

Molecular phylogenetics and classification of *Euphorbia* subgenus *Chamaesyce* (Euphorbiaceae)

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Abstract *Euphorbia* subg. *Chamaesyce* contains around 600 species and includes the largest New World radiation within the Old World-centered genus *Euphorbia*. It is one of the few plant lineages to include members with C₃, C₄ and CAM photosynthesis, showing multiple adaptations to warm and dry habitats. The subgenus includes North American-centered groups that were previously treated at various taxonomic ranks under the names of “*Agaloma*”, “*Poinsettia*”, and “*Chamaesyce*”. Here we provide a well-resolved phylogeny of *Euphorbia* subg. *Chamaesyce* using nuclear ribosomal ITS and chloroplast *ndhF* sequences, with substantially increased taxon sampling compared to previous studies. Based on the phylogeny, we discuss the Old World origin of the subgenus, the evolution of cyathial morphology and growth forms, and then provide a formal sectional classification, with descriptions and species lists for each section or subsection we recognize.

Key Words C₄; CAM; *Euphorbia* subgenus *Chamaesyce*; Euphorbiaceae; ITS; *ndhF*

Supplementary Material The alignment files are available in the Supplementary Data section of the online version of this article (<http://www.ingentaconnect.com/content/iapt/tax>).

■ INTRODUCTION

Euphorbia L. (Euphorbiaceae) has about 2000 species worldwide and is well known for the remarkable diversity of succulent and non-succulent plants that are avidly grown by horticultural enthusiasts. The entire genus is characterized by the presence of a cyathium, a unique inflorescence type (Prenner & Rudall, 2007; Prenner & al., 2011). The genus appears to have originated in the Old World (Steinmann & Porter, 2002), with multiple New World groups embedded in it. The largest New World lineage consists of more than 500 species that are characterized by the presence of petaloid appendages subtending the cyathial glands, although this feature has been subsequently lost a number of times. This petaloid appendage-bearing, New World group is deeply nested within Old World groups, and together they constitute *Euphorbia* subg. *Chamaesyce* Raf. (Steinmann & Porter, 2002; Bruyns & al., 2006; Horn & al., 2012a). Subgenus *Chamaesyce* is best known for its leafy, non-succulent, ornamental species, such as the Christmas Poinsettia (*E. pulcherrima* Willd. ex Klotzsch), one of the most profitable potted plants in the world. Other widely cultivated members are “Snow-on-the-Mountain” (*E. marginata* Pursh.) and “Diamond Frost” (a cultivar of *E. graminea* Jacq.). It also includes a large number of cosmopolitan weedy species such as the spotted spurge (*E. maculata* L., Fig. 1E).

Among the four subgenera of *Euphorbia*, *Euphorbia* subg. *Chamaesyce* is the second-most species-rich, encompassing around 600 species worldwide. It is highly diverse in growth forms, including annual and perennial herbs, shrubs, trees, and pencil-stem succulents (Fig. 1A–E). Notably, it is the only plant lineage at or below the level of genus that has all known photosynthetic types: C₃, C₄ and CAM (Webster & al., 1975), plus a C₂ system that represents an early stage of C₃ to C₄ transition (Sage & al., 2011). C₄ photosynthesis evolved once within *Euphorbia* subg. *Chamaesyce* sect. *Anisophyllum*, and this C₄ group subsequently diversified into approximately 350 species worldwide (Yang & Berry, 2011); C₂ photosynthesis also evolved once, again in sect. *Anisophyllum*, and is present in two species restricted to southwestern United States and northern Mexico (Sage & al., 2011). CAM photosynthesis, in contrast, evolved multiple times in subg. *Chamaesyce* in both the Old World and the New World (Horn & al., 2012b).

Due to widespread convergence in growth forms and cyathial characters, subgeneric classification within *Euphorbia* has been notoriously contentious. The current scheme of four subgenera is based on molecular evidence. All molecular phylogenetic studies to date support all cyathium-bearing species as forming a monophyletic *Euphorbia* s.l. (Steinmann & Porter, 2002; Bruyns & al., 2006, 2011; Park & Jansen, 2007; Zimmermann & al., 2010; Horn & al., 2012a). These studies

