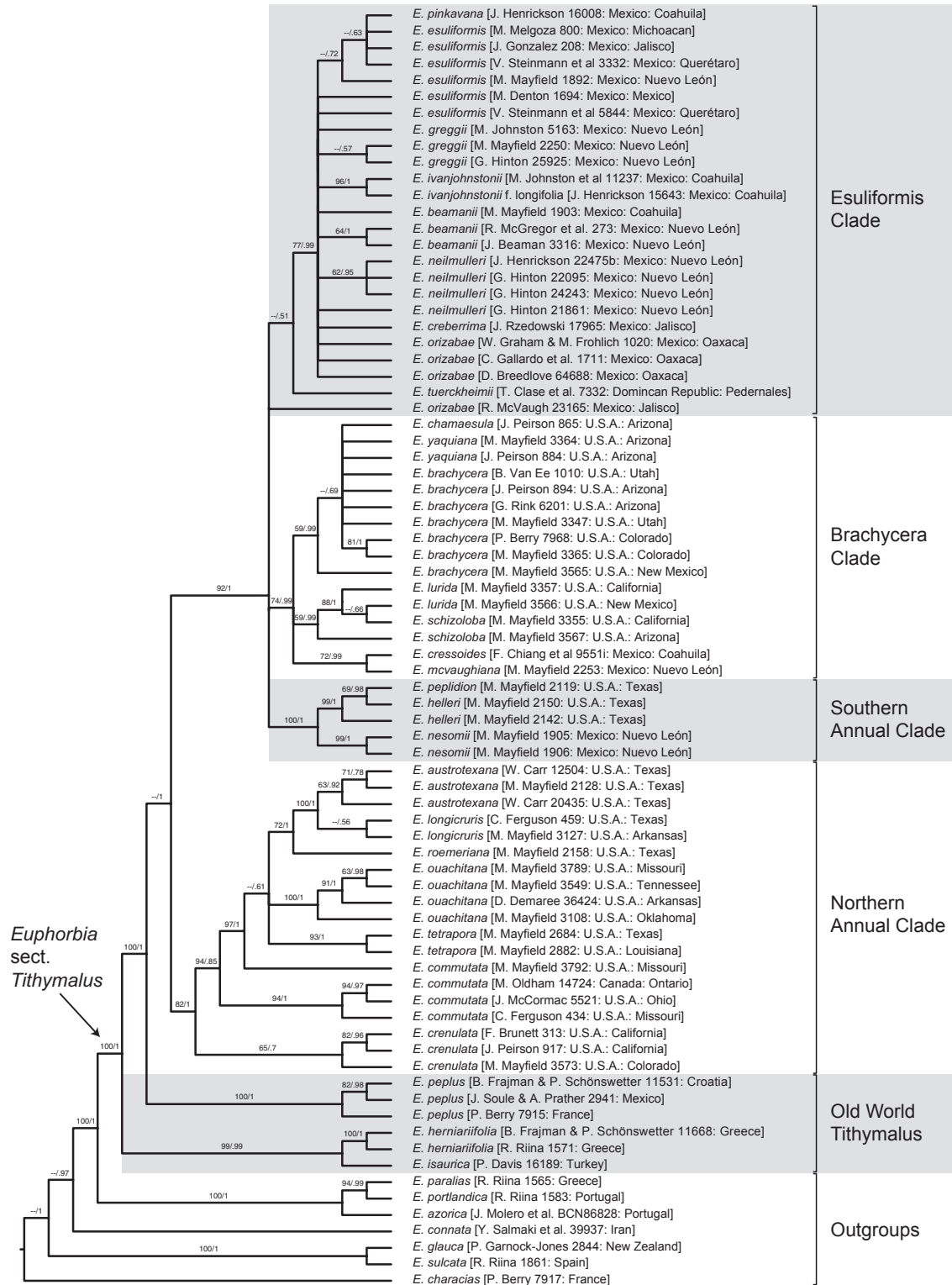


Figure 4. 50% majority-rule consensus cladogram from Bayesian analysis of the combined ITS + *ndhF* + plastid DNA spacer dataset (with scored indels included) of *Euphorbia* section *Tithymalus* and outgroups. Bayesian posterior probabilities (≥ 0.50) and maximum-likelihood bootstrap values from the RAxML analysis ($\geq 50\%$) are indicated above the branches, separated by a slash mark. Major clades recovered for New World taxa (and an Old World *Tithymalus* grade and outgroup taxa) are denoted to the right of the respective samples.

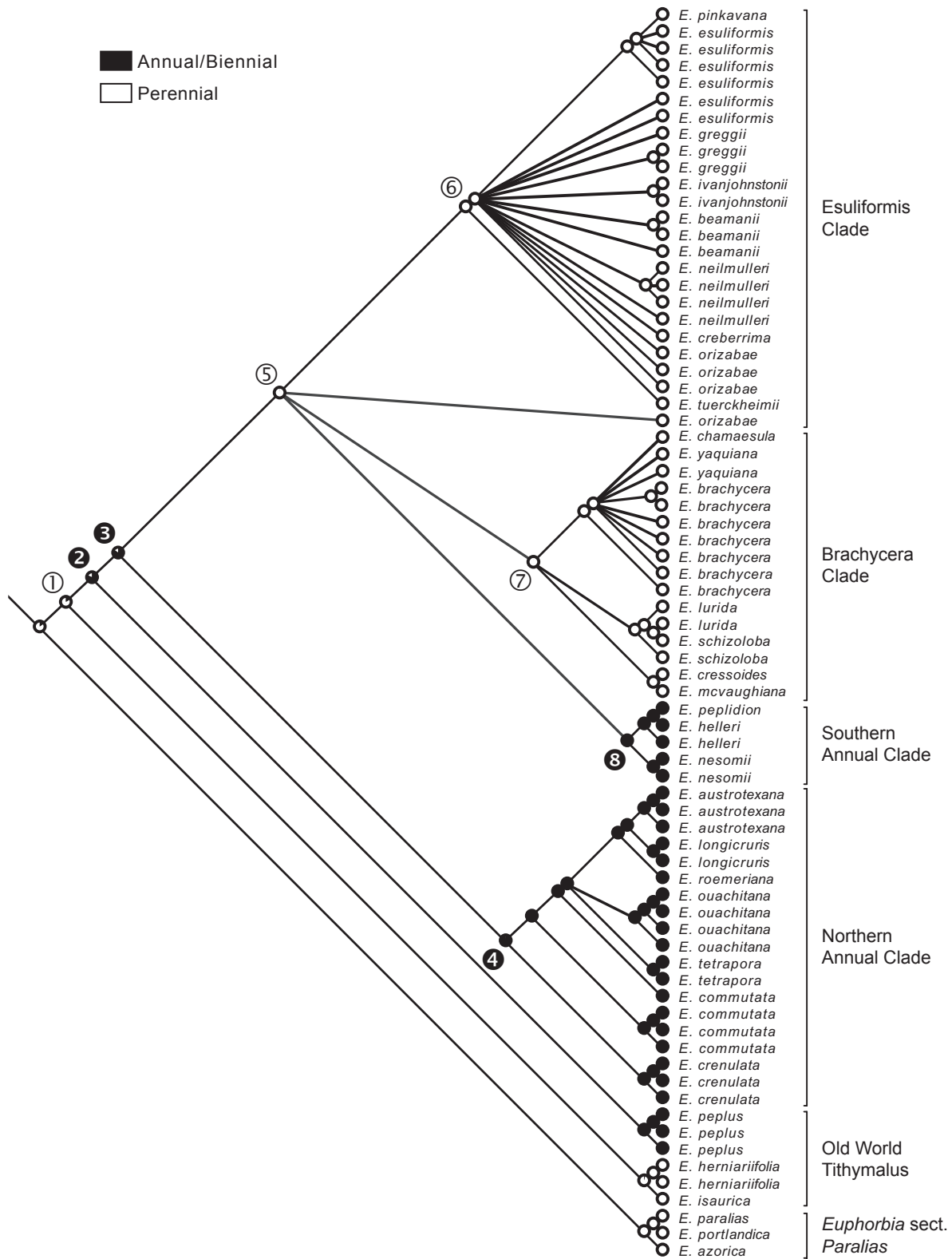


Figure 5. Maximum-likelihood character reconstructions of life history in *Euphorbia* section *Tithymalus* traced onto the 50% majority-rule BI consensus tree. Major clades recovered for New World taxa (and an Old World *Tithymalus* grade and outgroup taxa) are denoted to the right of the respective samples. Outgroups beyond section *Paralias* were pruned from the tree.

PHYLOGENETIC PATTERNS RELATIVE TO SPECIES
DELIMITATION

We used mainly morphological criteria to delimit species in section *Tithymalus*. Compared with other subgenera of *Euphorbia*, distinguishing characters between species are often more subtle, given the overall homogeneity of the sections of subgenus *Esula*. The annual species in the New World clade of section *Tithymalus* were generally more straightforward to circumscribe (even when differences between species were based on relatively few characters), whereas some members of the perennial clades tended to form complexes in which species boundaries were much less discrete (e.g. in the *E. brachycera* clade). We were also left with a residue of specimens that we could not place at this time with certainty; these are treated at the end of the Taxonomic Treatment as ‘unplaced or possibly new entities’ and we suggest that there will be additional taxa described in this section in the future.

Our phylogenetic results show that many of the annual species in section *Tithymalus* form discrete lineages, in which multiple accessions of species often form strongly supported clades (e.g. *E. peplus*, *E. crenulata* Engelm., *E. ouachitana* Mayfield and *E. austrotexana* Mayfield in Figs 4, S4). In the two perennial groups, however, there was generally insufficient resolution in the tree to determine whether currently recognized species form exclusive lineages, such as in the *E. brachycera*–*E. chamaesula*–*E. yaqui-ana* species group and broadly across the *Esuliformis* clade.

ANCESTRAL STATE RECONSTRUCTION

ML reconstructions based on our Bayesian tree indicate that the annual habit probably evolved twice in section *Tithymalus* (Fig. 5). The earliest diverging Old World members sampled in the phylogenetic analyses (*E. herniariifolia* and *E. isaurica*) are both perennial and the root node for the section was therefore reconstructed as perennial with high proportional likelihood (Node 1; 86%). The annual habit most probably evolved in the ancestor of *E. peplus* and the New World *Tithymalus* clade (Node 2; 70%) and was maintained in the northern annual clade (Nodes 3, 4; 72 and 100%, respectively). The reconstruction indicates a subsequent reversal to the perennial habit along the branch leading to the next major clade (Node 5; 99%) that was maintained in both the *Brachycera* clade (Node 6; 100%) and the *Esuliformis* clade (Node 7; 100%). A second origin of the annual habit probably evolved within this larger clade, along the branch leading to the southern annual clade (Node 8; 99%).

DISCUSSION

Euphorbia section *Tithymalus* is unique among the 21 sections of subgenus *Esula* in having greater species diversity in the New World than in the Old World. Our phylogenetic results now show convincingly that the 32 New World species of section *Tithymalus* form a strongly supported clade that is sister to the widespread, weedy *E. peplus* and these are in turn sister to other Old World members of the section (Fig. 4). In the New World group of section *Tithymalus*, four main clades can be recognized, two consisting of annual species primarily from the eastern and central United States and north-eastern Mexico and two consisting of perennial species from the western United States south to Honduras and on the island of Hispaniola.

ARRIVAL AND DIVERSIFICATION IN THE NEW WORLD

Most Old World members of section *Tithymalus* occur in relatively arid habitats from the eastern Mediterranean region to Iran and the Arabian Peninsula. *Euphorbia peplus* is also considered native to Europe and the Mediterranean region but is now widely distributed in temperate areas throughout the world, probably through recent human activities. In the Bayesian tree (Fig. 4), the New World members of section *Tithymalus* form a strongly supported clade, thus indicating a single origin from a presumably Old World ancestor. Age estimates suggest a late Miocene/early Pliocene stem age of c. 5 Ma for the New World clade of section *Tithymalus* (J. W. Horn *et al.*, unpubl. data). Similar ages have also been estimated for the stem age of the New World *E. spathulata* species group and for the split of the Appalachian *E. purpurea* from its European relatives in section *Helioscopia* (J. W. Horn *et al.*, unpubl. data). These ages are much more recent than those found for most dated intercontinental disjunctions of the Arcto-Tertiary flora (Harris, Wen & Xiang, 2013) and might suggest a long-distance dispersal mechanism to explain the disjunction pattern. Alternatively, some recent fossil and molecular evidence suggests that the North Atlantic Land Bridge may have functioned as a viable corridor for plant migration into the latest Miocene (Denk, Grimsson & Zetter, 2010) and this may have facilitated the migration of European taxa into North America. A possible scenario for the appearance of section *Tithymalus* in North America could have involved the arrival of an annual ancestor allied to *E. peplus* in the lowlands of eastern North America followed by a southward and westward spread and diversification of the group. Both perennial clades have diversified in montane habitats in western North America and Mexico and the ancestor of the

two Caribbean species could have arrived there from a common ancestor with the Mexican perennial species by long-distance dispersal. Hispaniola has the highest mountains (Pico Duarte reaches 3098 m) and the greatest extent of montane habitat of any island in the Caribbean, thus offering the best conditions for the establishment of montane elements in that region.

LIFE-HISTORY EVOLUTION

Euphorbia section *Tithymalus* contains both annual and perennial species and ancestral reconstructions suggest that multiple shifts in life history occurred in the section. The Old World members of the group are equally divided between annuals (*E. chamaepeplus* Boiss. & Gaill., *E. hieroglyphica* Coss. & Durieu ex Boiss., *E. peplus* and *E. punctata* Delile) and perennials (*E. caudiculosa* Boiss., *E. herniariifolia*, *E. isaurica* and *E. promecocarpa* Davis), whereas the New World species are predominantly perennial. Because the basal Old World members sampled in the phylogenetic analyses were perennial (*E. herniariifolia* and *E. isaurica*), the ancestral state for the section was reconstructed as perennial. The sister lineage to the New World clade in our Bayesian tree is the Old World annual *E. peplus*, however, and our character state reconstruction suggests that the annual habit evolved in the ancestor of *E. peplus* and the New World *Tithymalus* clade. A subsequent reversal to the perennial habit occurred in the New World lineage. Inclusion of the remaining Old World species in future phylogenetic studies and character state reconstructions, however, will be necessary to clarify life-history evolution further, especially in the earliest-diverging lineages of section *Tithymalus*.

Euphorbia section *Tithymalus* is another clear example of the lability of life-history evolution in the leafy spurge. Earlier sectional classifications in subgenus *Esula* relied heavily on the distinction between annual and perennial species, but they have proven to be largely incongruent with the evolutionary history of the group (Frajman & Schönswetter, 2011; Riina *et al.*, 2013). For example, Prokhanov (1949) included all annual species with bicornate nectary glands (e.g. *E. exigua* L., *E. falcata* L., *E. medicaginea* Boiss., *E. peplus*, *E. sulcata* Lens ex Loisel. and *E. turczanowii* Kar. & Kir.) in section *Cymatospermum* (Prokh.) Prokh., but we now know that these species belong to five separate sections of *Euphorbia*. Similarly, Prokhanov restricted section *Chamaebuxus* Lázaro to perennial species with oval nectary glands and verrucose capsules, but Riina *et al.* (2013) showed those species to belong to a larger section *Helioscopia* that also has annual species embedded in it.

Our phylogenetic results show relatively high molecular differentiation among the New World

annual species in section *Tithymalus*. Both the northern and the southern annual clades are strongly supported and relationships within the clades are mostly well resolved. As in some other groups (e.g. flowering plants in general: Smith & Donoghue, 2008; *Veronica* L.: Müller & Albach, 2010), branch lengths in the annual clades of section *Tithymalus* are longer than those in the perennial clades (e.g. northern annual clade vs. *Esuliformis* clade in Fig. S4). Shorter generation times in the annual clades probably provided more opportunities for genetic changes/mutations to occur (Smith & Donoghue, 2008). In each of the two perennial clades, phylogenetic relationships are less resolved and there is poor differentiation in some of the species complexes (e.g. in *E. brachycera* Engelm. and *E. esuliformis* S.Schauer). In *Lupinus* L., Drummond *et al.* (2012) found that increased rates of diversification were strongly correlated with shifts to a perennial life history and invasion of montane habitats in western North America and Mexico. It is possible that a similar scenario has occurred in the two perennial clades in section *Tithymalus*.

CYTOLOGICAL OBSERVATIONS

The sister species to the New World clade of section *Tithymalus*, *E. peplus*, is well documented cytologically and is one of just two Old World species that have been studied thus far, with numerous counts of $2n = 16$ (reviewed in Bauer, 1971). The other Old World species that has been counted, *E. herniariifolia*, has two counts of $2n = 16$ (Strid & Franzen, 1981; Franzen & Gustavsson, 1983) and one of $2n = 18$ (Strid, 1983). Perry (1943) considered $x = 8$ to be the base chromosome number for *Euphorbia*, although other low numbers of $x = 6, 7, 9$ and 10 have been recorded for the genus.

Among the New World members of the section, Mayfield (2013) reported two different chromosome numbers, $2n = 28$ for *E. brachycera*, *E. commutata* Engelm. ex A. Gray, *E. peplidion* Engelm. and *E. roemeriana* Scheele versus $2n = 26$ for *E. austrotexana* var. *austrotexana*, *E. chamaesula*, *E. longicurris* Scheele, *E. aff. lurida* Engelm., *E. lurida* Engelm., *E. ouachitana* and *E. yaquiana* Tidestr. These data indicate that the North American members of *E.* section *Tithymalus* are probably tetraploid derivatives of Old World ancestors, either from a now extinct ancestor with $2n = 14$ or from an ancestor like *E. peplus* having $2n = 16$, followed by subsequent aneuploid reduction in chromosome number. In the North American clade, the northern annual clade and the perennial *Brachycera* each have species with $2n = 28$ and $2n = 26$, which indicates that aneuploid losses or gains have occurred at least twice independently in that group. Given the hypotheses of phylogenetic rela-

tionships generated by the molecular data, further cytological study of the remaining New and Old World species would be very promising.

NON-NATIVE LEAFY SPURGES IN NORTH AMERICA

In addition to the 32 native species, two non-native members of section *Tithymalus* have been recorded in North America. Most notably, *E. peplus*, the sister lineage to the New World clade of section *Tithymalus*, occurs as an introduced species in the New World. Unlike a number of other introduced members of subgenus *Esula*, however, it is not an aggressive invader of rangeland but typically occurs in gardens and waste places. The Old World native *E. herniariifolia* was collected once as a waif on an ore pile at the Port of Baltimore, Maryland (Reed, 1964), but it has not been documented since. The capsules of *E. peplus* (Fig. 3D) and *E. herniariifolia* both possess distinctive, longitudinal crests or ridges that make these species easy to distinguish, whereas the capsules of all New World members of the section are smooth (e.g. Fig. 3H, J).

Thirteen additional non-native species of leafy spurges from other sections of subgenus *Esula* have also become established in North America (Berry *et al.*, in press). These species represent eight different sections of subgenus *Esula* (Riina *et al.*, 2013) and none of the species is closely related to the New World clade of section *Tithymalus*. Most notable among them are several members of section *Esula*, including *E. virgata* Waldst. & Kit., a widely distributed invasive weed that has caused considerable concern among range managers in the United States and Canada (Watson, 1985). *Euphorbia virgata* (leafy spurge) has been widely treated as *E. esula* L. in North America, but the latter is actually a distinct, non-weedy European species that has never been widespread in North America (Berry *et al.*, in press).

TAXONOMIC TREATMENT

This taxonomic review provides a much-improved understanding of the diversity in the group and points to the need for additional fieldwork in Mexico and the south-western United States to understand population-level variation better, especially in the perennial clades. In the treatment that follows, we provide a list of all species currently placed in section *Tithymalus*, together with distribution maps, a key, comprehensive synonymy, typification and phylogenetic placement for the New World species. Among the perennials, there are a number of specimens that are difficult to place to species and that may represent yet unrecognized species; these are discussed at the end of the treatment. Geltman *et al.* (2011) provided synonymy and type information for the species that

occur in the United States and Canada. We include that information below along with updates. Because *E. peplus* is a common, garden weed in the New World, we include it in the key to species but not in the taxonomic treatment. Exsiccatae examined for this study and georeferenced to produce the distribution maps (Figs 6–14) are listed in Appendix S1.

EUPHORBIA SECTION TITHYMALUS (GAERTN.)

Roep. in Duby, Bot. Gall., ed. 2: 412. 1828 = *Tithymalus* Gaertn., Fruct. Sem. Pl. 2: 115 (1790), nom. cons. = *E.* section *Peplus* Lázaro, Comp. Fl. Españ. 2: 282. 1896. = *E.* subsection *Foveospermae* Hurusawa, J. Jap. Bot. 16: 342. 1940 – Type: *E. peplus* L. (= *T. peplus* (L.) Gaertn.; type cons. for *Tithymalus*).

Annual, biennial or perennial herbs or subshrubs, glabrous, pubescent or rarely papillose. Stem leaves alternate, margin entire or rarely serrulate, venation pinnate, usually obscure (midrib usually prominent). Cyathia arranged in terminal pleiochasia; individual pleiochasia branches unbranched or two- to four-branched at one or more successive nodes; bracts subtending pleiochasia (pleiochasia bracts) whorled, green, similar in shape and size to distal stem leaves or distinctly different; bracts on branches and subtending cyathia (dichasia and subcyathial bracts) opposite, free or partially connate; additional cymose branches often present in axils of distal leaves, but alternately arranged and not subtended by whorled bracts. Cyathial (involucral) glands four, oblong to crescent-shaped, margin entire or dentate/crenate, two horn-like appendages usually present. Capsule globose to oblong-ovoid, usually smooth or in some cases slightly punctulate, glabrous or pubescent, cocci rounded or crested-winged. Seeds oblong to subovoid, pitted, sulcate, shallowly sculptured, or foveolate, rarely smooth, white, grey to brown, or mottled, carunculate. $2n = 16, 26, 28$.

Included species (40, those included in the current or previous molecular phylogenetic studies are in bold) – *E. austrotexana* Mayfield, *E. beamanii* M.C.Johnst., *E. brachycera* Engelm., *E. caudiculosa* Boiss., *E. chamaepeplus* Boiss. & Gaill., *E. chamaesula* Boiss., *E. chiribensis* V.W.Steinm. & Felger, *E. commutata* Engelm. ex A.Gray, *E. correllii* M.C.Johnst., *E. creberrima* McVaugh, *E. crenulata* Engelm., *E. cressoides* M.C.Johnst., *E. eggertii* Urb., *E. esuliformis* S.Schauer, *E. furcillata* Kunth, *E. georgiana* Mayfield, *E. greggii* Engelm. ex Boiss., *E. helleri* Millsp., *E. herniariifolia* Willd., *E. hieroglyphica* Coss. & Durieu ex Boiss., *E. isaurica* M.S.Khan, *E. ivanjohnstonii* M.C.Johnst., *E. longicornuta* S.Watson, *E. longicruris* Scheele, *E. lurida* Engelm., *E. mcvaughiana* M.C.Johnst., *E. neilmulleri* M.C.Johnst., *E. nesomii* Mayfield,

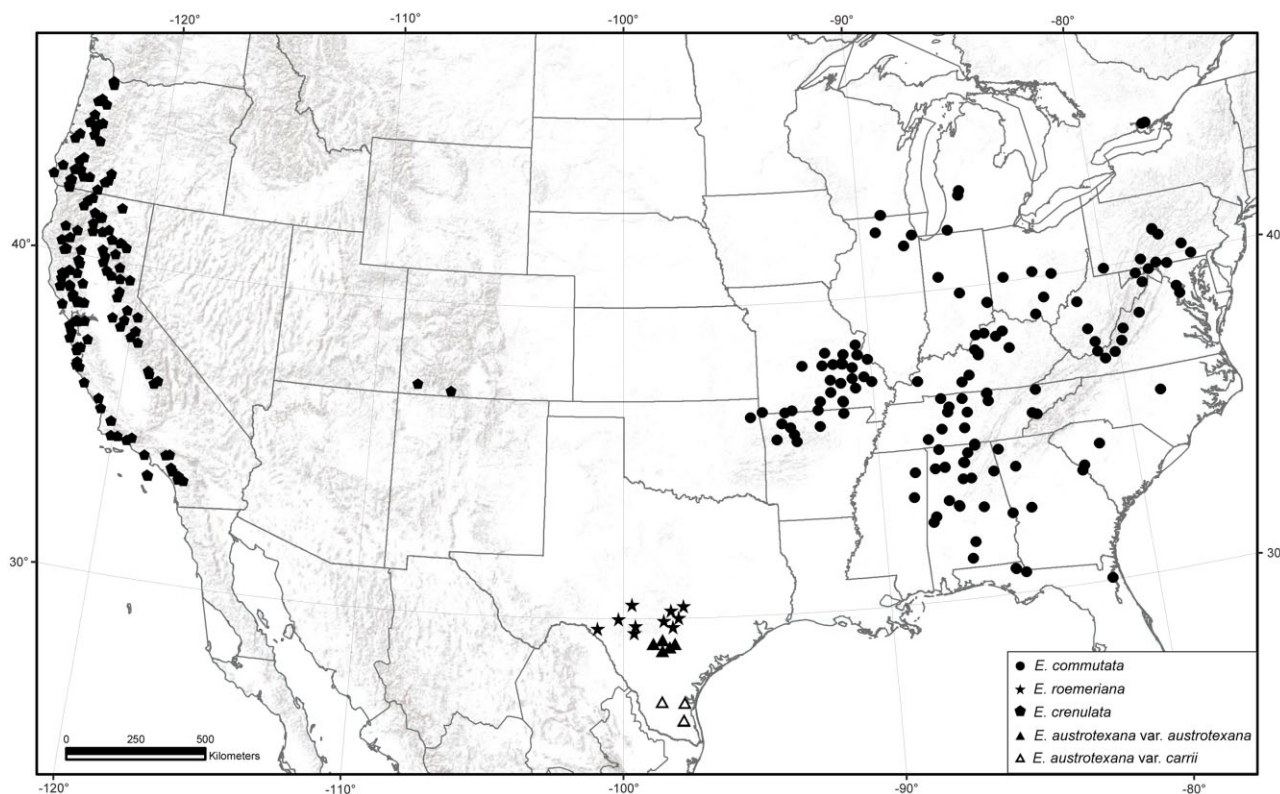


Figure 6. Geographical distribution of *Euphorbia austrotexana*, *E. commutata*, *E. crenulata* and *E. roemeriana* in the USA and Canada. For these and successive figures, see the Taxonomic Treatment for overall range extensions and Appendix S1 for a spreadsheet containing all georeferenced specimens used to generate the maps.

E. orizabae Boiss., *E. ouachitana* Mayfield, *E. pep- lidion* Engelm., *E. peplus* L., *E. pinkavana* M.C.Johnst., *E. promecocarpa* Davis, *E. punctata* Delile, *E. roemeriana* Scheele, *E. schizoloba* Engelm., *E. tetrapora* Engelm., *E. tuerckheimii* Urb., *E. yaquiana* (Cockerell) Tidestr.

Distribution and habitat: Eight species (*E. caudiculo- losa*, *E. chamaepeplus*, *E. herniariifolia*, *E. hiero- glyphica*, *E. isaurica*, *E. peplus*, *E. promecocarpa* and *E. punctata*) are native to the Old World, from the eastern Mediterranean region to the Arabian Penin- sula and Iran. The weedy *E. peplus* is considered native to the Mediterranean region but is now wide- spread in temperate regions worldwide. The remain- ing 32 species in the section are native to the New World and are distributed from the United States and Canada south to Guatemala and Honduras and on Hispaniola. Many of the New World perennial species are restricted to montane habitats at relatively high elevations, whereas the annual species typically occur at lower elevations. Some species (e.g. *E. brachycera* and *E. esuliformis*) are widespread, whereas others are quite local and narrowly distributed (e.g. *E. geor- giana* and *E. cressoides*).

Taxonomic remarks: Leafy spurges are rather homo- geneous in aspect compared with the diverse array of growth forms and succulent species found in the other subgenera of *Euphorbia* and they can sometimes be difficult to distinguish. In section *Tithymalus*, one of the most useful characters to separate species is the difference of annual/biennial (Fig. 3C, I) vs. perennial habit (Fig. 3A, E). Life history is generally easily categorized in the group and is the first step in the key below. Vegetatively, most species in the section are glabrous, including all of the annual species. There are, however, a few perennial species that are characteristically densely hairy, such as *E. cressoides*, *E. mcvaughiana*, *E. neilmulleri* and *E. yaquiana* (Fig. 3A, B). Another group of four perennial species [*E. creberrima* (Fig. 3E, F), *E. ivanjohnstonii*, *E. longi- cornuta* and *E. pinkavana*] is characterized by short, papillose pubescence. Whereas most New World leafy spurges are fibrous-rooted, *E. greggii* is unique in the group in having discrete underground tubers. In terms of the cyathia, the majority of species in section *Tithymalus* have the typical, two-horned gland appendages that are prevalent in the subgenus (Fig. 3D, F–H, J, L). Several New World species [e.g. *E. schizoloba*, *E. yaquiana* (Fig. 3B) and occasionally

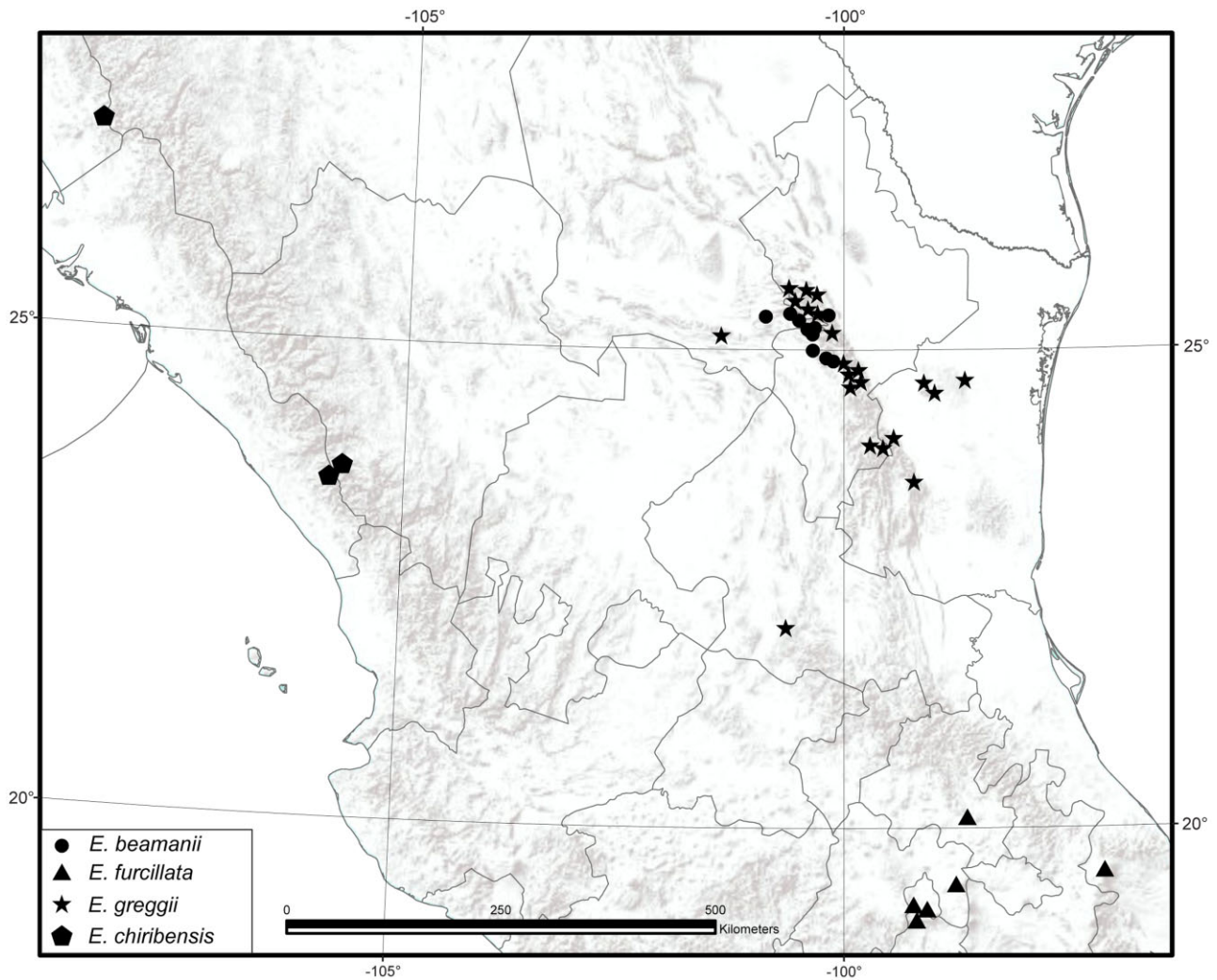


Figure 7. Geographical distribution of *Euphorbia beamanii*, *E. chiribensis*, *E. furcillata* and *E. greggii* in Mexico.

E. brachycera and *E. commutata* (Fig. 3K) to a limited extent], however, have dentate or crenate gland margins without evident horns.

Seed characters are especially useful for distinguishing some species in section *Tithymalus* (Fig. 2; see key below). The seeds of all species in the group possess a caruncle, but differences in the size and shape of the caruncle are pronounced. *Euphorbia isaurica*, from arid parts of the Old World, has a massive caruncle about half the size of the seed itself (Fig. 2J), whereas *E. orizabae*, from mesic forests of Mexico and Guatemala, has a small, almost vestigial caruncle (Fig. 2N). Seed size and ornamentation also vary considerably. The size of the seeds varies by a factor of nearly two in the section, with small seeds typical among the annual species (Fig. 2A–I, K–L) and larger seeds more common in the perennial species of the *Brachycera* clade (Fig. 2U–Y). Perhaps the most distinctive feature of seeds from this section

is the ornamentation of the seed coat. *Euphorbia pepus*, the sister species to the New World clade, has very different types of pitting on the dorsal and ventral sides of its seeds (Fig. 2A). This pattern of pitting is shared with other Old World species (e.g. *E. isaurica*; Fig. 2J) and the New World *E. peplidion* (Morawetz *et al.*, 2010). *Euphorbia nesomii* and *E. longicornuta* (Fig. 2B, S) both show an intermediate degree of surface dimorphism between the dorsal and ventral faces. *Euphorbia helleri* (Fig. 2E) is unusual in its essentially smooth seed surface and *E. orizabae*, *E. neilmulleri* and *E. tuerckheimii* (Fig. 2N, T, M) are also quite smooth, with only faint sculpturing evident below the whitish surface layer. Other species such as *E. austrotexana*, *E. georgiana* and *E. esuliformis* (Fig. 2C, G, R) have seeds with deeply pitted or conspicuously reticulate surfaces. The seeds of *E. ouachitana* (Fig. 2H) are distinctive with their lustrous brown surface that lacks the

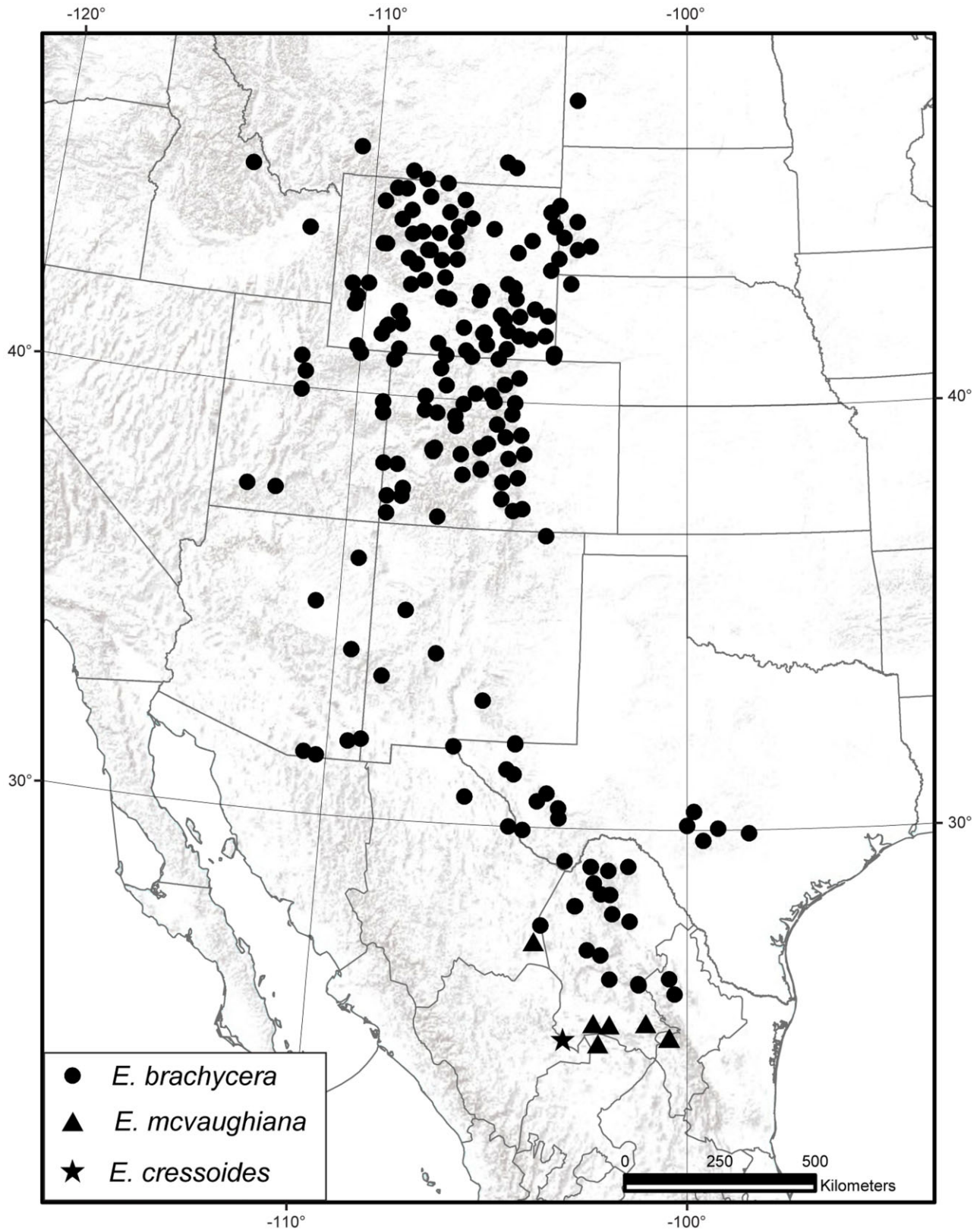


Figure 8. Geographical distribution of *Euphorbia brachycera*, *E. cressoides* and *E. mcvaughiana* in northern Mexico and the USA.