also support the monophyly of four major clades within *Euphorbia*, which were informally named by Steinmann & Porter (2002) as clades A, B, C and D. Among them, clade D was later recognized by Bruyns & al. (2006) as subg. *Chamaesyce* Raf. These studies either have limited taxon sampling within subg. *Chamaesyce*, or else they have low statistical support within subg. *Chamaesyce*. Steinmann & Porter (2002) sampled 82 of the 600 species in subg. *Chamaesyce* for nuclear ribosomal internal transcribed spacer (ITS), among which 40 also had *ndhF* sequences. Using maximum parsimony, they found that the majority of deep nodes within the genus received low statistical support. Four subsequent genus-wide molecular phylogenetic studies each added only a small number of species within subg. *Chamaesyce*, and relationships among major groups of the subgenus remained poorly supported (Bruyns & al., 2006, 2011; Park & Jansen, 2007; Zimmermann & al., 2010). This problem was partly addressed by the “backbone” phylogeny of Horn & al. (2012a), which sampled 176 species across *Euphorbia* using ten loci, including nuclear, mitochondrial and chloroplast regions, with 31 representative species within subg. *Chamaesyce*. This study had much improved support values within subg. *Chamaesyce*, and it highly supported the monophyly of subg. *Chamaesyce*, as well as its sister relationship to *Euphorbia* subg. *Euphorbia*. Of all six previous genus-wide molecular studies, three of them support a monophyletic, primarily New World clade nested in a basal Old World grade (Steinmann & Porter, 2002; Zimmermann & al., 2010; Horn & al., 2012a). The other three studies lack statistical support for deep nodes within subg. *Chamaesyce* (Bruyns & al., 2006, 2011; Park & Jansen, 2007). In addition to these studies, Yang & Berry (2011) constructed a robust phylogeny of *Euphorbia* subg. *Chamaesyce* sect. *Anisophyllum*, which corresponds to the former segregate genus *Chamaesyce* S.F. Gray. In their analysis, 138 ingroup species were sequenced with two nuclear loci and three chloroplast loci, and the monophyly of sect. *Anisophyllum* was well supported. Taking all seven previous molecular studies into account, about a third of the species in subg. *Chamaesyce* were sampled, and most species outside of sect. *Anisophyllum* only have ITS sequences available.

With the international collaborative network established by the *Euphorbia* Planetary Biodiversity Inventory (*Euphorbia* PBI) project (www.euphorbiaceae.org), we have been able to greatly expand our worldwide taxon sampling to reconstruct a well-sampled, and well-supported molecular phylogeny. The main purpose of this paper is to propose a revised sectional and subsectional classification of *Euphorbia* subg. *Chamaesyce* in light of the updated phylogeny we have produced. This will provide a stable nomenclatural base for subsequent research.

■ MATERIALS AND METHODS

Taxon sampling. — Silica-preserved leaf samples were collected in all major areas where *Euphorbia* occurs during 2006–2009. Sampling was supplemented by leaf materials taken from herbarium sheets. To include as many taxa as possible belonging to subg. *Chamaesyce*, we conducted a