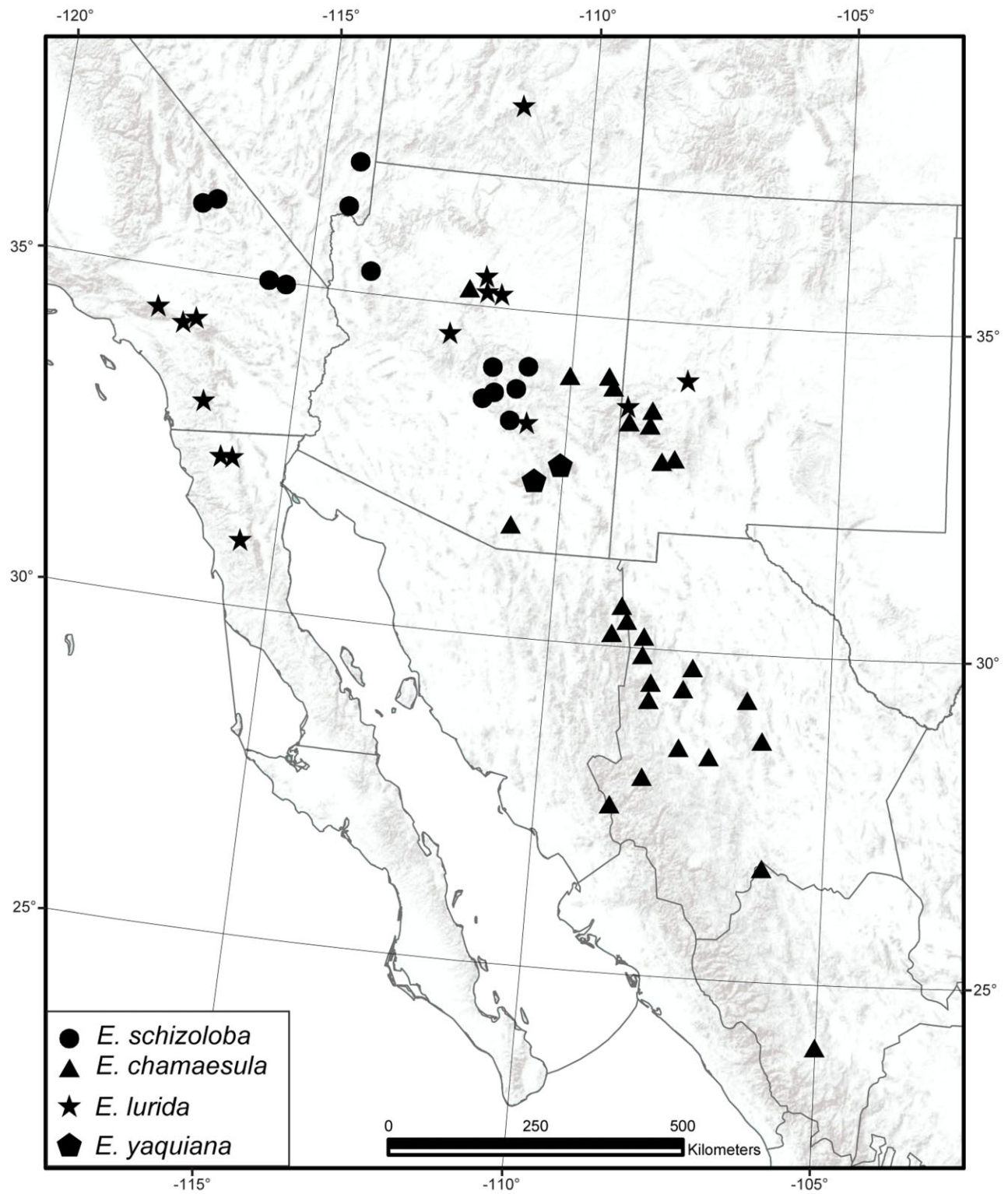


Figure 9. Geographical distribution of *Euphorbia chamaesula*, *E. lurida*, *E. schizoloba* and *E. yaquiana* in northern Mexico and the USA.

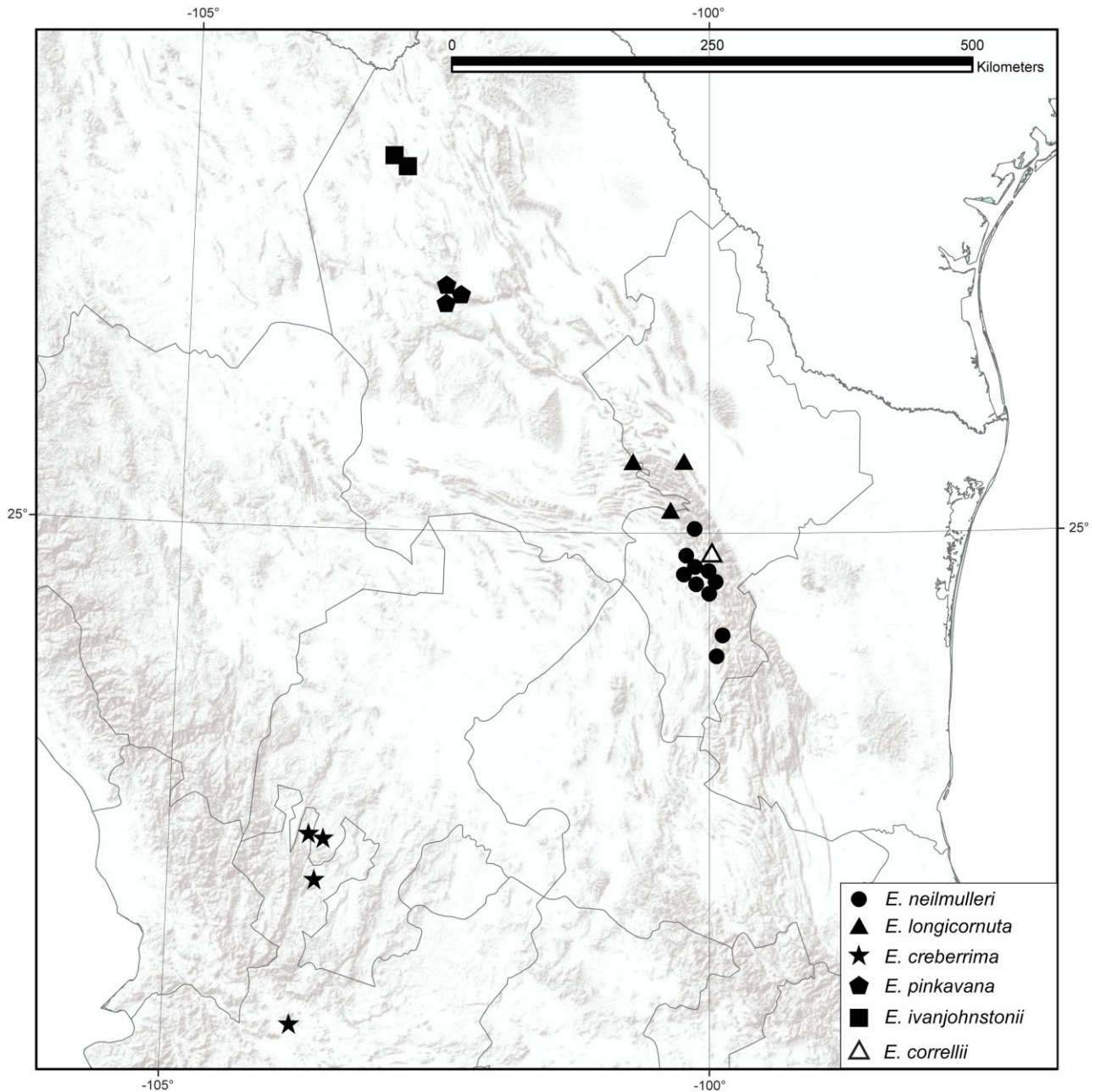


Figure 10. Geographical distribution of *Euphorbia correllii*, *E. creberrima*, *E. ivanjohnstonii*, *E. longicornuta*, *E. neilmulleri* and *E. pinkavana* in Mexico.

whitish/grey outer surface of the other species and their large pits aligned in vertical rows.

TIPIFICATION, SYNONYMY, DISTRIBUTION AND
PHYLOGENETIC PLACEMENT OF NEW WORLD SPECIES
OF *EUPHORBIA* SECTION *TITHYMALUS*

1. *EUPHORBIA AUSTROTEXANA* Mayfield, J. Bot. Res. Inst. Texas 7: 634. 2013 – Type: USA, Texas, Atas-

cosa Co., along FM 476, 5.2 mi N of Rossville from junction FM 2405, 0.2 mi S of Hartung Road, 216 m, 29°09'55"N, 98°40'55"W, 4 Apr 1993, *M.H. Mayfield, J. Mendenhall & J. Panero* 1717 (holotype, TEX!; isotypes, BRIT!, DAV!, F!, GH!, KSC!, LSU!, MICH!, MO!, NY!, PH!, RSA!, TAES!, UC!, US!).

Distribution and habitat: Endemic to southeastern Texas, in stabilized sandy soil habitats, extending

KEY TO THE SPECIES OF *EUPHORBIA* SECTION *TITHYMALUS* IN THE NEW WORLD

1. Annual herbs from a taproot (*E. commutata* and *E. crenulata* often biennial from overwintering buds at base of stem) 2
- 1'. Perennial herbs from woody or rhizomatous rootstock or woody taproot 13
2. Seeds smooth (Fig. 2E) *E. helleri*
- 2'. Seeds transversally or longitudinally sulcate or pitted (Fig. 2A–D, F–I, K–L) 3
3. Seeds longitudinally sulcate on ventral faces, with large pits on dorsal faces (Fig. 2A) 4
- 3'. Seeds pitted 5
4. Leaves linear-cuneate to narrowly cuneate-spatulate, largest leaves 1–4 mm wide; capsules without wings
..... *E. peplidion*
- 4'. Leaves obovate, oblong or suborbiculate, largest leaves 4–15 mm wide; capsules with low longitudinal wings (Fig. 3D) *E. peplus*
5. Dichasial bracts connate $\frac{1}{4}$ – $\frac{1}{2}$ length (often only on one side or rarely only basally in *E. crenulata*) 6
- 5'. Dichasial bracts usually distinct (occasionally subconnate basally) 8
6. Biennial or occasionally annual herbs; dichasial bract margins erose denticulate to subentire (Fig. 3J); involucre glands 1.5–2.3 mm wide, horns 0.4–0.6 mm long; capsules 2.5–3.0 mm long; seeds 2.0–2.5 mm long (Fig. 2I); California, Oregon, southwestern Colorado, northern New Mexico *E. crenulata*
- 6'. Annual herbs; dichasial bract margins entire; involucre glands 0.7–1.2 mm wide, horns 0.1–0.4 mm long; capsules 2.0–2.7 mm long; seeds 1.6–2.0 mm long; east of Rocky Mountains 7
7. Petioles 2–5 mm long; capsules subglobose, 2.0–2.5 mm long; styles 0.6–1.0 mm long; seeds with broad, shallow connected pits not in obvious rows (Fig. 2K); central Texas *E. roemeriana*
- 7'. Petioles 0–3 mm long; capsules ovoid-globose, 2.6–2.7 mm long; styles 0.3–0.5 mm long; seeds with deep, rounded, well-separated pits in three or four regular, vertical rows (Fig. 2H); central United States, in Texas only along the eastern Oklahoma border *E. ouachitana*
8. Dichasial bracts strongly imbricate; seeds grey to purple-grey or occasionally nearly black (Fig. 2F)
..... *E. longicuris*
- 8'. Dichasial bracts usually not imbricate (only rarely slightly overlapping); seeds white to grey or tan or red-brown to brown 9
9. Petioles of proximal leaves up to 10 mm long; leaf blades oblanceolate to obovate, subrhombic, or rhombic-obovate, 3–10 mm wide (usually at least some leaves > 5 mm wide) 10
- 9'. Petioles of proximal leaves 0–2 mm long; leaf blades narrowly oblanceolate, spatulate-cuneate or spatulate to linear or sometimes slightly lanceolate, 0.5–5.0 mm wide 11
10. Biennial or occasionally annual herbs; petioles of proximal leaves 5–10 mm long; leaf blades oblanceolate to obovate, rarely ovate, largest leaves 5–10 mm wide; capsules 2.5–3.2 mm long; seeds 1.5–2.0 mm long (Fig. 2F); eastern to central United States and eastern Canada *E. commutata*
- 10'. Annual herbs; petioles of proximal leaves 3–6 mm long; leaf blades subrhombic to rhombic-obovate, 3–7 mm wide; capsules 1.8–1.9 mm long; seeds 1.3–1.5 mm long (Fig. 2B); Mexico *E. nesomii*
11. Seeds reddish brown to brown, 1.3–1.4 × 0.8–0.9 mm, with four to six shallow pits or irregular oblong grooves on adaxial face, small-pitted or nearly smooth on abaxial face (Fig. 2D) *E. tetrapora*
- 11'. Seeds white to grey, 1.4–1.7 × 1–1.6 mm, with pits scattered over entire surface 12
12. Leaf blades narrowly oblanceolate or spatulate to linear or sometimes slightly lanceolate, 0.5–2.5 mm wide; seeds ellipsoid, 1.4–1.7 × 1.0–1.3 mm (Fig. 2C); sandy-soil habitats in Texas *E. austrotexana*
- 12'. Leaf blades oblanceolate, 3–5 mm wide; seeds ovoid, 1.6–1.7 × 1.4–1.6 mm (Fig. 2G); granitic outcrops in Georgia *E. georgiana*
13. Foliage and/or stems (at least the young stems) hairy or papillose (use magnification) 14
- 13'. Foliage and/or stems essentially glabrous 25
14. Leaves and/or stems papillose, ± densely covered with minute, translucent papillae < 0.1 mm long 15
- 14'. Leaves and/or stems pubescent, sparsely to densely covered with elongate, non-papillose trichomes, trichomes usually 0.1–0.3 mm long (shorter in *E. orizabae*) 18
15. Stems glabrous; known only from Sierra de la Madera, northwest of Cuatro Ciénegas (Coahuila)
..... *E. pinkavana*
- 15'. Stems papillose, like the leaves; other parts of northern Mexico but not in Sierra de la Madera 16
16. Involucre glands 1.0–1.5 mm wide; Jalisco and westernmost Zacatecas, Mexico *E. creberrima*
- 16'. Involucre glands 0.3–0.8 mm wide; Coahuila and Nuevo León, Mexico 17
17. Middle and upper stem leaves linear-elliptical to linear- or narrowly lanceolate, mostly 4–9 × 1–3 mm; involucre glands 0.3–0.4 mm wide, horns c. 1 mm long; central Nuevo León and southern Coahuila, Mexico
..... *E. longicornuta*

- 17'. Middle and upper stem leaves ovate to lanceolate or lanceolate-elliptical (sometimes narrowly so), 7–25 × 3–7 mm; involucre glands 0.5–0.8 mm wide, horns 0.5–0.7 mm long; northwestern Coahuila, Mexico *E. ivanjohnstonii*
18. Leaves glabrous, elliptic to narrowly elliptical, 25–60(–90) × 8–15 mm, evenly long-tapered at both ends, widest at the middle; central and southern Mexico (Chiapas, Hidalgo, Jalisco, Michoacán, Oaxaca and Veracruz) and Guatemala *E. orizabae*
- 18'. Leaves pubescent, narrowly lanceolate to ovate, oblanceolate, obovate or spatulate, rarely elliptical or orbicular, 4–22 × 2–13 mm, the ends not evenly long-tapered, usually not widest at the middle; northern Mexico (Chihuahua, Coahuila and Nuevo León) and southwestern United States 19
19. Largest leaves 5–9 × 2–3 mm, closely spaced, overlapping and ascending on the stems, base acute; Nuevo León, Mexico, mostly specialized on gypsum substrates *E. neilmulleri*
- 19'. Largest leaves 6–22 × 5–13 mm, more loosely spaced, generally not overlapping or ascending on the stems, base rounded to truncate; more widespread, including Nuevo León, Mexico, but not specialized on gypsum substrates 20
20. Plants with erect, untangled trichomes (c. 0.1 mm long); western United States and northwestern Coahuila, Mexico 21
- 20'. Plants with spreading, more tangled trichomes (0.2–0.4 mm long); southern Arizona and southern Coahuila and adjacent Chihuahua, Mexico 23
21. Involucre gland margin entire to occasionally slightly crenate or dentate, horns present, longer than teeth on gland margin; pubescent forms of this species uncommon but scattered across the species range *E. brachycera* (in part)
- 21'. Involucre gland margin irregularly to strongly crenate or dentate, horns present or absent, slightly longer than or generally indistinguishable from teeth on margin of gland 22
22. Leaf blade apex obtuse to rounded; involucre glands oblong to broadly ovate, 0.5–0.8 mm wide, margin irregularly crenate to strongly dentate, horns present or absent, slightly longer than or occasionally indistinguishable from teeth on gland margin; pubescent plants of this species from Yavapai County, Arizona *E. lurida* (in part)
- 22'. Leaf blade apex acute to acuminate; involucre glands semicircular to trapezoidal, 0.8–1.5 mm wide, margin strongly crenate or dentate, horns usually absent or indistinguishable from teeth on gland margin; pubescent plants of this species from Gila County, Arizona *E. schizoloba* (in part)
23. Involucre glands lacking horns or horns indistinct, margin of gland crenate; Santa Catalina and Pinaleno mountains in southern Arizona *E. yaquiiana*
- 23'. Involucre glands with a pair of well-developed horns, margin mostly entire in between; Coahuila, Mexico 24
24. Leaves and stems densely tomentose; petioles of stem leaves 0.5–1.0 mm long; glands 0.8–1.0 mm wide; southwestern Coahuila, Mexico *E. cressoides*
- 24'. Leaves and stems moderately pubescent; petioles of stem leaves 1.0–2.5 mm long; glands 0.4–0.5 mm wide; Chihuahua, Coahuila, Nuevo León and northernmost Zacatecas, Mexico *E. mcvaughiana*
25. Seeds smooth to obscurely reticulate (Fig. 2M); plants native to Hispaniola 26
- 25'. Seeds irregularly shallowly pitted to foveolate or alveolate, sometimes only faintly so (Fig. 2N–Y); plants native to the western United States, Mexico, Guatemala and Honduras 27
26. Stem leaves narrowly spatulate, 5–12 mm long, apex obtuse to rounded or shortly apiculate; dichasial bracts broadly deltate; peduncle 0.5–2.0 mm long; involucre glands shortly stipitate *E. eggersii*
- 26'. Stem leaves linear to linear-lanceolate, 15–25 mm long, apex acute to acuminate; dichasial bracts lanceolate; peduncle 3–5 mm long; involucre glands sessile *E. tuerckheimii*
27. Sterile leafy shoots arising from axils of some of the leaves of the primary stem (after the initiation of flowers and then mostly along the upper portion) or from within the pleiochasium; peduncles 1–3 mm long; involucre gland horns present; capsules 4.3–5.0 mm long; seeds 3.0–3.4 × 2.3–2.5 mm *E. chamaesula*
- 27'. Sterile leafy shoots lacking; peduncles 0.3–1.0 mm long; involucre gland horns present or absent; capsules 2–4 mm long; seeds 1.8–3.1 × 1.2–1.8 mm 28
28. Upper stem leaves 6–8 mm long; involucre glands hornless; seeds faintly foveolate, with the surface microtuberculate; known so far from a single collection on gypsum flats in Nuevo León, Mexico *E. correllii*
- 28'. Upper stem leaves at least 10 mm long, often several centimetres long; involucre glands with horns; seeds more obviously foveolate or shallowly pitted, surface not microtuberculate; more widespread in the western United States and Mexico 29
29. Both stem leaves and pleiochasial bracts ± linear, the stem leaves reflexed; longest stem leaves > 3.5 cm long; Sonora, Sinaloa and Durango, Mexico *E. chiribensis*
- 29'. Stem leaves variously shaped but only rarely linear (e.g. some specimens of *E. greggii* and *E. esuliformis*), not reflexed; pleiochasial bracts not linear (except rarely in *E. greggii*); longest stem leaves usually < 3.2 cm long (if longer then clearly not linear) 30

30. Involucral gland margin irregularly to strongly crenate or dentate, horns present or absent, slightly longer than or generally indistinguishable from teeth on margin of gland; southwestern United States and Baja California, Mexico 31
- 30'. Involucral gland margin entire to occasionally slightly crenate to dentate, horns present, longer than teeth on gland margin; throughout the western United States, Mexico (not Baja California), Guatemala and Honduras 32
31. Leaf blade apex obtuse to rounded; involucral glands oblong to broadly ovate, 0.5–0.8 mm wide, margin irregularly crenate to strongly dentate, horns present or absent, slightly longer than or occasionally indistinguishable from teeth on gland margin *E. lurida* (in part)
- 31'. Leaf blade apex acute to acuminate; involucral glands semicircular to trapezoidal, 0.8–1.5 mm wide, margin strongly crenate or dentate, horns usually absent or indistinguishable from teeth on gland margin *E. schizoloba* (in part)
32. Slender herbs, usually less than 50 cm tall; stems thin and wiry (especially evident on underground portions), often arising singly or in small groups from deep underground rhizomes or tubers 33
- 32'. Robust herbs to subshrubs, 30–120 cm tall; stems thicker, often clumped with numerous stems arising from a ± woody base 34
33. Small herbs, to 25 cm tall, from rhizomes; stem leaves narrowly ovate-elliptical to slightly obovate, ascending, generally overlapping, 6–15 × 2–6 mm; pleiochasia bracts ovate to cordate-ovate, slightly wider than but generally similar to distal stem leaves; high elevations (2900–3900 m) of central Mexico (Distrito Federal, Hidalgo, Mexico and Veracruz) *E. furcillata*
- 33'. Small to medium-sized herbs, usually over 25 cm tall, often with underground tubers; stem leaves highly variable, ranging from linear to elliptical or obovate-emarginate to spatulate, generally not ascending, not overlapping, 15–115 × 2–12 mm; pleiochasia bracts linear or linear-lanceolate or often abruptly constricted from a broader cordate base, usually similar in size to distal stem leaves; lower to middle elevations (720–2100 m) of north-east Mexico (Coahuila, Nuevo León, San Luis Potosí and Tamaulipas) *E. greggii*
34. Plants compact and densely branched; leaves densely spiralled, overlapping; internodes not visible; mostly subalpine habitats at elevations of (2500–)3300–3750 m on the high peaks of Cerro Potosí, Sierra la Viga, Sierra la Marta and Sierra Coahuilón in Coahuila and Nuevo León, Mexico *E. beamanii*
- 34'. Plants more diffuse and laxly branched; leaves loosely spiralled and not overlapping; stem internodes visible; low to high elevations (500–3300 m) in western United States, Mexico, Guatemala and Honduras 35
35. Upper stem after leaf-fall with prominent dark leaf scars; upper stem leaves narrowly oblanceolate to elliptical or lance-linear to narrowly lanceolate, 15–60 × 2–6(–9) mm, at least five to ten times as long as broad; southern Coahuila, Mexico (mainly south of 27°N) south to Honduras, not occurring in Sonora or Chihuahua, Mexico ... *E. esuliformis*
- 35'. Upper stem after leaf-fall without prominent dark leaf scars; upper stem leaves broadly oblong-elliptical to lanceolate, oblanceolate or ovate, 5–25 × 2–7 mm; less than four times as long as broad; western United States and northern to central Coahuila, Chihuahua and Sonora, Mexico (mainly north of 27°N) *E. brachycera* (in part)

through a wide swath of the south Texas plains in Atascosa, Bexar, Jim Hogg, Kenedy and Wilson Counties, 10–250 m elevation.

Phylogenetic placement: Northern annual clade.

Taxonomic remarks: *Euphorbia austrotexana* is closely related to *E. longicuris*. It differs from *E. longicuris* in its smaller stature; narrower, almost linear leaves; dichasia bracts that are not strongly imbricate; and smaller ellipsoid seeds covered with minute, crowded concave depressions (Fig. 2C). Mayfield (2013) recognized two varieties in the species.

1a. *E. austrotexana* var. *austrotexana*

Distribution and habitat: Endemic and locally distributed on stabilized sandy soils in southern central

Texas, in northern Atascosa, southern Bexar and western Wilson Counties, 140–200 m elevation (Fig. 6).

1b. *E. AUSTROTEXANA* var. *CARRII* Mayfield, J. Bot. Res. Inst. Texas 7: 636. 2013 – Type: USA, Texas, Kenedy Co., 50–200 ft W of a major N-S pipeline clearing on Hunke Ranch, 0.6 mi N of a major internal fence, 1.2–1.3 air mi W to WNW of jct. of Hidalgo, Kenedy and Willacy counties, at 26°36'53.3"N, 097°58'38.1"W, 50 ft, 16 Mar 2004, W.R. Carr & M. Pons 22784 (holotype, TEX!).

Distribution and habitat: Endemic to southern Texas, probably extending through a wide swathe of the south Texas plains in Jim Hogg and Kenedy Counties, 10–15 m elevation (Fig. 6).

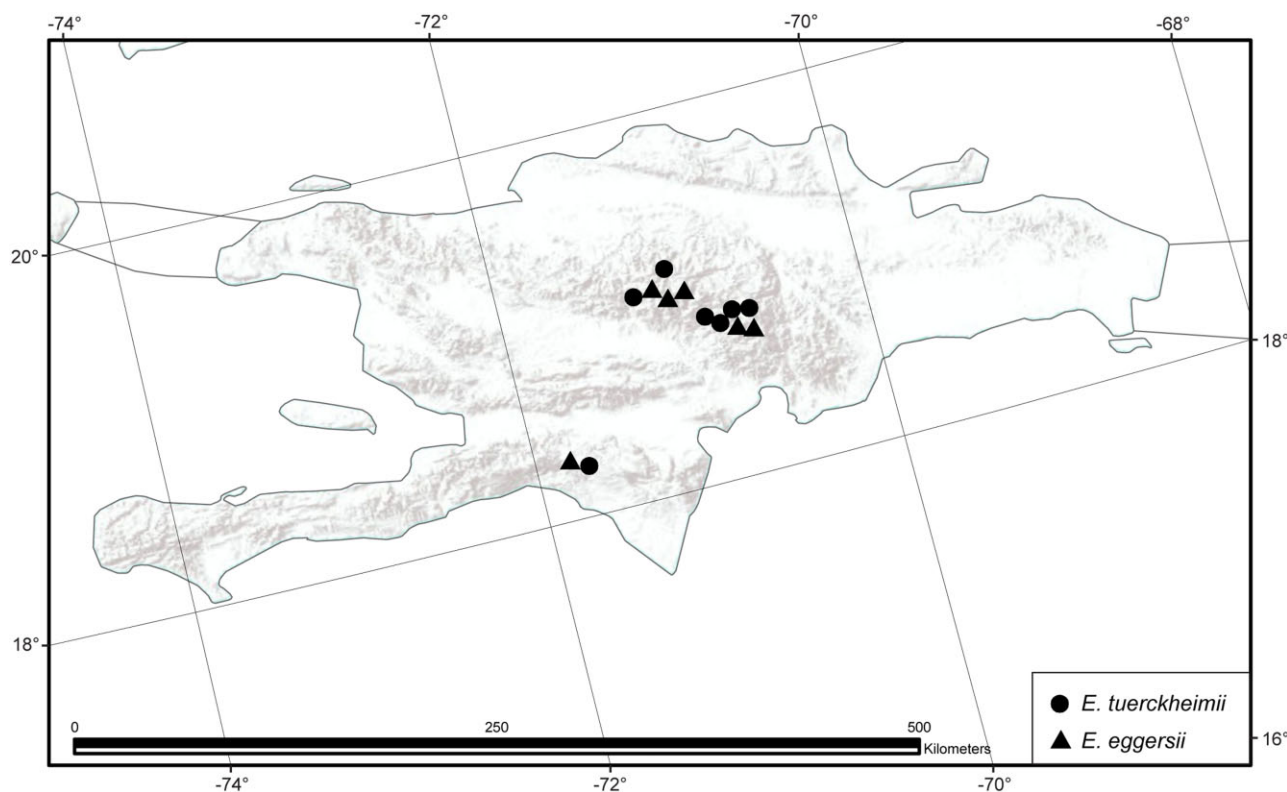


Figure 11. Geographical distribution of *Euphorbia eggersii* and *E. tuerckheimii* on the Caribbean island of Hispaniola.

KEY TO THE VARIETIES OF *E. AUSTROTEXANA*

1. Plants generally 10–22 cm tall, with a single dominant erect main stem and two or three more or less erect, subdominant stems; stem leaves linear-oblongate and strictly ascending, apex rounded; dichasial bracts reniform-ovate to subdeltate-ovate with a short-acuminate apex, base truncate, 3–7 mm long; seeds generally larger, 1.6–1.7 × 1.1–1.3 mm, surface pits of circular concave depressions *E. austrotexana* var. *austrotexana*
- 1'. Plants generally 6–13 cm tall, with one to several subequal virgate main stems from the base; stem leaves linear to scarcely lanceolate, the apices acute, divergent from the stem; dichasial bracts broadly ovate-lanceolate, the bases rotund, 8–15 mm long; seeds generally smaller, 1.4–1.5 × 1.0–1.1 mm, surface pits more irregular, not obviously concave *E. austrotexana* var. *carrii*

Taxonomic remarks: Populations of this variety were mistaken by Turner (2011b) to be evidence for the persistence of *E. exigua* in Texas. The latter taxon is native to Europe and has been introduced into the United States, including Texas (as reported by Johnston, 1969). The two species are not closely related and can be distinguished by the tuberculate seeds of *E. exigua* (Morawetz *et al.*, 2010).

2. *EUPHORBIA BEAMANII* M.C.Johnst., *Wrightia* 5: 126. 1975 ≡ *Tithymalus beamanii* (M.C.Johnst.) Soják, *Cas. Nár. Mus., Odd. Prír.* 148: 199. 1980 – Type: Mexico, Nuevo León, Cerro Potosí, 24°53'30"N, 100°10'30"W, 10 500 ft, 18 Jun 1966, L. Gilbert 2 (holotype, TEX!).

Distribution and habitat: Endemic to north-central Mexico (Nuevo León and Coahuila), in high-montane meadows, (2150–)3300–3750 m elevation (Fig. 7).

Phylogenetic placement: *Esuliformis* clade.

Taxonomic remarks: *Euphorbia beamanii* is endemic to the high mountains of north-central Mexico. It was described from subalpine meadows on the upper slopes of Cerro Potosí in Nuevo León but also occurs on the slopes of Sierra de Santa Marta, Cerro de La Viga and Sierra Coahuilón in Coahuila state. Its compact habit and closely spaced, strongly overlapping stem leaves give *E. beamanii* a distinctive

appearance that is easily recognized. This species is probably closely related to *E. esuliformis* (Fig. 4) and may represent a high mountain form of that species. Specimens from high elevations along the Tamaulipas–Nuevo León border on Peña Nevada approach *E. beamanii* in form, but we have placed them provisionally with *E. esuliformis* (see below).

3. *EUPHORBIA BRACHYCERA* Engelm. in W.H. Emory, Rep. U.S. Mex. Bound. 2(1): 192. 1859 ≡ *Tithymalus brachycerus* (Engelm.) Small, Fl. S.E. U.S., ed. 2:1349. 1913 – Type: USA, Texas, Nueces Co., pebbly bars of the Nueces [c. 7 mi WNW of Uvalde], 15 May 1851 [specimen labels state erroneously ‘N. Mex., Donana, above El Paso’], C. Wright 1821 (holotype, MO 149763!; isotypes, BM!, G!, GH!, NY!, P!).

= *Tithymalus fendleri* Klotzsch & Garcke, Abh. Königl. Akad. Wiss. Berlin 1859: 85. 1860 – Type: USA, New Mexico, Plantae Novo-Mexicanae, on Santa Fe Creek and the base and declivities of the mountains, May–Jul 1847, A. Fendler 786 (holotype, B, destroyed; isotypes, MO 149776!, NY 263148!).

= *Euphorbia odontadenia* Boiss. in A.P. de Candolle, Prodr. 15(2): 148. 1862 – Type: USA, [New Mexico/Texas], mountains, El Paso, ‘N. Mex.’ April–May 1852, C. Wright 1825 (holotype, G-BOISS-Suppl.!; isotypes, BM!, GH!, K! (two sheets), MO!).

= *Euphorbia robusta* (Engelm.) Small in N.L. Britton & A. Brown, Ill. Fl. N. U.S. 2: 381. 1897 ≡ *Euphorbia montana* var. *robusta* Engelm. in W.H. Emory, Rep. U.S. Mex. Bound. 2(1): 192. 1859, nom. illeg. ≡ *Tithymalus robustus* (Engelm.) Small in N.L. Britton & A. Brown, Ill. Fl. N. U.S., ed. 2, 2: 475. 1913 ≡ *Galarhoeus robustus* (Engelm.) Rydb., Brittonia 1: 93. 1931 ≡ *Euphorbia brachycera* var. *robusta* (Engelm.) Dorn, Vasc. Pl. Wyoming 296. 1988 – Type: USA, ‘Frémont’s expedition to the Rocky Mountains, on the upper Platte,’ 1842, J.C. Frémont s.n. (lectotype, Geltman *et al.*, 2011: 145, NY 263150!).

= *Euphorbia robusta* var. *interioris* Norton, N. Amer. Euphorbia 49, pl. 49. 1899 – Type: USA, Utah, Wasatch Mts., 9 Jun 1869, S. Watson 1081 (lectotype, Geltman *et al.*, 2011: 145, US 19574!; isolectotypes, GH!, NY!).

= *Tithymalus philorus* f. *dichotomus* Daniels, Univ. Missouri Stud., Sci. Ser. 2: 165. 1911 ≡ *Euphorbia brachycera* f. *dichotoma* (Daniels) Oudejans, Collect. Bot. (Barcelona) 21: 184. 1992 publ. 1993 – Type: USA, Colorado, from the high ridges of Green Mt., F.P. Daniels 367 (holotype, COLO!).

= *Tithymalus philorus* Cockerell, Muhlenbergia 4: 56. 1908 ≡ *Euphorbia montana* Engelm. in W.H. Emory, Rep. U.S. Mex. Bound. 2(1): 192. 1859, nom. illeg., non Raf., Amer. Monthly Mag. & Crit. Rev. 1(6):440. 1817 ≡ *Euphorbia montana* var. *gracilior*

Engelm. in W.H. Emory, Rep. U.S. Mex. Bound. 2(1): 192. 1859, nom. illeg. ≡ *Euphorbia philora* (Cockerell) Tidestr., Proc. Biol. Soc. Wash. 48: 41. 1935 – Type: USA, New Mexico, Plantae Novo-Mexicanae, on Santa Fe Creek and the base and declivities of the mountains, May–Jul 1847, A. Fendler 786 (lectotype, Norton 1899: 44, MO 149776!; isolectotype, NY 263148!).

Distribution and habitat: Widespread in western North America from northern Mexico (Chihuahua, Coahuila, Nuevo León and Sonora mainly north of 27°N) to Arizona, Colorado, Idaho, Montana, Nebraska, New Mexico, North Dakota, South Dakota, Texas, Utah and Wyoming, in mountain canyons, rock crevices, sandy or gravelly slopes, pine–oak woodlands, ponderosa pine and mixed coniferous forests; 500–3200 m elevation (Fig. 8).

Phylogenetic placement: *Brachycera* clade.

Taxonomic remarks: *Euphorbia brachycera* as delimited here constitutes a widespread and variable species. Populations that most closely resemble the type of the species range from northern Mexico (Chihuahua, Coahuila, Nuevo León and Sonora states) north and west through Texas into southern New Mexico and southeastern Arizona. Generally more robust but lower-growing plants from the northern portions of the range of the species occur in northern Arizona, Colorado, Idaho, Montana, Nebraska, northern New Mexico, North Dakota, South Dakota, Utah and Wyoming and have at times been recognized as a distinct species, *E. robusta*. Plants that are similar to the type of *E. robusta* var. *interioris* occur from Utah south to the Mogollon Rim area of Arizona and western New Mexico. Kearney & Peebles (1960) recognized *E. odontadenia* as an uncertain entity that was closely allied to *E. schizoloba* (as *E. incisa*). Geltman *et al.* (2011) considered *E. odontadenia* to be a synonym of *E. schizoloba*, but closer examination of the type specimen and locality data indicate that it is consistent with the morphology and range of *E. brachycera* and was collected much farther east than the known distribution of *E. schizoloba*. In addition to the type locality in the Franklin Mountains of western Texas, populations of plants consistent with type of *E. odontadenia* occur from the Grand Canyon in northern Arizona to the Mesa Verde area of southwestern Colorado and the Ladrone and Fra Cristobal Mountains of New Mexico. We provisionally include *E. odontadenia* and *E. robusta* here in *E. brachycera* but acknowledge that this complex requires a detailed population-level study across its range.

Euphorbia brachycera is usually glabrous, but sparsely pubescent plants can be found scattered

nearly throughout its distribution. Pubescent forms are most consistently encountered in populations discussed above as *E. odontadenia* and in plants from Utah and in more typical *E. brachycera* plants from the Huachuca Mountains in southern Arizona and the Chisos Mountains in southwest Texas.

4. *EUPHORBIA CHAMAESULA* Boiss., Cent. Euphorb. 38. 1860 = *Tithymalus chamaesula* (Boiss.) Wootton & Standl., Contr. U.S. Natl. Herb. 16: 145. 1913 – Type: U.S.A. [New Mexico], ‘N. Mex., 1851–52,’ C. Wright 1820 (holotype, G!; isotypes, BM!, F! [fragment ex G], GH!, K! (2 sheets), MO!, NY!, US!).

= *Euphorbia esuliformis* var. *subdentata* Engelm. in W.H. Emory, Rep. U.S. Mex. Bound. 2(1): 192. 1859 = *E. chamaesula* var. *subdentata* (Engelm.) Norton, N. Amer. Euphorbia 47, pl. 47. 1899 – Type: U.S.A. [probably Arizona. Coconino Co.], San Francisco Spring, Mar 1852, C.C. Parry s.n. (holotype, MO 149764!).

Distribution and habitat: Mexico (Sonora, Chihuahua) and south-western United States in Arizona and New Mexico, in meadows and open pine woodlands, 1700–2700 m (Fig. 9).

Phylogenetic placement: *Brachycera* clade.

Taxonomic remarks: *Euphorbia chamaesula* occurs on the high plains of the southwestern United States and northwestern Mexico. In contrast to the other perennial members of the *Brachycera* clade, *E. chamaesula* appears to flower later in the year, with the onset of summer monsoonal rains. Plants are usually taller than other species in the group, with longer leaves and larger fruits and seeds (Fig. 2Y). The conspicuous, sterile branches at the upper nodes of the stem, with their smaller, closely spaced leaves, are characteristic of this species.