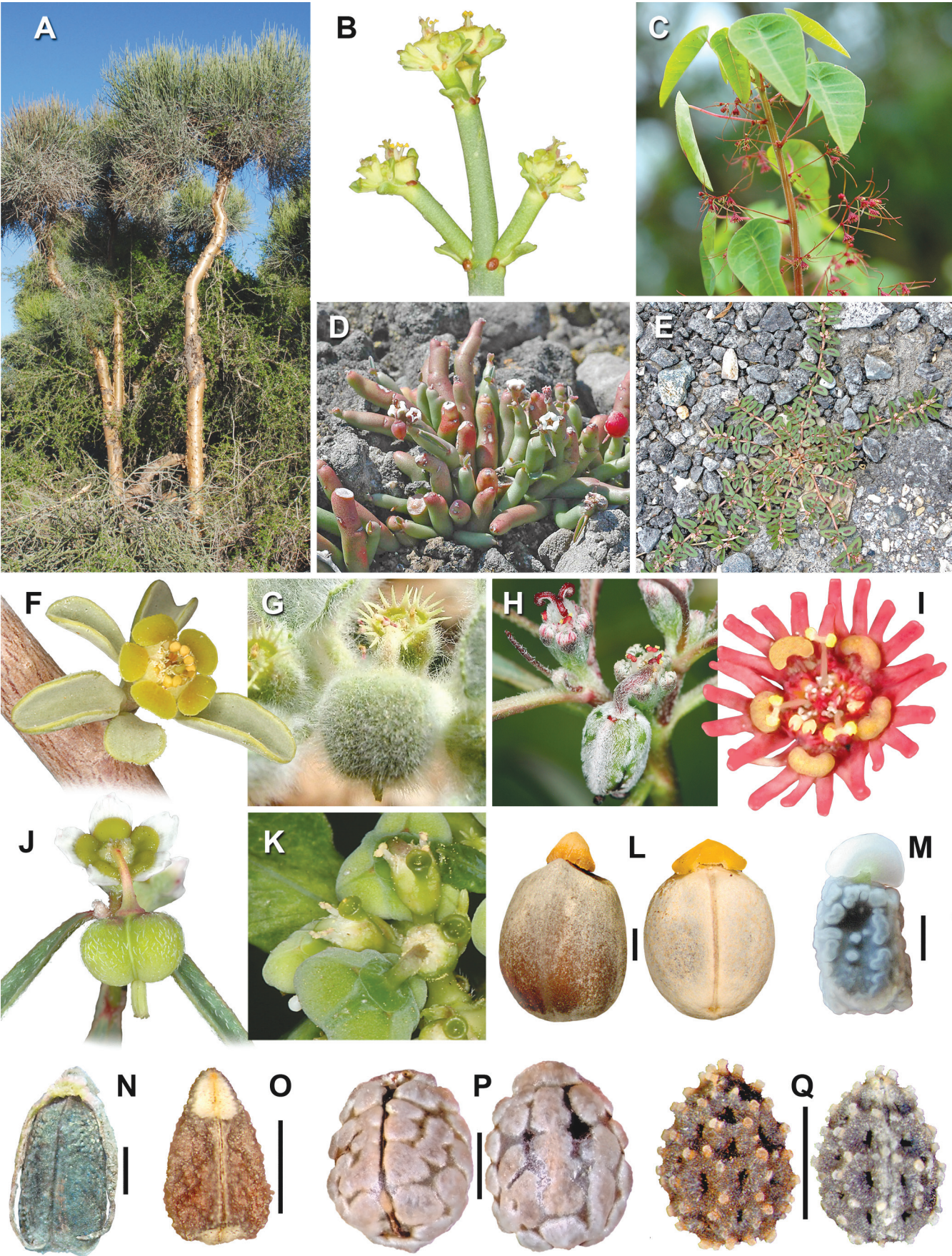
preliminary maximum parsimony analysis in PAUP* (Swofford, 2003), using *ndhF* sequences to assign each taxon to one of the four subgenera in *Euphorbia*. In addition, all sequences in GenBank that belong to subg. *Chamaesyce* were included. In total, our taxon sampling covered 291 out of the total of 600 species in the subgenus, with all previously recognized sections and most subsections represented. Since the monophyly and subclade structure within sect. *Anisophyllum* was well established in an earlier study (Yang & Berry, 2011), we reduced taxon sampling within sect. *Anisophyllum* to 15 species representing all major subclades. About 80 DNA accessions that grouped together with conspecific sequences during our preliminary analysis were excluded. In total, our final matrices include 174 taxa (163 ingroup taxa and 11 species representing the other three subgenera of *Euphorbia* as outgroups). All taxa sampled for the molecular phylogeny are associated with herbarium voucher specimens and are listed in the Appendix.

DNA extraction, amplification, and sequencing. — DNA extraction and PCR amplification of the ITS region were carried out following Yang & Berry (2011). The chloroplast *NADH dehydrogenase F* (*ndhF*) coding region was PCR-amplified in two pieces: the 5' half was amplified using primers 536 and 1318R (Olmstead & Sweere, 1994), and the 3' half using primers 972 (Olmstead & Sweere, 1994) and 2110Ri (Steinmann & Porter, 2002). The PCR mixture contained 0.15 µL of 5 units/µL *Ex Taq* (Takara Bio Inc., Otsu, Shiga, Japan), 2.5 µL 10× *Ex Taq* Buffer, 2.0 µL dNTP (2.5 mM), 1.0 µL of each primer (10 µM), 2 µL of diluted template DNA (dilution varies from 1/20 to 1/80), and ddH₂O to bring the final volume to 25 µL. The PCR profile consisted of an initial 4 min denaturing step at 95°C followed by 40 cycles of 45 s denaturing at 95°C, 45 s annealing at 53.6°C, and 2 min “slow and cold” extension at 65°C (Shaw & al., 2007). PCR products were purified with ExoSap-IT (USB Corporation, Cleveland, Ohio, U.S.A.), or QIAquick PCR Purification Kit (Qiagen, Valencia, California, U.S.A.). Cleaned PCR products were sequenced at the University of Michigan DNA Sequencing Core using the respective PCR primers.