5. *EUPHORBIA CHIRIBENSIS* V.W.Steinm. & Felger, Mexico (Sonora), Aliso 16: 52. 1997 – Type: Mexico, Sonora, Municipio Álamos, Sierra Saguaribo, c. 1 km E of El Chiribo by the road to Saguaribo, c. 27°17'30"N, 108°42'W, 1400 m, 24 Aug 1993, V. Steinmann 93–270 (holotype, ARIZ!; isotypes, MEXU!, RSA!, TEX!).

Distribution and habitat: Known from the Sierra de Saguaribo in southern Sonora and in the Sierra Madre Occidental of Sinaloa and Durango, Mexico, in pine–oak forests, at 1400–2100 m elevation (Fig. 7).

Phylogenetic placement: *Esuliformis* clade.

Taxonomic remarks: *Euphorbia chiribensis* was formerly known only from the type specimen in southern Sonora, but here we have identified two additional specimens belonging to the species from adjacent areas of the Sierra Madre Occidental in Sinaloa and Durango farther south. We were able to amplify and sequence only the *trnH-psbA* spacer for this species and in the ML analysis of the plastid DNA spacer dataset *E. chiribensis* was weakly placed with members of the *Esuliformis* clade (Fig. S3). This is consistent with morphology as *E. chiribensis* is quite similar to narrow-leaved forms of *E. esuliformis*. The species is easily recognized by its distinctive linear, reflexed leaves and pleiochasial bracts.

6. *EUPHORBIA COMMUTATA* Engelm. ex A.Gray, Manual, ed. 2: 389. 1856 = *Tithymalus commutatus* (Engelm. ex A.Gray) Klotzsch & Garcke, Abh. Königl. Akad. Wiss. Berlin 1859: 82. 1860 = *Galarhoeus commutatus* (Engelm. ex A.Gray) Small ex Rydb., Fl. Plains N. Amer. 520. 1932 – Type: USA, Missouri, in Herculaneum Gasconade, May 1835, [G. Engelmann] 82 (lectotype, Geltman *et al.*, 2011: 146, MO 1910962!).

= *Euphorbia ohiotica* Steud. & Hochst. ex Boiss. in A.P. de Candolle, Prodr. 15(2): 142. 1862 – Type: U.S.A. [South Carolina], in silvis montanis Carolina sept., May 1841, F. Ruegel s.n. (lectotype, Geltman *et al.*, 2011: 146, G!).

= *Euphorbia commutata* var. *erecta* Norton, N. Amer. Euphorbia 35. 1899 = *Tithymalus commutatus* var. *erectus* (Norton) Small, Fl. S.E. U.S. 720. 1903 = *Galarhoeus commutatus* var. *erectus* (Norton) Small, Man. S.E. Fl. 801. 1933 – Type: USA, Florida, Hibernia, Mar 1869, W.M. Canby s.n. (lectotype, Geltman *et al.*, 2011: 146, GH!; isolectotypes, MO!, NY!).

Distribution and habitat: Widespread throughout eastern North America from Florida to Alabama and north to Iowa, Wisconsin, Pennsylvania and southern Ontario, Canada, in forests, on bluffs, ledges and glades and along streams and rivers, 50–1000 m elevation (Fig. 6).

Phylogenetic placement: Northern annual clade.

Taxonomic remarks: *Euphorbia commutata* is the most widespread of the native New World annual species of section *Tithymalus*. It is closely related to *E. crenulata* from the western United States and together these two species form the basal lineage within the northern annual clade (Fig. 4). Morphologically *E. commutata* is quite similar to *E. ouachitana* but can be distinguished from that species by its free dichasial bracts and white to grey seeds, vs. the

partially connate bracts and dark brown lustrous seeds in *E. ouachitana* (Fig. 2L). The two species apparently also differ in chromosome number, with *E. commutata* having $2n = 28$ and *E. ouachitana* $2n = 26$ (Mayfield, 2013).

7. *EUPHORBIA CORRELLII* M.C. Johnst., *Wrightia* 5: 130. 1975 \equiv *Tithymalus correllii* (M.C. Johnst.) Soják, *Cas. Nár. Mus., Odd. Prír.* 148: 199. [1979] 1980 – Type: Mexico, Nuevo León, 5 km E of Entronque Galeana, gypsum flats in valley, 24°45'N, 100°00'W, 1600 m, 21 July 1958, *D.S. Correll & I.M. Johnston 19959* (holotype, TEX!).

Distribution and habitat: From east of Entronque Galeana, Nuevo León, Mexico, on gypsum flats, 1600 m elevation (Fig. 10).

Phylogenetic placement: *Esuliformis* clade.

Taxonomic remarks: *Euphorbia correllii* is known only from a single collection on gypsum flats in central Nuevo León, Mexico. This species is unique in section *Tithymalus*, possessing hornless cyathial glands and seeds that are faintly foveolate with a microreticulate surface. We were unable to include the species in our phylogenetic analyses, but morphologically it is most similar to other small-leaved species in the *Esuliformis* clade that occur in similar, specialized habitats.

8. *EUPHORBIA CREBERRIMA* McVaugh, *Contr. Univ. Michigan Herb.* 19: 218. 1993 – Type: Mexico, Jalisco, about 8–10 km SE of El Mortero, near Mezquitic, on Zacatecas–Jalisco border, along road to Monte Escobedo, Zacatecas, 2450 m, 5 Nov 1963, *C. Feddema 2452* (holotype, MICH 1104842!; isotypes, CAS!, G! (2 sheets), IEB!).

Distribution and habitat: Endemic to the Sierra Madre Occidental in Jalisco and probably western Zacatecas, Mexico, in oak–pine forests, 1800–2700 m elevation (Fig. 10).

Phylogenetic placement: *Esuliformis* clade.

Taxonomic remarks: *Euphorbia creberrima* is closely related to *E. esuliformis* but can be distinguished from that species by its distinctive, papillose indument on the leaves and upper portions of the stem.

9. *EUPHORBIA CRENULATA* Engelm. in *W.H. Emory, Rep. U.S. Mex. Bound.* 2(1): 192. 1859 \equiv *Euphorbia leptocera* var. *crenulata* (Engelm.) Boiss. in *A.P. de Candolle, Prodr.* 15(2): 143. 1862 \equiv *Tithymalus crenulatus* (Engelm.) A. Heller, *Muhlenbergia* 1: 55. 1904 – Type: USA, California, Monterey Co.,

Monterey, 1850, *C.C. Parry s.n.* (lectotype, Geltman *et al.*, 2011: 146, NY 263094!).

= *Euphorbia leptocera* Engelm. ex Boiss. in *A.P. de Candolle, Prodr.* 15(2): 143. 1862 \equiv *Tithymalus leptocerus* (Engelm. ex Boiss.) Arthur, *Torreya* 22: 30. 1922 – Type: USA, California, [Sonoma Co.], Colonia Ross, 1833, *F.P. Wrangel s.n.* (lectotype, Geltman *et al.*, 2011: 146, LE!).

= *Euphorbia crenulata* var. *franciscana* Norton, *N. Amer. Euphorbia* 38. 1899 \equiv *Tithymalus franciscanus* (Norton) A. Heller, *Muhlenbergia* 1: 56. 1904 – Type: USA, California, [San Francisco Co.] San Francisco, Mission hills, on cultivated fields, May 1865, *H. Bolander 20* (lectotype, Geltman *et al.*, 2011: 146, MO 1910115!).

= *Euphorbia manca* A. Nelson, *Bot. Gaz.* 47: 437. 1909 \equiv *Tithymalus mancus* (A. Nelson) A. Heller, *Muhlenbergia* 9: 67. 1913 – Type: USA, Colorado, southern Colorado, Mancos, common about edges of thickets along river bottom, 23 Jun 1898, *C.F. Baker, F.S. Earle & S.M. Tracy 23* (holotype, RMI!; isotypes, GH!, NY!, US!).

= *Euphorbia nortoniana* A. Nelson, *Bot. Gaz.* 47: 437. 1909 – Type: USA, California, sand hills near the Marine Hospital, San Francisco, 25 Apr 1903, *A.A. Heller 6625* (lectotype, Geltman *et al.*, 2011: 146, RMI!; isolectotypes, GH!, LE!, MO!, NY!, PH!, US!).

Distribution and habitat: Widespread in northern California and Oregon, less common in north-western New Mexico and south-western Colorado, in conifer forest borders, open shale outcrops and riverine thickets, 30–1800 m elevation (Fig. 6).

Phylogenetic placement: Northern annual clade.

Taxonomic remarks: Geltman *et al.* (2011) hypothesized that despite being an annual, *E. crenulata* may in fact be more closely related to members of the *E. brachycera* group, based on similarities in seed and leaf morphology with *E. lurida*. However, our results indicate that Norton (1900) was correct in proposing a close relationship with *E. commutata*, as shown in the Bayesian tree (Fig. 4).

10. *EUPHORBIA CRESSOIDES* M.C. Johnst., *Wrightia* 5: 123. 1975 \equiv *Tithymalus cressoides* (M.C. Johnst.) Soják, *Cas. Nár. Mus., Odd. Prír.* 148: 199. [1979] 1980 – Type: Mexico, Coahuila, Sierra de Jimulco approached from the south at Mina San José 8 km N of Estación Otto, 25°08'N, 103°13'30'W, 3000 m, 27 Sep 1972, *M.C. Johnston, T. Wendt, & F. Chiang 9551i* (holotype, TEX!).

Distribution and habitat: Known only from the summit area of Sierra de Jimulco in south-western Coahuila, Mexico, in chaparral, 3000 m elevation (Fig. 8).

Phylogenetic placement: *Brachycera* clade.

Taxonomic remarks: *Euphorbia cressoides* is morphologically quite similar to *E. mcvaughiana* and is placed sister to that species in the phylogenetic tree (Fig. 4). It can be distinguished from *E. mcvaughiana* by its more densely tomentose stems, shorter petioles and wider involucre glands. These two species are the only Mexican endemic members of the *Brachycera* clade.

11. *EUPHORBIA EGGERSII* Urb., Symb. Antill. 1: 343. 1899 – Type: Dominican Republic, inter saxa in Valle Nuevo, 2270 m, 29 May 1887, *H.V.A. von Eggers 2181* (lectotype, K!, here designated; isolecotypes, BM!, F!, G! [3 sheets], GOET!, NY!, US!).

Distribution and habitat: Haiti and the Dominican Republic, at the upper elevations of the Cordillera Central of Hispaniola in open and rocky sites, 1600–2300 m elevation (Fig. 11).

Phylogenetic placement: *Esuliformis* clade.

Taxonomic remarks: *Euphorbia eggersii* is one of two species of section *Tithymalus* native to Hispaniola; although unsampled in our analyses, it is presumably closely related to the *Esuliformis* clade, as indicated by the position of *E. tuerckheimii* in the Bayesian tree (Fig. 4). *Euphorbia eggersii* generally occurs at slightly higher elevations and has generally smaller, rounder, more obtuse leaves and smoother seeds than *E. tuerckheimii*.

12. *EUPHORBIA ESULIFORMIS* S.Schauer ex Nees & S.Schauer, Linnaea 20: 729. 1847 ≡ *Tithymalus esuliformis* (S.Schauer ex Nees & S.Schauer) Klotzsch & Garcke, Abh. Königl. Akad. Wiss. Berlin 1859: 59. 1860 ≡ *E. campestris* var. *esuliformis* (S.Schauer ex Nees & S.Schauer) Boiss. in DC, Prodr. 15(2): 147. 1862 – Type: Mexico, A. *Aschenborn 19* (holotype, B [destroyed], fragment at MO!).

= *Euphorbia campestris* Schldl. & Cham., Linnaea 5: 84. 1830, nom. illeg., non S. Geuns, 1788 – Type: Mexico, in planitie inter Tlachichuca [Puebla, W of Pico de Orizaba] et Tepetitlán [Hidalgo], Sep 1828, *C.J.W. Schiede & F. Deppe 384* (holotype, B [destroyed]; isotypes, HAL-71081!, MO! [fragment of B specimen]).

= *Euphorbia furcillata* var. *ribana* M.C.Johnst., Wrightia 5: 128. 1975 – Type: Mexico, Nuevo León,

0.5 km NE of Rancho Zaragoza, 4 km E of el Barroquito, 2050 m, 19 Jun 1972, *M.C. Johnston, T. Wendt & F. Chiang 8025* (holotype, TEX 00371672!; isotype, MEXU 00244398!).

= *Euphorbia seemannii* Klotzsch, Bot. Voy. Herald 276. 1856 ≡ *E. campestris* var. *seemannii* (Klotzsch) Boiss. in DC, Prodr. 15(2): 147. 1862 – Type: Mexico, Sierra Madre, NW Mexico [either between Mazatlán and Durango, in either Sinaloa or Durango States, or else between Durango and Tepic, in either Durango or Nayarit States], Jan. 1850, *B.C. Seemann 2160* (holotype, K 000253759!).

= *Euphorbia campestris* var. *foliosa* Millsp., Bull. Torrey Bot. Club 16: 66. 1889 – Type: Mexico, Nuevo León, wooded slopes of Sierra Madre near Monterey [sic], 23 Jun 1888, *C.G. Pringle 2068* (holotype, F 0056376!; isotype, GH!).

Distribution and habitat: Known from the states of Chiapas, Coahuila, Colima, Distrito Federal, Durango, Guanajuato, Hidalgo, Jalisco, Mexico, Michoacán, Nayarit, Nuevo León, Oaxaca, Puebla, Querétaro, San Luis Potosí, Tamaulipas, Tlaxcala and Zacatecas, Mexico and in the departments of Quiché and Huehuetenango, Guatemala and El Paraíso, Honduras, in dry to mesic montane forests and grasslands, 1300–3300 m elevation (Fig. 12).

Phylogenetic placement: *Esuliformis* clade.

Taxonomic remarks: *Euphorbia esuliformis* is one of the most widespread and morphologically variable species in section *Tithymalus*. The species occurs from northern Mexico south into Guatemala and Honduras. It displays a remarkable range in plant stature and leaf shape and size. Johnston (1975) described *E. furcillata* var. *ribana* as a distinct taxon that inhabited drier and generally lower habitats than more typical *E. esuliformis* (which he recognized as *E. furcillata* var. *furcillata*). These plants resemble the narrow-leaved forms of *E. esuliformis* that occur throughout its distribution and we place them here in synonymy. This widespread and variable species deserves critical study across its range.

13. *EUPHORBIA FURCILLATA* Kunth, Nov. Gen. Sp. 2: 60. 1817 ≡ *Tithymalus furcillatus* (Kunth) Klotzsch & Garcke, Abh. Königl. Akad. Wiss. Berlin 1859: 86. 1860 – Type: Mexico, [Hidalgo], ‘Juxta Morán, Real del Monte et Pachuca,’ May 1803, *A. Bonpland & A. von Humboldt s.n.* (holotype, P-Bonpl 00669832!; isotype, B [destroyed]).

Distribution and habitat: Endemic to central Mexico in the Distrito Federal and the states of Hidalgo,

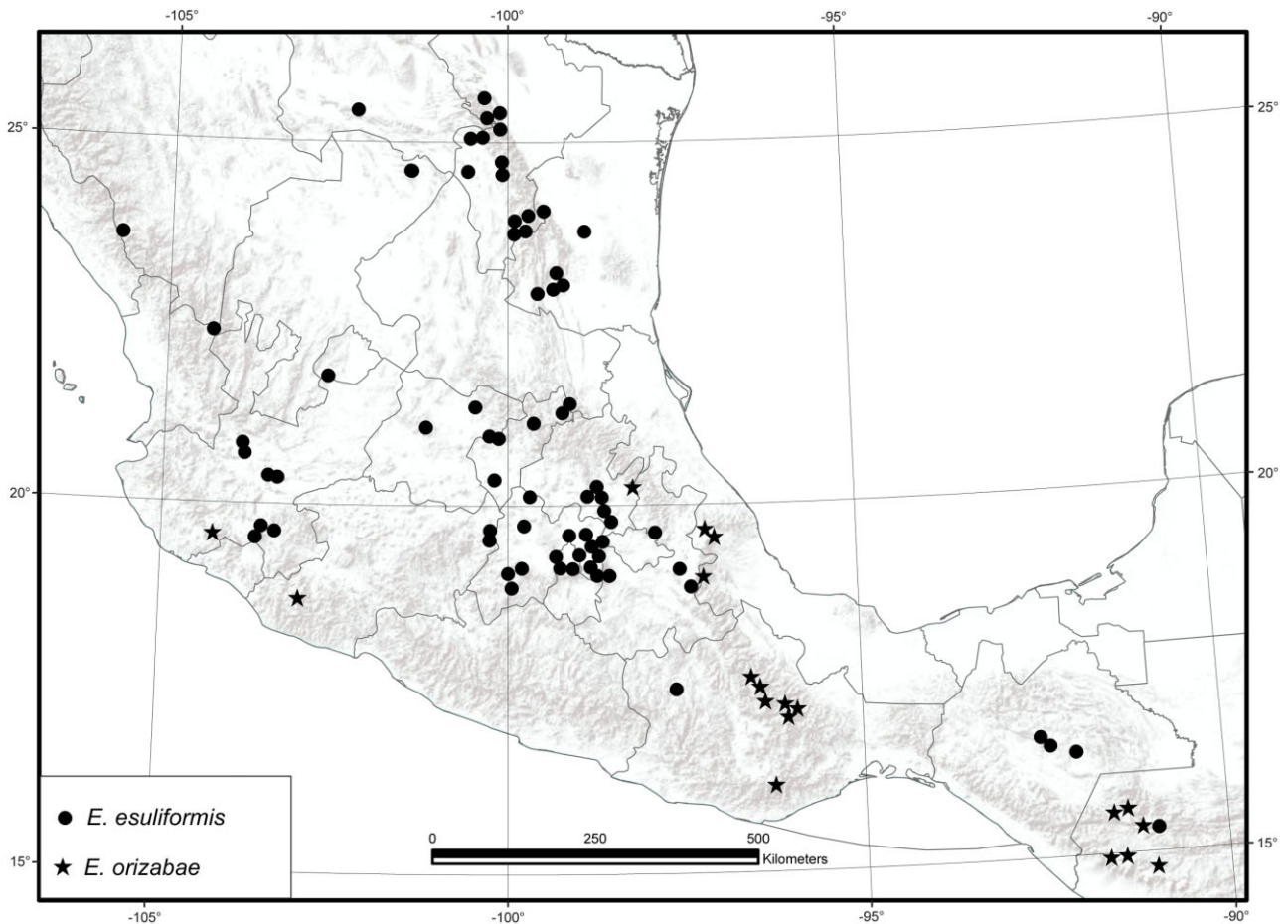


Figure 12. Geographical distribution of *Euphorbia esuliformis* and *E. orizabae* in Mexico and Guatemala. Missing is a collection of *E. esuliformis* from above Monte de Agua Fria, El Paraíso Department, Honduras (off the east end of the map close to the Nicaraguan border).

Mexico and Veracruz, in high montane habitats, 2900–3750(–4000) m elevation (Fig. 7).

Phylogenetic placement: *Esuliformis* clade.

Taxonomic remarks: As delimited here, *Euphorbia furcillata* is a small-leaved species restricted to relatively high-elevation habitats in central Mexico. Johnston (1975) took a much broader view of the species and also included what we are now recognizing as *E. esuliformis*. We were able to amplify and sequence only the *trnH-psbA* spacer for this species and in the analysis of the plastid DNA spacer dataset *E. furcillata* was placed in the *Esuliformis* clade with weak support (Fig. S3).

14. *EUPHORBIA GEORGIANA* Mayfield, J. Bot. Res. Inst. Texas 7: 639. 2013 – Type: USA, Georgia, Oglethorpe Co., shallow soil, newly exposed area, Echols Mill granitic outcrop, 9.3 mi N, 45° east of

Lexington. Piedmont Province, 13 May 1965. *D. Blake and F. Montgomery 136* (holotype, GA!).

Distribution and habitat: Endemic to south-eastern USA in Georgia, in semi-open forests and open areas, on granite outcrops, 100–200 m elevation (Fig. 13).

Phylogenetic placement: Northern annual clade.

Taxonomic remarks: *Euphorbia georgiana* is a newly described species that is restricted to granitic outcrops in the Piedmont Province of Georgia, to where it is most probably endemic (Mayfield, 2013). It is similar to *E. austrotexana* but has larger seeds that are much more deeply pitted (Fig. 2G) and leaves that are oblanceolate instead of linear-oblanceolate to linear. It is quite distinct from the more robust, biennial *E. commutata*, the only other closely related species that occurs in the area.

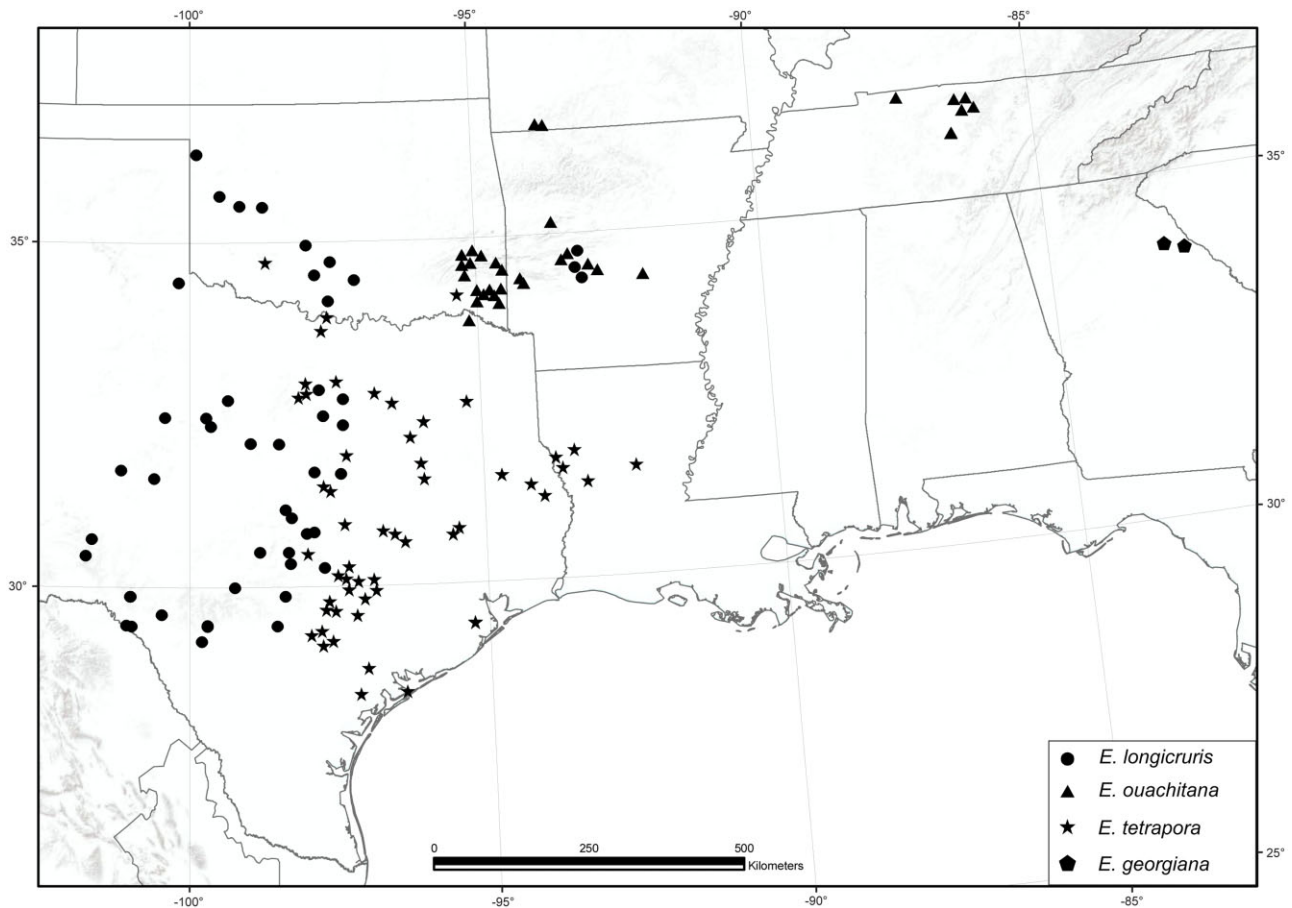


Figure 13. Geographical distribution of *Euphorbia georgiana*, *E. longicuris*, *E. ouachitana* and *E. tetrapora* in the USA.

15. *EUPHORBIA GREGGII* Engelm. ex Boiss., Prodr. 15(2). 147. 1862 \equiv *E. brachycera* var. *greggii* (Engelm. ex Boiss.) M.C.Johnst., Wrightia 5: 129. 1975 – Type: Mexico, Coahuila, San Antonio near Saltillo, 31 Aug 1848, *J. Gregg* 429 (holotype, MO!; isotype, F!).

Distribution and habitat: Known from north-eastern Mexico in the states of Coahuila, Nuevo León, Tamaulipas and San Luis Potosí, in oak forests on limestone and gypsum, 720–2100 m elevation (Fig. 7).

Phylogenetic placement: *Esuliformis* clade.

Taxonomic remarks: *Euphorbia greggii* grows on mesic slopes in otherwise rather dry montane forests on limestone and on open gypsum outcrops. The species has distinctive rounded tubers at the ends of long, wiry, underground stems/roots, a character that has not been previously documented and that is not shared with any other species in section *Tithymalus*. When growing on gypsum, the underground portions of the stem become thickened and subligneous. The

leaves vary from linear to orbicular and the bracts at the base of the rays often differ greatly in length and shape within the same inflorescence. Johnston (1975) interpreted *E. greggii* as a wide-leaved variety or synonym of *E. brachycera*, occurring further north and west than we map it here (Fig. 7). Our understanding of the tuberous-rooted *E. greggii* places it south and mostly east of Saltillo, Coahuila, whereas *E. brachycera* is only found west and north of there. Our phylogenetic analyses clearly place *E. greggii* within the *Esuliformis* clade.

16. *EUPHORBIA HELLERI* Millsp., Bot. Gaz. 26: 268. 1898 \equiv *Tithymalus helleri* (Millsp.) Small, Fl. S.E. U.S. 719. 1903 – Type: USA, Texas, southern Texas, ad Corpus Christi, Nueces County, 23–30 Mar 1894, A.A. Heller 1509 (holotype, F 196474!; isotypes, G!, GH!, MICH!, MSC!, NY!, PH!, TEX!, US (two sheets)!).

Distribution and habitat: Southern Texas and northern Nuevo León, Mexico, in forests, along stream banks, roadsides and in shaded areas with sandy, calcareous soils; 0–50 m elevation (Fig. 14).

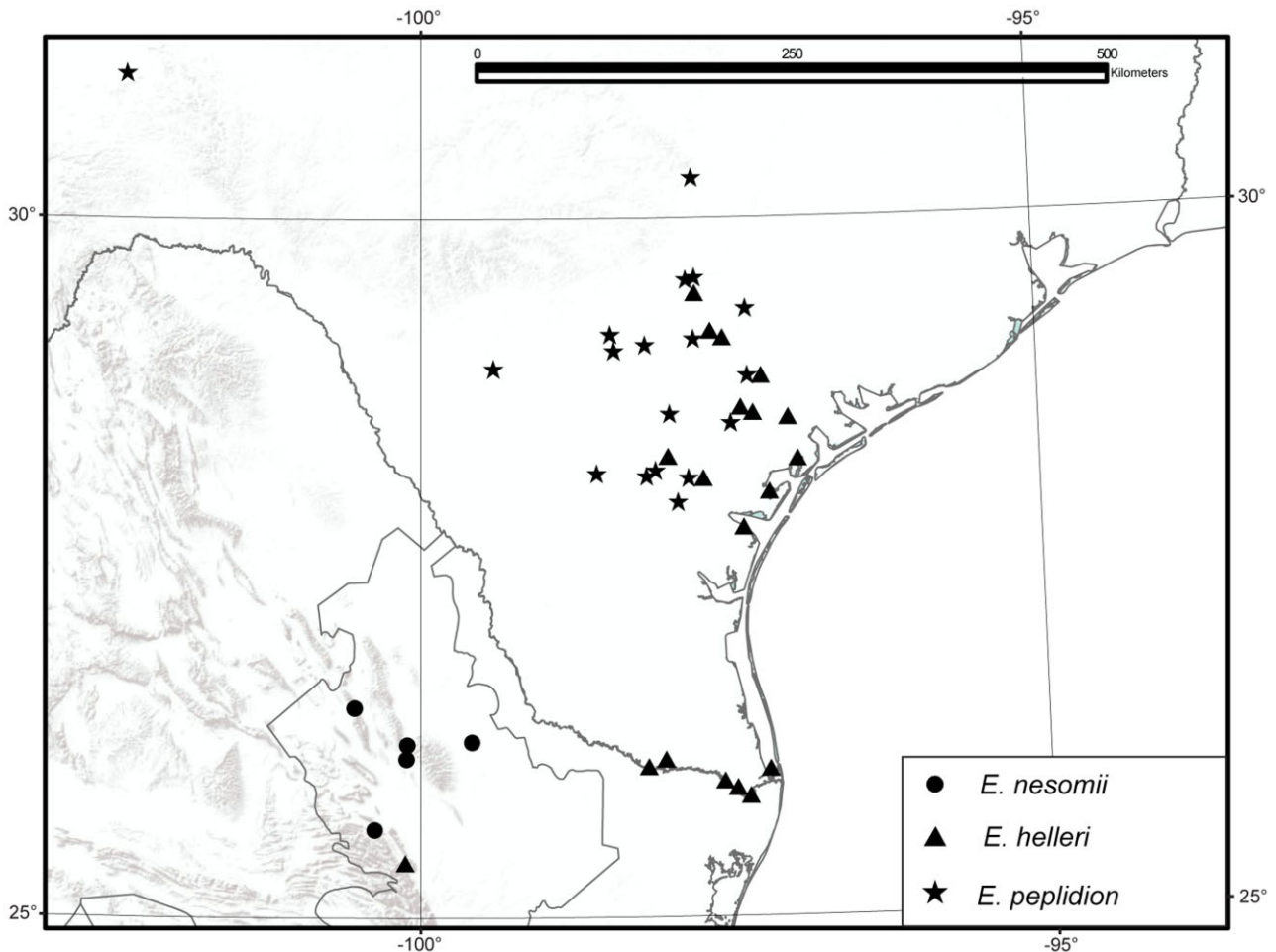


Figure 14. Geographical distribution of *Euphorbia helleri*, *E. nesomii* and *E. peplidion* in northern Mexico and the USA.

Phylogenetic placement: Southern annual clade.

Taxonomic remarks: *Euphorbia helleri* is most easily recognized by its smooth, white to light grey seeds that lack any kind of ornamentation (Fig. 2E). It is part of a strongly supported clade that includes two other annual species, *E. nesomii* and *E. peplidion*. *Euphorbia helleri* was reported by Thomas & Allen (1996) as introduced in Webster Parish, Louisiana (Thompson 503, LTU), but we could not confirm this record and so do not include it in the distribution.

17. *EUPHORBIA IVANJOHNSTONII* M.C.Johnst., *Wrightia* 5: 129. 1975 – Type: Mexico, Coahuila, Sierra Santa Fé del Pino, near and just west of the highest peaks in a WNW of Hacebuches and in broad canyon between the two main ridges, 28°13'30"–8°14'30"N, 103°02'–103°03'W, 2200–2600 m, 26 May 1973, M.C. Johnston, T. Wendt & F. Chiang 11237 (holotype, TEX!; isotypes, CAS!, MEXU!).

= *Euphorbia ivanjohnstonii* f. *longifolia* B.L.Turner, *Phytoneuron* 2011–14: 2. 2011 – Type: Mexico. Coahuila. Mpio. Ocampo, ca 63 (air) miles S of the S-most Mexico–US border of Big Bend, in Sierra Santa Fé del Pino, Cañon del Pino (VACA), on NE-facing limestone slope, c. 5 miles above the main ranch, in narrow canyon, 6000 ft, 28°10'N, 103°01'W, 12 Oct 1976, J. Henrickson & M. Dillon 15643 (holotype, TEX!).

Distribution and habitat: Endemic to upper slopes of the Sierra Santa Fé del Pino, in Coahuila, Mexico, 2000–2600 m elevation (Fig. 10).

Phylogenetic placement: *Esuliformis* clade.

Taxonomic remarks: Johnston (1975) proposed that *E. ivanjohnstonii* was presumably closely related to *E. brachycera* but that it differed in its distinctive indument. When Turner (2011a) described *E. ivanjohnstonii* f. *longifolia* as a distinct taxon, however, he hypothesized a close relationship between *E. ivan-*

johnstonii and *E. longicornuta*. Our phylogenetic analyses clearly place *E. ivanjohnstonii* (including f. *longifolia*) in the *Esuliformis* clade, to which *E. longicornuta* also belongs.

18. *EUPHORBIA LONGICORNUTA* S.Watson, Proc. Amer. Acad. Arts 25: 161. 1890 [as '*longecornuta*,' Article 60 of the ICN considers this to be an orthographical error to be corrected] – Type: Mexico, Nuevo León, summit of Sierra de la Silla, crevices of cliffs, 5000 ft, 3 Jun 1889, C.G. Pringle 2545 (holotype, GH 00047788!; isotypes, AC!, BKL!, BM!, BR! [two sheets], F!, G! [three sheets], GOET!, HBG!, K!, MEXU! [two sheets], LL!, MICH!, MO!, MPU!, MSC!, MU!, P!, PH! [2 sheets], PUL!, S!, US! [two sheets]).

Distribution and habitat: Endemic to Nuevo León and Coahuila, Mexico, on montane slopes, 1500–3400 m (Fig. 10).

Phylogenetic placement: *Esuliformis* clade.

Taxonomic remarks: *Euphorbia longicornuta* was described from the Sierra de la Silla, on the eastern edge of the city of Monterrey in northern Nuevo León, Mexico. The specimens from the type locality have long horns on the cyathial glands (hence the specific epithet) and also small leaves. Turner (2011a) included a second collection under this species from the nearby Sierra de la Marta (Nuevo León), based on the geographical proximity of the specimen, overall similarity and papillose stems. We add here a third specimen from the Sierra San José de los Nuncios (adjacent Coahuila). Both of these collections have leaves that are slightly larger and gland horns that are somewhat shorter than the type.

19. *EUPHORBIA LONGICRURIS* Scheele, Linnaea 22: 152. 1849 ≡ *Tithymalus longicruris* (Scheele) Small, Fl. S.E. U.S. 719. 1903 – Type: USA, Texas, [Comal Co.], 'bei Neu-Braunfels [New Braunfels]', 16 Apr 1846, F. Lindheimer 529 (90a) (neotype, Geltman *et al.*, 2011: 146, MO 1911068!; isoneotypes, BM!, G (two sheets)!, LE!).

= *Euphorbia peploides* Nutt., Trans. Amer. Philos. Soc., n.s., 5: 172. 1835, nom. illeg., non Gouan, Fl. Monsp. 174. 1764.

Distribution and habitat: Arkansas, Kansas, Texas and Oklahoma in grasslands, open prairies, sites with rocky, usually calcareous, soils, 300–800 m elevation (Fig. 13).

Phylogenetic placement: Northern annual clade.

Taxonomic remarks: *Euphorbia longicruris* is quite similar to the other small, annual members of section *Tithymalus* in the south-central United States but can be best distinguished from those species by its imbricate dichasial bracts that form little tufts of overlapping leaves at the ends of the pleiochasial branches. It is closely related to the newly described *E. austrotexana* (Fig. 4).

20. *EUPHORBIA LURIDA* Engelm., Proc. Amer. Acad. Arts 5: 173. 1861 ≡ *Tithymalus luridus* (Engelm.) Wootton & Standl., Contr. U.S. Natl. Herb. 16: 145. 1913 – Type: USA, Arizona, Camps 81–82 near Leroux's Spring, foot of Bill Williams Mtn., 7000–8000 ft, 27 Apr 1858, J.S. Newberry s.n. (holotype, MO 149770!; isotypes, G!, GH!).

= *Euphorbia palmeri* Engelm. ex S.Watson, Bot. California 2: 75. 1880 ≡ *Tithymalus palmeri* (Engelm. ex S.Watson) Dayton, Misc. Publ. U.S. Dept. Agric. 101: 93. 1931 – Type: USA, California [San Diego Co.], Talley's Ranch in the Cuyamaca Mountains, Jul 1875, E. Palmer 450 (holotype, GH!; isotypes, F!, MO 149780!, NY!, PH!).

= *Euphorbia subpubens* Engelm. ex S.Watson, Bot. California 2:76. 1880 ≡ *Tithymalus subpubens* (Engelm.) Norton, Contr. U.S. Natl. Herb. 35: 342. 1925 ≡ *E. palmeri* var. *subpubens* (Engelm.) L.C.Wheeler, J. Wash. Acad. Sci. 30:473. 1940 – Type: USA, Arizona, Prescott Mt., 20 Apr 1876, E. Palmer 512 (lectotype, Geltman *et al.*, 2011: 147, GH 47742!; isolectotypes, MO 149784!, MO 149785! –with sketch by S. Watson, NY!).

= *Euphorbia palmeri* var. *peplofolia* Norton, N. Amer. Euphorbia 41. 1899 ≡ *Euphorbia peplofolia* Engelm. ex Patt., Checklist N. Amer. Pl. 114. 1887, nom. nud. – Type: USA, 'southern Utah, Arizona &c, 1877,' E. Palmer 440 (lectotype, Geltman *et al.*, 2011: 147, MO 149781!).

= *Euphorbia lurida* var. *pringlei* Norton, N. Amer. Euphorbia 39. 1899 – Type: USA, Arizona, Santa Rita Mountains, 5500 ft, 2 May 1881, C.G. Pringle s.n. (lectotype, Geltman *et al.*, 2011: 147, MO 149771!; isolectotypes, MICH!, MO 202563!, NY!, US!).

Distribution and habitat: Arizona, California, Nevada, New Mexico, Utah and northern Mexico (Baja California), in open pine–oak forests, dry slopes and canyons, 1300–2800 m elevation (Fig. 9).

Phylogenetic placement: *Brachycera* clade.

Taxonomic remarks: *Euphorbia lurida* is an early spring perennial that occurs from southern Utah south to the western edge of New Mexico, southern Arizona, southern California and to the highest mountains of Baja California, Mexico. *Euphorbia*

lurida is usually glabrous, but plants from the vicinity of Prescott, Arizona (Yavapai Co.) are often sparsely puberulent and correspond closely to the type of *E. palmeri* var. *subpubens*. It is sometimes difficult to distinguish *E. lurida* from *E. brachycera* where they come into contact in the Mogollon Rim area of Arizona and some individuals in this region appear intermediate between the two species. The most reliable features to distinguish the two are the closely spaced and often significantly overlapping stem leaves in *E. lurida* relative to *E. brachycera*, and the crenate-margined glands that tend to lack horns in the former. Plants from southern Nevada and the Clark Mountains in California (San Bernardino County, California, and Clark County, Nevada) are distinctive in having orbicular leaves and bracts and short, spreading soboliferous stems (c. 15 cm tall). These populations may represent an undescribed species.