Phylogenetic analyses. — Chromatograms were assembled and edited in the program Sequencher v.4.10.1 (Gene Codes, Ann Arbor, Michigan, U.S.A.). Sequence alignments were performed in the program MUSCLE v.3.8 (Edgar, 2004) using the default parameters, and manually adjusted in the program MacClade v.4.08 (Simmons, 2004; Maddison & Maddison, 2005). The full-length data matrices are in the online supplementary data, and sequences are deposited in GenBank (Appendix).

Phylogenetic analyses using maximum likelihood (ML) and Bayesian inference (BI) were conducted on the ITS and *ndhF* matrices separately, with gaps treated as missing data. Congruence between the resulting ITS and *ndhF* trees was visually inspected before concatenating them into a combined matrix. ITS, *ndhF* and the combined matrices were each subjected to the analyses described below.

Maximum likelihood analyses were carried out in the program RAxML v.7.0.3 (Stamatakis, 2006), partitioning ITS vs. *ndhF* regions. The nucleotide substitution model was set to



GTR+G as recommended by the RAxML manual; 500 ML bootstrap replicates were performed, followed by a thorough search for the best tree. Bayesian inference was conducted in the program MrBayes v.3.1.2 (Huelsenbeck & Ronquist, 2001; Ronquist & Huelsenbeck, 2003). Two independent runs (four for the combined dataset) of four chains each (three heated, one cold), starting from random trees, using the default temperature of 0.2, were run for 15 million generations. Trees were sampled every 1000 generations. Each analysis was conducted using the nucleotide substitution model GTR+I+G as selected by Akaike information criterion (AIC) in the program MrModeltest v.2.3 (Nylander, 2004). To prevent unrealistically long branches, “br lenspr=unconstrained:exponential(100.0)” was applied (Brown & al., 2010; Marshall, 2010). The relevant parameters for convergence were visually examined in the program Tracer v.1.5 (Rambaut & Drummond, 2007) to verify stationary status. Trees from the first 2.5 million generations were discarded as burn-in; the remaining trees were used to compute the majority-rule consensus tree and support statistics.

■ RESULTS

Overall statistics of the gene regions sequenced for this study are summarized in Table 1. Results of phylogenetic analyses are shown in Figs. 2 and 3 and are summarized in Fig. 4. For each of the three analyses (ITS, *ndhF*, combined ITS+*ndhF*), BI and ML results are congruent for nodes with ML bootstrap support (MLB) ≥50 and Bayesian posterior probability (PP) ≥0.80; monophyly of subg. *Chamaesyce* and its sister relationship to *Euphorbia* subg. *Euphorbia* are both highly supported (MLB ≥ 80; PP = 1). Groups are numbered consistently across

Figs. 2–4, and labels for sections, subsections, and subclades are shown on the combined tree only in Fig. 3.

ITS dataset. — The ITS dataset has a relatively high proportion of variable sites compared to *ndhF* (71.1% vs. 45.1%, Table 1). The alignment required some manual adjustment in parts, and all characters were included in the subsequent phylogenetic analysis. Monophyly of each section is strongly supported by MLB ≥ 70 (not shown) and PP = 1 (Fig. 2), except that sect. *Gueinzia* (11) is nested in sect. *Crossadenia* (12) with MLB = 72 (not shown) and PP = 0.81.

***ndhF* dataset.** — The *ndhF* coding region could be unambiguously aligned, with relatively fewer variable sites compared to ITS (Table 1). Monophyly of each section is supported by MLB ≥ 81 (not shown) and PP ≥ 0.88 (Fig. 2), except for sect. *Poinsettia*, where *E. jaliscensis* is sister to sect. *Poinsettia* (14) + sect. *Alectoroctonum* (15) with MLB = 62 (not shown) and PP = 0.75 (Fig. 2).