21. *EUPHORBIA MCVAUGHIANA* M.C. Johnst., *Wrightia* 5: 123. 1975 ≡ *Tithymalus mcvaughiana* (M.C. Johnst.) Soják, *Cas. Nár. Mus., Odd. Prír.* 148: 199. [1979] 1980 – Type: Mexico, Coahuila, 9 km S of Parras on Sierras Negras, 2400 m, 3 July 1941, L.R. Stanford, K.L. Retherford & R.D. Northcraft 220 (holotype, TEX!; isotypes, MO!, WTU!).

Distribution and habitat: Most common in the Mexican states of Coahuila and Nuevo León, but also known from south-eastern Chihuahua and northern Zacatecas, Mexico; in scrubby woodlands (chaparral) with pines, junipers and oaks, 2000–2850 m elevation (Fig. 8).

Phylogenetic placement: *Brachycera* clade.

Taxonomic remarks: *Euphorbia mcvaughiana* is closely related to *E. cressoides* and these are the only Mexican endemic members of the *Brachycera* clade (Fig. 4).

22. *EUPHORBIA NEILMULLERI* M.C. Johnst., *Wrightia* 5: 125. 1975 – Type: Mexico, Nuevo León, Sierra Madre Oriental, foothills below Pablillo, a ranch 15 mi S of Pueblo Galeana, 21 May 1934, C.H. Mueller & M.T. Mueller 501 (holotype, TEX!; isotypes, A!, F!, MICH!).

Distribution and habitat: Known only from Nuevo León, Mexico, in juniper–pine-dominated scrub on gypsum substrates, (1400)–1900–2150 m elevation (Fig. 10).

Phylogenetic placement: *Esuliformis* clade.

Taxonomic remarks: *Euphorbia neilmulleri* is a distinctive, small-leaved, densely woolly pubescent species that is endemic to the area around Galeana, Nuevo León, Mexico. The species is mainly confined almost entirely to gypsum substrates.

23. *EUPHORBIA NESOMII* Mayfield, *J. Bot. Res. Inst. Texas* 7: 639. 2013 – Type: Mexico, Nuevo León, Mun. Higuera, Cuesta Mamulique, along old unused road through pass (north of the summit), north facing slope above road to 1 km west of highway [85], 26°12'10"N, 100°06'25"W (WGS84), 600 m, 17 Mar 1994, M.H. Mayfield, C.J. Ferguson, & A.L. Hempel 1905 (holotype, MEXU!; isotypes, ANSM!, LSU!, KSC!, MICH!, TEX!).

Distribution and habitat: Endemic to northern Mexico in the state of Nuevo León, on relatively mesic limestone slopes in the mountains and in montane oak chaparral habitat, 400–600 m elevation (Fig. 14).

Phylogenetic placement: Southern annual clade.

Taxonomic remarks: *Euphorbia nesomii* is the only annual species in section *Tithymalus* that is endemic to Mexico. It is similar to *E. roemeriana* in having petiolate leaves and a multibranching habit, but differs in having stem leaves that are rhombic-ovate to elliptical, dichasial bracts that are free to the base and involucre glands that are narrower with longer horns. *Euphorbia nesomii* forms part of a strongly supported clade with two other annual species, *E. helleri* and *E. peplidion*.

24. *EUPHORBIA ORIZABAE* Boiss., *Prodr.* 15(2): 147. 1862 – Type: Mexico, Veracruz, in regione alpina montis Orizaba loco Vaquería del Jacal, Aug. 1838, J.J. Linden 791 (lectotype, K 000253760!, designated here; isolectotypes, BR!, FI-Webb!, G!, LG!, MICH! [ex LG]). The other syntype, *H. Galeotti* 3737, comes from the same Orizaba area, with specimens seen at BR!, F!, G! and K!.

= *Euphorbia campestris* var. *subpuberula* Greenm., *Proc. Amer. Acad. Arts* 41: 240. 1905 – Type: Mexico, Hidalgo, wet banks of river below Trinidad Iron Works, 5700 ft, 25 Apr 1904, C.G. Pringle 8906 (holotype, GH 00047758!; isotypes, E!, FR!, G! (four sheets), GOET!, JE!, K!, LL!, MEXU! (four sheets), MIN!, MPU!, MSC!, NY!, P!, PH!, R!, RSA!, S!, TEX!, US!).

Distribution and habitat: Southern Mexico (Chiapas, Hidalgo, Jalisco, Michoacán, Oaxaca, Veracruz) to Guatemala [Chimaltenango (Volcán de Acatenango), Huehuetenango, Quezaltenango, Quiché, San Marcos

and Totoncapán departments], in mesic montane forests, 2000–3100 m elevation (Fig. 12).

Phylogenetic placement: *Esuliformis* clade.

Taxonomic remarks: *Euphorbia orizabae* is one of the southernmost of the New World species of section *Tithymalus*. It can be distinguished from *E. esuliformis*, the only other sympatric species in the section, by short pubescence on the upper parts of the stem and floral branches in the former and by its less crowded and broader, elliptical-lanceolate leaves. Populations on the western side of Mexico in Jalisco and Michoacán are disjunct from the main area of the species distribution and differ in their long gland horns, as compared with the rather short horns that are typical of the species. The species is probably present in Puebla as well, as the type of *E. campestris* var. *subpuberula* is from a site on the Hidalgo–Puebla border.

25. *EUPHORBIA OUACHITANA* Mayfield, J. Bot. Res. Inst. Texas 7: 642. 2013 – Type: USA, Oklahoma, Pushmataha Co., 3.2 mi SE (130°) of Nashoba, slopes north of the mouth of Watson Creek (Little River), elev. 640 ft, 34.45261°N, 95.17233°W, 25 Apr 2002, *M.H. Mayfield 3551* (holotype, BRIT!; isotypes, KANU!, KSC!, MICH!, OKL!, OKLA!, TEX!, UARK!).

Distribution and habitat: Arkansas, Missouri, Oklahoma, Tennessee and Texas, in semi-open forests, on bluffs and ledges and glades and along stream banks, 100–400 m elevation (Fig. 13).

Phylogenetic placement: Northern annual clade.

Taxonomic remarks: *Euphorbia ouachitana* is a newly described species that is restricted to semi-open forests and woodlands in the south-central United States. It is most common in the Ouachita Mountains from south-eastern Oklahoma to Hot Springs County, Arkansas. *Euphorbia ouachitana* is similar to *E. commutata* and has been most commonly identified as that species in the past. It differs, however, in its consistently brown seeds that have pits in regular, vertical rows (Fig. 2H). Aside from the restricted distribution of *E. ouachitana* in Missouri and Tennessee, the ranges of *E. ouachitana* and *E. commutata* do not overlap (for a detailed discussion of the distribution see Mayfield, 2013).

26. *EUPHORBIA PEPLIDION* Engelm. in W.H. Emory, Rep. U.S. Mex. Bound. 2(1): 191. 1859 ≡ *Tithymalus peplidion* (Engelm.) Small, Fl. S.E. U.S. 720. 1903 – Type: USA, Texas, [Val Verde Co.], stony prairies east of San Pedro, [21–22 May]

1851, *C. Wright 1823* (holotype, MO 1911115!; isotypes, BM!, G!, GH!, K!, NY!, P!, US!).

Distribution and habitat: Endemic to south-central and western Texas, in dry, sandy habitats and open areas with poor soils, 100–300 m elevation (Fig. 14).

Phylogenetic placement: Southern annual clade.

Taxonomic remarks: *Euphorbia peplidion* forms part of a strongly supported clade with two other annual species, *E. helleri* and *E. nesomii*. This species has seeds that are similar to the European *E. peplus* (Morawetz *et al.*, 2010).

27. *EUPHORBIA PINKAVANA* M.C. Johnston, Wrightia 5: 126. 1975, – Type: Mexico, Coahuila, Sierra de la Madera, north side, upper part of Cañón de la Hacienda, 27°02'30"N, 102°26'30"W, 2550 m, 10 May 1973, *M.C. Johnston, T. Wendt & F. Chiang 10958* (holotype, TEX-LL!; isotype, CAS!).

Distribution and habitat: Known from the state of Coahuila, Mexico, on limestone crests and shaley slopes along pine–oak forests, 2550–2700 m elevation (Fig. 10).

Phylogenetic placement: *Esuliformis* clade.

Taxonomic remarks: *Euphorbia pinkavana* is known only from the Sierra de la Madera north-west of Cuatrociénegas in Coahuila, Mexico. It grows near the top of the mountains where the forest is thin. It is similar to *E. esuliformis* but can be distinguished primarily by its more compact habit and micropapillose leaf epidermis. *Euphorbia creberrima*, *E. ivan-johnstonii* and *E. longicornuta* all have a similar micropapillose vestiture.

28. *EUPHORBIA ROEMERIANA* Scheele, Linnaea 22: 151. 1849 ≡ *Tithymalus roemerianus* (Scheele) Small, Fl. S.E. U.S. 720. 1903 – Type: USA, Texas [Comal Co.], [New Braunfels], Apr 1846, *F. Lindheimer 528* (89) (neotype, Geltman *et al.*, 2011: 148, MO 1911159!; isoneotypes, BM!, G!, LE!).

Distribution and habitat: Endemic to central Texas (Bandera, Comal, Edwards Hays, Kerr and Travis Counties), near spring-fed streams that flow from the Edwards Aquifer along the Balcones Escarpment and also on floodplain terraces along rocky limestone stream valleys, often under live oak and elm in openings, 100–300 m elevation (Fig. 6).

Phylogenetic placement: Northern annual clade.

Taxonomic remarks: Correll & Johnston (1970) suggested that *E. roemeriana* was the southern counterpart of *E. commutata*, to which it is morphologically similar. *Euphorbia roemeriana* can be distinguished from *E. commutata* by the partly connate dichasial bracts of the former. Our phylogenetic analyses indicate that it is most closely related to *E. austrotexana* and *E. longicuris*.

29. *EUPHORBIA SCHIZOLOBA* Engelm., Proc. Amer. Acad. Arts 5: 173. 1861 = *Tithymalus schizolobus* (Engelm.) Norton, Contr. U.S. Natl. Herb. 25: 343. 1925 = *Euphorbia incisa* Engelm. in Ives, Rep. Colorado R. 4: 27. 1861 = *Tithymalus incisus* (Engelm.) W.A. Weber, Phytologia 67: 428. 1989 – Type: USA, Arizona, Camp 62, Central Range, in eastern Arizona, east of Colorado river, Railroad Pass, 3346 ft, 26 Mar 1858, *J.S. Newberry s.n.* (holotype, MO 144648!; isotypes, G!, GH 277308! [specimen on the left], NY 263179!).

Distribution and habitat: Arizona, California and Nevada, in desert canyons and on protected rock ledges, 500–1800 m elevation (Fig. 9).

Phylogenetic placement: *Brachycera* clade.

Taxonomic remarks: *Euphorbia schizoloba* is a desert perennial that occurs on bluffs and ledges from Death Valley, California, in the Mojave Desert to the Sonoran Desert of southern and central Arizona. Pubescent populations of *E. schizoloba* are known from Arizona and are best represented by several collections from the Mazatzal and Sierra Ancha Mountains in Gila County, Arizona. *Euphorbia schizoloba* is most easily recognized by its conspicuous, large involucre glands with jagged margins.

30. *EUPHORBIA TETRAPORA* Engelm. in W.H. Emory, Rep. U.S. Mex. Bound. 2(1): 191. 1859 = *Tithymalus tetraporus* (Engelm.) Small, Fl. S.E. U.S. 720. 1903 – Type: USA, [Louisiana], ‘Red River, Louisiana,’ *J. Hale s.n.* (lectotype, Geltman *et al.*, 2011: 149, MO 191173!; isolectotype, G!).

= *Euphorbia tetrapora* var. *berlandieri* Boiss. in A.P. de Candolle, Prodr. 15(2): 142. 1862 – Type: USA, Texas, de Bejar ad Rio de la Trinidad, May 1828, *J.L. Berlandier 1664* (holotype, G!; isotypes, G!, P 00716338!).

Distribution and habitat: Endemic to Texas, Oklahoma and Louisiana, in dry open woods and sandy soil habitats, 0–300 m elevation (Fig. 13).

Phylogenetic placement: Northern annual clade.

Taxonomic remarks: Correll & Johnston (1970) included Alabama and Georgia in the distribution of *Euphorbia tetrapora*, but we have excluded those states from the distribution because no specimens from the eastern Gulf Coastal Plain have been found.

31. *EUPHORBIA TUERCKHEIMII* Urb., Symb. Antill. 7: 265. 1912 – Type: Dominican Republic, prope Constanza, 1200 m in pinetum, Mar 1910, *H. von Tuerckheim 3009* (holotype, S!; isotypes, BM!, E!, F! [two sheets], G!, GH!, HBG! [two sheets], K!, MIN!, MO!, NY!, P!, U!).

Distribution and habitat: Known from the Dominican Republic, in openings of pine and mixed forest in the mountains of the Cordillera Central and Sierra de Bahoruco, 1200–2000 m elevation (Fig. 11).

Phylogenetic placement: *Esuliformis* clade.

Taxonomic remarks: *Euphorbia tuerckheimii* is one of only two native species of section *Tithymalus* that occur on Hispaniola. It differs from *E. eggersii* in its more lanceolate, sharply acute leaves. This species is weakly supported as sister to the other members of the *Esuliformis* clade in the Bayesian tree (Fig. 4).

32. *EUPHORBIA YAQUIANA* Tidestr., Proc. Biol. Soc. Wash. 48: 41. 1935 = *E. mollis* Engelm. ex Patt., Checklist N. Amer. Pl. 114. 1887, nom. nud. = *E. schizoloba* var. *mollis* Norton, N. Amer. Euphorbia 43, pl. 43. 1899 = *E. incisa* var. *mollis* (Norton) L.C. Wheeler, J. Wash. Acad. Sci. 30: 473. 1940 – Type: USA, Arizona, canyons, Santa Catalina Mts., 19 Apr 1881, *C.G. Pringle s.n.* (lectotype, Geltman *et al.*, 2011: 149, MO 149782!; isolectotypes, AC!, F! [2 sheets], G! [3 sheets], GH!, K!, ISC!, NY! [4 sheets], P!, PH! [3 sheets]).

Distribution and habitat: Sky island mountains and canyons of southern Arizona, in ponderosa pine forests, oak–pine mixed forests, along creek banks and dry stream beds, 1000–2200 m elevation (Fig. 9).

Phylogenetic placement: *Brachycera* clade.

Taxonomic remarks: *Euphorbia yaquiana* is a perennial species in the *E. brachycera* group that is endemic to Pima and Graham Counties in southern Arizona. This species appears to comprise a densely pubescent set of southern populations with crenate gland margins that is closely related to *E. brachycera* and *E. chamaesula*. At this time, the species is only known to occur in the Santa Catalina and Pinaleno Mountains.

UNPLACED OR POSSIBLY NEW ENTITIES

During the course of this study, it became clear that a number of Mexican specimens belonging to section *Tithymalus* do not fit well in any previously described species. Below we list and discuss nine distinct groups of specimens that we were unable to clearly place in our taxonomic treatment. For each of them, we indicate the species they most closely resemble. It is probable that at least some of these groups represent new species and we hope that clarifying our current understanding of this diversity will advance work on the group. We encourage others to actively seek out these plants in the field and herbarium and to critically evaluate them. Leafy spurge are generally undercollected and increased collections in the floristically diverse area of northern and central Mexico are critical to furthering our understanding of the taxonomy and evolution of this group.

Euphorbia sp. 1 (aff. *E. furcillata*). This entity is represented by several collections from the states of Jalisco and Michoacán. The plants arise from thin, wiry stems and appear to be most similar to *E. furcillata*. They differ, however, in their longer, lanceolate to lance-elliptical leaves. These populations are separated from the main range of *E. furcillata* by around 300 km. Included here are *Gaona 402* (MICH; Jalisco, Municipio Tamazula, 26 km east of Ciudad Guzmán, road from Tamazula and 34 km from Vista Hermosa); *Pérez-Ramírez 137* (TEX; Michoacán, Municipio Paracho, 5 km SW of Paracho); *Zamudio 9843* (TEX; Michoacán, Municipio Pátzcuaro, Cerro El Estribo); *Leavenworth 248* (MICH; Michoacán, Municipio Tancítaro, on mesa above Tancítaro); and *Díaz-Barriga 2526* (TEX; Michoacán, base of Cerro La Calabaza, near the turnoff to Coeneo).

Euphorbia sp. 2 (aff. *E. furcillata*). This entity is represented by two collections from the states of San Luis Potosí and Tamaulipas. The plants are most similar to *E. furcillata*, arising from thin wiry stems and with strongly ascending, overlapping leaves. These specimens are more robust than *E. furcillata* and the localities are separated from the main range of the species by around 400 km. Included here are *Torres-Colin et al. 14982* (TEX; San Luis Potosí, Municipio Guadalucazar, 15 km N of Realejo, towards San José de Las Flores) and *Martínez et al. 354* (TEX; Tamaulipas, Municipio Tula, La Presita, Ejido Ricardo García, km 66 of the Tula-Ciudad Victoria road).

Euphorbia sp. 3 (aff. *E. furcillata*). This diminutive plant is represented here by a single collection from the state of Durango. The plant is most similar to *E. furcillata*, arising from thin wiry stems, but they have small, spreading to reflexed leaves and sparsely short-pubescent stems. The locality is separated from

the main range *E. furcillata* by 850 km. Included here is *Maysilles 7899* (MICH; Durango, Laguna del Progreso, 34 road miles north of railroad at Coyotes, 2500–2600 m elevation).

Euphorbia sp. 4 (aff. *E. creberrima*). This entity is represented by several collections from near Suratato in the state of Sinaloa and near Xoconostle in the state of Durango. The plants appear to be most similar to *E. creberrima*, but they are glabrous or sparsely pubescent (not conspicuously papillose) and geographically disjunct from that species. Included here are *González 1184* (MEXU; Durango, from camino El Durazno a Xoconostle, Municipio Mezquital) and *Breedlove 15560* (CAS, MICH), *Breedlove & Thorne 18312* (CAS, MICH), *Gentry 6190* (MICH) and *Martínez et al. 4190* (DAV), all from Sinaloa state in the Sierra Suratato near Los Ornos.

Euphorbia sp. 5 (aff. *E. creberrima*). These two collections from the state of Durango are generally similar to *E. creberrima*, but they have glaucescent stems and only the upper leaves are minutely papillose. Included here are *Corral-Díaz 236/Worthington 10942* (TEX; Municipio Santiago Papasquiario, Sierra Madre Occidental, c. 22 air mi WNW of Santiago Papasquiario, 3.3 mi by Topia Rd W crest of sierra from road to antenna, 8750 ft, 25°04'N, 105°51'W) and *Palmer 72* (K, US) from the vicinity of Santiago Papasquiario.

Euphorbia sp. 6. This conspicuously pubescent plant is represented by two collections from the state of Durango. Its affinities are unclear. Included here are *Bacon & Spellenberg 1238* (CIIDIR, KSC, NMC, TEX; c. 130 air km W of Santiago Papasquiario, along road from Santiago Papasquiario to Canelas, 13 km E of Canelas, on W edge of Cuevecillas, 1.6 km W of junction of road to Topia) and *Pennell 18436* (PH, US; Metates, north of Cueva, waterfall in pineland, 2600–2650 m).

Euphorbia sp. 7. This entity is represented by several collections from the states of Hidalgo, Querétaro and Veracruz. The plants are probably related to *E. orizabae* in that the specimens appear to be low shrubs or subshrubs with thin stems that have a distinctive, forked branching pattern. They are also apparently restricted to montane cloud forests with *Pinus patula* and *Quercus* spp. Included here are *Moore & Wood 4344* (MICH; Hidalgo, Municipio Zimapán, from Encarnación to Mt. Cangandho); *Poole et al. 2383* (TEX; Hidalgo, c. 14.3 mi S of Jacala on Hwy 85 from Tamazunchale to Pachuca); *Webster et al. 11325* (DAV; Hidalgo, 13.5 km by road SW of Jacala); *Tenorio & R. Hernández 351* (DAV, MEXU; Querétaro, Municipio Pinal de Amoles, 12 km SE of Pinal de Amoles); and *Fay & Calzada 699* (US; Veracruz, carretera Huayacocotla a Vibrillas, 1 km de Huayacocotla, 2300 m).

Euphorbia sp. 8. This is a small, weak-stemmed perennial herb, represented by a number of collections from the Mexican states of Chihuahua and Sonora. It is most common in the Basaseachic area of south-western Chihuahua. Steinmann & Felger, (1997) included this entity in their treatment as '*Euphorbia* species 2'. It is not clear to which perennial clade it belongs. Included here are Steinmann 484 (ARIZ; Sonora, Municipio Álamos, Sierra Saguaribo, Barranca Huicochic, c. 27°18'30"N, 108°39'30"W); Van Devender 97-404 (ARIZ; Sonora, Municipio Yécora, Ciénaga de Camilo, 6.3 km E of El Kipor, 11.2 km W of the Chihuahua border, 28°43'05"N, 108°34'05"W); and Spellenberg et al. 8106 (MICH, NMC; Chihuahua, Municipio Ocampo, Parque Nacional de Cascada Baseachic).

Euphorbia sp. 9. This entity is represented by a few collections from the western part of the state of Chihuahua. The plants have somewhat thin, wiry stems and lanceolate to lance-elliptical leaves with irregular, slightly undulate margins. Its affinities are unclear. Included here are Spellenberg et al. 8413 (NMC, TEX; Chihuahua, Municipios Guerrero/El Progreso boundary, 16 mi W of Tomochic, 6400 ft elevation); Palmer 311 (US; Chihuahua, vicinity of Madera, 2250 m); and Jenkins 95-54 (ARIZ; Chihuahua, Sierra de los Ajos, Municipio Bacoachi, 30°53'N, 109°55'W, 2080 m).

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APPENDIX 1

Taxon and authority, sample origin, voucher information (herbarium acronym) and ITS, *ndhF*, *trnH-psbA*, *trnS-trnG* and *trnD-trnT* GenBank accession numbers for samples included in the phylogenetic analyses. GenBank accession numbers for newly generated sequences are preceded by an asterisk. A region that was not sequenced for a particular sample is indicated by –.

Euphorbia austrotexana M.Mayfield, USA: Texas, W. Carr 12504 (KSC, MICH), *KJ149580, *KJ149625, *KJ149708, *KJ149773, *KJ149683. *Euphorbia austrotexana* M.Mayfield, USA: Texas, M. Mayfield 2128 (KSC, MICH), *KJ149581, –, *KJ149709, *KJ149774, *KJ149684. *Euphorbia austrotexana* M.Mayfield, USA: Texas, W. Carr 20435 (MICH), *KJ149582, *KJ149626, *KJ149710, –, –. *Euphorbia azorica* Hochst. in M.A.Seubert, Portugal, J. Molero et al. BCN86828 (BCN), KC212182, KC212448, –, –, –. *Euphorbia beamanii* M.C.Johnst., Mexico: Coahuila, M. Mayfield 1903 (MICH), *KJ149583, *KJ149627, *KJ149711, –, –. *Euphorbia beamanii* M.C.Johnst., Mexico: Coahuila, G. McPherson 889 (MICH), *KJ149586, –, *KJ149714, –, –. *Euphorbia beamanii* M.C.Johnst., Mexico: Nuevo León, R. McGregor et al. 273 (MICH), *KJ149584, *KJ149628, *KJ149712, –, –, –. *Euphorbia beamanii* M.C.Johnst., Mexico: Nuevo León, E. Perez & S. Zamudio 2078 (MICH), *KJ149585, –, *KJ149713, –, –. *Euphorbia beamanii* M.C.Johnst., Mexico: Nuevo León, J. Beaman 3316 (MSC), –, *KJ149629, *KJ149715, –, –, –. *Euphorbia brachycera* Engelm., USA: Arizona, J. Peirson 894 (MICH), –, *KJ149632, *KJ149718, –, –, –. *Euphorbia brachycera* Engelm., USA: Arizona, G. Rink 6201 (NY), JN250186, JN249176, –, –, –. *Euphorbia brachycera* Engelm., USA: Colorado, P. Berry 7968 (MICH), –, KC212457, –, –, –. *Euphorbia brachycera* Engelm., USA: Colorado, M. Mayfield 3365 (KSC, MICH), –, *KJ149630, *KJ149716, *KJ149775, *KJ149685. *Euphorbia brachycera* Engelm., USA: New Mexico, M. Mayfield 3565 (KSC, MICH), *KJ149587, *KJ149631, *KJ149717, *KJ149776, *KJ149686. *Euphorbia brachycera* Engelm., USA: Utah, B. Van Ee 1010 (MICH), KC212194, KC212458, –, –, –. *Euphorbia brachycera* Engelm., USA: Utah, M. Mayfield 3347 (KSC, MICH), *KJ149588, *KJ149633, *KJ149719, *KJ149777, *KJ149687. *Euphorbia chamaesula* Boiss., USA: Arizona, J. Peirson 865 (MICH),

*KJ149589, *KJ149634, *KJ149720, –, –, –. *Euphorbia characias* L., France, P.E. Berry 7917 (MICH), KC212205, KC212470, –, –, –. *Euphorbia chiribensis* V.W.Steinm. & Felger, Mexico: Sonora, V. Steinmann et al. 93270 (TEX), –, –, *KJ149721, –, –, –. *Euphorbia commutata* Engelm. ex A.Gray, Canada: Ontario, M. Oldham 14724 (MICH), KC212207, KC212472, *KJ149724, –, –, –. *Euphorbia commutata* Engelm. ex A.Gray, USA: Arkansas, C. Ferguson 434 (LSU), *KJ149590, *KJ149635, *KJ149722, *KJ149778, *KJ149688. *Euphorbia commutata* Engelm. ex A.Gray, USA: Missouri, M. Mayfield 3792 (KSC, MICH), *KJ149591, *KJ149636, *KJ149723, –, –, –. *Euphorbia commutata* Engelm. ex A.Gray, USA: Ohio, J. McCormac 5521 (MICH), *KJ149592, *KJ149637, *KJ149725, –, –, –. *Euphorbia connata* Boiss., Iran, Y. Salmaki et al. 39937 (TUH), KC212211, KC212475, –, –, –. *Euphorbia creberrima* McVaugh, Mexico: Jalisco, M. Cházaro & A. Garcia-Guerrero 7433 (MICH), –, –, *KJ149726, –, –, –. *Euphorbia creberrima* McVaugh, Mexico: Jalisco, J. Rzedowski 17965 (MICH), –, *KJ149638, *KJ149727, –, –, –. *Euphorbia crenulata* Engelm., USA: California, F. Brunett 313 (MICH), *KJ149593, *KJ149640, *KJ149729, –, –, –. *Euphorbia crenulata* Engelm., USA: California, J. Peirson 917 (MICH), *KJ149594, *KJ149641, *KJ149730, –, –, –. *Euphorbia crenulata* Engelm., USA: Colorado, M. Mayfield 3573 (KSC, MICH), –, *KJ149639, *KJ149728, *KJ149779, *KJ149689. *Euphorbia cressoides* M.C.Johnst., Mexico: Coahuila, M. Johnston et al. 9551i (TEX), –, *KJ149642, *KJ149731, –, –, –. *Euphorbia esuliformis* S.Schauer, Mexico: Coahuila, F. Gould 6366 (MICH), *KJ149599, –, *KJ149737, –, –, –. *Euphorbia esuliformis* S.Schauer, Mexico: Jalisco, J. Gonzalez 208 (IEB), *KJ149596, *KJ149644, *KJ149733, –, –, –. *Euphorbia esuliformis* S.Schauer, Mexico: Mexico, M. Denton 1694 (MICH), *KJ149595, *KJ149643, *KJ149732, –, –, –. *Euphorbia esuliformis* S.Schauer, Mexico: Michoacan, M. Melgoza 800 (MEXU), –, KC212518, –, –, –. *Euphorbia esuliformis* S.Schauer, Mexico: Michoacan, E. Pérez-Calix 4485 (IEB/MICH), *KJ149597, –, *KJ149734, –, –, –. *Euphorbia esuliformis* S.Schauer, Mexico: Nuevo León, M. Mayfield 1892 (Redo) (MICH), *KJ149598, *KJ149645, *KJ149735, –, –, –. *Euphorbia esuliformis* S.Schauer, Mexico: Querétaro, V. Steinmann et al. 5844 (MICH), –, KC212464, –, –, –. *Euphorbia esuliformis* S.Schauer, Mexico: Querétaro, V. Steinmann et al. 3332 (MICH), –, *KJ149646, *KJ149736, –, –, –. *Euphorbia furcillata* Kunth, Mexico: Federal District, J. Rzedowski 35747 (MICH), –, –, *KJ149738, –, –, –. *Euphorbia glauca* G.Forst., New Zealand, P. Garnock-Jones 2844 –, KC212261, KC212523, –, –, –. *Euphorbia greggii* Engelm. ex Boiss., Mexico: Nuevo León, M. Mayfield 2250 (KSC, MICH), *KJ149600, *KJ149647, *KJ149739, *KJ149780, *KJ149690. *Euphorbia*

- greggii* Engelm. ex Boiss., Mexico: Nuevo León, *M. Johnston* 5163 (MICH), *KJ149601, *KJ149648, *KJ149740, –, –, *Euphorbia greggii* Engelm. ex Boiss., Mexico: Nuevo León, *G. Hinton* 25925 (IEB), –, *KJ149649, –, –, *Euphorbia helleri* Millsp., USA: Texas, *M. Mayfield* 2142 (MICH), *KJ149602, *KJ149650, *KJ149741, *KJ149781, *KJ149691. *Euphorbia helleri* Millsp., USA: Texas, *M. Mayfield* 2150 (MICH), *KJ149603, *KJ149651, *KJ149742, –, –, *Euphorbia herniariifolia* Willd., Greece, *B. Frajman & P. Schönswetter* 11668 (IB), JN010054, KC212536, –, –, *Euphorbia herniariifolia* Willd., Greece, *R. Riina* 1571 (MICH), JN250169, JN249159, –, –, *Euphorbia isaurica* M.S.Khan, Turkey, *P. Davis* 16189 (E), –, KC212547, *KJ149743, –, –, *Euphorbia ivanjohnstonii* M.C.Johnst., Mexico: Coahuila, *M. Johnston et al* 11237 (CAS), –, *KJ149652, *KJ149744, –, –, *Euphorbia ivanjohnstonii* f. *longifolia* B.L.Turner, Mexico: Coahuila, *J. Henrickson* 15643 (TEX), –, *KJ149653, *KJ149745, –, –, *Euphorbia longicuris* Scheele, USA: Arkansas, *M. Mayfield* 3127 (KSC, MICH), *KJ149605, *KJ149655, *KJ149747, *KJ149783, *KJ149693. *Euphorbia longicuris* Scheele, USA: Texas, *C. Ferguson* 459 (LSU), *KJ149604, *KJ149654, *KJ149746, *KJ149782, *KJ149692. *Euphorbia lurida* Engelm., Mexico: Baja California, *R. Moran* 14918 (MICH), *KJ149608, –, *KJ149750, –, –, *Euphorbia lurida* Engelm., USA: California, *M. Mayfield* 3357 (KSC, MICH), *KJ149606, *KJ149656, *KJ149748, *KJ149784, *KJ149694. *Euphorbia lurida* Engelm., USA: New Mexico, *M. Mayfield* 3566 (KSC, MICH), *KJ149607, *KJ149657, *KJ149749, *KJ149785, *KJ149695. *Euphorbia mcvaughiana* M.C.Johnst., Mexico: Nuevo León, *M. Mayfield* 2253 (KSC, MICH), *KJ149609, *KJ149658, *KJ149751, *KJ149786, *KJ149696. *Euphorbia neilmulleri* M.C.Johnst., Mexico: Nuevo León, *J. Henrickson* 22475b (IEB), –, KC212578, –, –, *Euphorbia neilmulleri* M.C.Johnst., Mexico: Nuevo León, *G. Hinton* 21861 (MICH), –, *KJ149659, *KJ149752, –, –, *Euphorbia neilmulleri* M.C.Johnst., Mexico: Nuevo León, *G. Hinton* 22095 (MICH), –, *KJ149660, *KJ149753, –, –, *Euphorbia neilmulleri* M.C.Johnst., Mexico: Nuevo León, *G. Hinton* 24243 (MEXU), –, *KJ149661, –, –, *Euphorbia nesomii* M.Mayfield, Mexico: Nuevo León, *M. Mayfield* 1905 (KSC, MICH), *KJ149610, *KJ149662, *KJ149754, *KJ149787, *KJ149697. *Euphorbia nesomii* M.Mayfield, Mexico: Nuevo León, *M. Mayfield* 1906 (KSC, MICH), *KJ149611, *KJ149663, *KJ149755, *KJ149788, *KJ149698. *Euphorbia orizabae* Boiss., Mexico: Jalisco, *R. McVaugh* 23165 (MICH), *KJ149614, *KJ149668, *KJ149758, –, –, *Euphorbia orizabae* Boiss., Mexico: Oaxaca, *W. Graham & M. Frohlich* 1020 (MICH), *KJ149612, *KJ149664, *KJ149756, –, –, *Euphorbia orizabae* Boiss., Mexico: Oaxaca, *G. Webster et al.* 11555 (MICH), *KJ149613, –, –, –, *Euphorbia orizabae* Boiss., Mexico: Oaxaca, *C. Galardo et al.* 1711 (MEXU), –, *KJ149665, –, –, –, *Euphorbia orizabae* Boiss., Mexico: Oaxaca, *J. Rivera-Reyes* 1902 (MEXU), –, *KJ149666, –, –, –, *Euphorbia orizabae* Boiss., Mexico: Oaxaca, *D. Breedlove* 64688 (MICH), –, *KJ149667, *KJ149757, –, –, *Euphorbia ouachitana* M.Mayfield, USA: Arkansas, *D. Demaree* 36424 (MICH), *KJ149617, *KJ149671, *KJ149761, –, –, *Euphorbia ouachitana* M.Mayfield, USA: Missouri, *M. Mayfield* 3789 (KSC, MICH), *KJ149616, *KJ149670, *KJ149760, –, –, *Euphorbia ouachitana* M.Mayfield, USA: Oklahoma, *M. Mayfield* 3108 (KSC, MICH), *KJ149615, *KJ149669, *KJ149759, *KJ149789, *KJ149699. *Euphorbia ouachitana* M.Mayfield, USA: Tennessee, *M. Mayfield* 3549 (KSC, MICH), *KJ149618, *KJ149672, *KJ149762, *KJ149790, *KJ149700. *Euphorbia paralias* L., Greece, *R. Riina* 1565 (MICH), JN250207, JN249194, –, –, –, *Euphorbia peplidion* Engelm., USA: Texas, *M. Mayfield* 2119 (TEX), *KJ149619, *KJ149673, *KJ149763, *KJ149791, *KJ149701. *Euphorbia peplus* L., Croatia, *B. Frajman & P. Schönswetter* 11531 (IB), JN010076, KC212597, –, –, –, *Euphorbia peplus* L., France, *P. Berry* 7915 (MICH), KC212334, KC212598, –, –, –, *Euphorbia peplus* L., Mexico: Puebla, *J. Soule & A. Prather* 2941 (MO), –, *KJ149674, *KJ149764, –, –, *Euphorbia pinkavana* M.C.Johnst., Mexico: Coahuila, *J. Henrickson* 16008 (IEB), –, KC212601, –, –, –, *Euphorbia portlandica* L., Portugal, *R. Riina* 1583 (MICH), KC212345, KC212609, –, –, –, *Euphorbia roemeriana* Scheele, USA: Texas, *M. Mayfield* 2158 (TEX), *KJ149620, *KJ149675, *KJ149765, *KJ149792, *KJ149702. *Euphorbia schizoloba* Engelm., USA: Arizona, *M. Mayfield* 3567 (KSC, MICH), *KJ149621, *KJ149677, *KJ149767, *KJ149794, *KJ149704. *Euphorbia schizoloba* Engelm., USA: California, *M. Mayfield* 3355 (KSC, MICH), –, *KJ149676, *KJ149766, *KJ149793, *KJ149703. *Euphorbia sulcata* Lens ex Loisel., Spain, *R. Riina* 1861 (MA), KC212400, KC212652, –, –, –, *Euphorbia tetrapora* Engelm., USA: Louisiana, *M. Mayfield* 2882 (LSU), *KJ149623, *KJ149679, *KJ149769, *KJ149796, *KJ149706. *Euphorbia tetrapora* Engelm., USA: Texas, *M. Mayfield* 2684 (LSU), *KJ149622, *KJ149678, *KJ149768, *KJ149795, *KJ149705. *Euphorbia tuerckheimii* Urb., Dominican Republic: Pedernales, *T. Clase et al.* 7332 (MICH), –, *KJ149680, *KJ149770, –, –, *Euphorbia yaquiana* (Cockerell) Tidestr., USA: Arizona, *M. Mayfield* 3364 (KSC, MICH), *KJ149624, *KJ149681, *KJ149771, *KJ149797, *KJ149707. *Euphorbia yaquiana* (Cockerell) Tidestr., USA: Arizona, *J. Peirson* 884 (MICH), –, *KJ149682, *KJ149772, –, –.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Figure S1. Maximum-likelihood phylogram from RAxML analysis of the complete ITS dataset of *Euphorbia* section *Tithymalus* and outgroups. Maximum-likelihood bootstrap values ($\geq 50\%$) are indicated. The scale bar indicates the mean number of nucleotide substitutions per site.

Figure S2. Maximum-likelihood phylogram from RAxML analysis of the complete *ndhF* dataset of *Euphorbia* section *Tithymalus* and outgroups. Maximum-likelihood bootstrap values ($\geq 50\%$) are indicated. The scale bar indicates the mean number of nucleotide substitutions per site.

Figure S3. Maximum-likelihood phylogram from RAxML analysis of the complete plastid DNA spacer dataset of *Euphorbia* section *Tithymalus* and outgroups. Maximum-likelihood bootstrap values ($\geq 50\%$) are indicated. The scale bar indicates the mean number of nucleotide substitutions per site.

Figure S4. Maximum-likelihood phylogram from RAxML analysis of the combined ITS + *ndhF* + plastid DNA spacer dataset (without scored indels) of *Euphorbia* section *Tithymalus* and outgroups. Maximum-likelihood bootstrap values ($\geq 50\%$) are indicated. The scale bar indicates the mean number of nucleotide substitutions per site.

Appendix S1. Herbarium specimens and associated specimen data examined during the course of this study. Georeferenced specimens in this table are the basis for the distribution maps (Figs 6–14) in the article.