Combined ITS+*ndhF* dataset. — Analysis of the combined dataset produced a well-resolved phylogeny (Fig. 3). Monophyly of each section is supported by MLB ≥ 92 and PP ≥ 0.92, except for sect. *Crossadenia*, which has sect. *Gueinzia* nested within it. Relationships within each clade are well resolved in general, except for certain nodes in sect. *Alectoroctonum* and sect. *Articulofruticosae*. There are five instances of moderately (thin continuous lines) to strongly supported (thick lines) incongruence between the ITS and *ndhF* datasets, and such incongruences affect the combined analysis in different ways (Figs. 2, 3). (1) In sect. *Alectoroctonum*, the two clades marked with an asterisk (*) are strongly supported as sister to each other in the combined analysis and in the *ndhF* phylogeny, while ITS strongly supports them forming a paraphyletic grade. (2) *Euphorbia jaliscensis* is strongly supported as nested

Table 1. Summary statistics for the aligned molecular data matrices.

	<i>ndhF</i>	ITS	combined <i>ndhF</i> + ITS
No. of accessions	147	172	182
Range of raw length ^a [bp]	762–1480	336–651	584–2123
Aligned length	1547	714	2261
Variable characters (proportion)	697 (45.1%)	508 (71.1%)	1205 (53.3%)

^a Lower ends of raw lengths are from partial sequences that the full-length sequences failed to amplify or sequence.

◀ **Fig. 1.** *Euphorbia* subg. *Chamaesyce*: **A–E**, representative growth forms; **F–K**, cyathial morphologies; **L–Q**, seed morphologies. **A**, *Euphorbia plagiantha*, a broom-like tree (sect. *Plagianthae*; Dorsey 164, MICH); **B**, *E. burmannii*, a stem-succulent shrub with opposite or dichotomous branching and terminal cymes (sect. *Articulofruticosae*; Becker & Moller 1141, UNIN); **C**, *E. subpeltata*, a herb with indeterminate main shoots and axillary cymes (sect. *Alectoroctonum*; Steinmann 5585, IEB); **D**, *E. gumaroi*, a stem-succulent herb with alternate branching and single, terminal cyathia (sect. *Alectoroctonum*; Steinmann 5813, MICH); **E**, *E. maculata*, a prostrate herb with early termination of main shoots typical of sect. *Anisophyllum*; **F**, *E. guerichiana*, showing exappendiculate glands (sect. *Espinosa*; Becker & Moller 929, UNIN); **G**, *E. petiolata*, showing pectinate cyathial glands (sect. *Cheirolepidium*; Zarre & Salmaki 39514, TUH); **H**, *E. eriantha*, showing gland appendages arching over and concealing the glands (sect. *Erianthae*; field photo, California); **I**, *E. subpeltata*, showing cyathial appendages with finger-like lobes (sect. *Alectoroctonum*; Steinmann 5585, IEB); **J**, *E. sphaerorrhiza*, showing cyathial morphology typical in sect. *Alectoroctonum* (Yang 110, MICH); **K**, *E. heterophylla*, showing single, stalked and cupped glands typical of sect. *Poinsettia* subsect. *Stormieae* (Riina 1825, VEN); **L**, *E. espinosa* (sect. *Espinosa*; Leach 15938, UNIN); **M**, *E. petiolata* (sect. *Cheirolepidium*; Zarre & Salmaki 39514, TUH); **N**, *E. cheirolepis* (sect. *Cheirolepidium*); **O**, *E. mundii* (sect. *Articulofruticosae*; Leach 17110, UNIN); **P**, *E. goyazensis* (sect. *Crossadenia*; Caruzo 139, HUEFS); **Q**, *E. sonorae* (sect. *Alectoroctonum*; Fishbein 2455, RSA). — Photo credits: A, B.L. Dorsey; B & F, A. Moller; C, D, I & J, V.W. Steinmann; E, P.E. Berry; G & M, Y. Salmaki and S. Zarre; H, S. Matson; K, R. Riina; L, O & Q, B. Wagner; N, A.H. Pahlevani; P, J.J. Morawetz.

within sect. *Poinsettia* in the combined analysis and with ITS, but not with the *ndhF* data alone. (3) *Euphorbia gueinzii* is nested within sect. *Crossadenia* in the ITS analysis with strong support, while *ndhF* provides low support (dashed line) for *E. gueinzii* being sister to sect. *Crossadenia*; the combined analysis is congruent with the ITS topology in this case but with weaker support values. (4) *Euphorbia salota* is strongly supported by the combined and *ndhF* analyses to be nested within the Madagascar clade, while ITS places it sister to sect. *Cheirolepidium*+sect. *Eremophyton* with moderate support, separated from the rest of the Madagascan species. (5) Within sect. *Articulofruticosae*, results from ITS either conflict with *ndhF* or are poorly resolved, and the combined tree is also poorly resolved.

DISCUSSION

Our results are consistent with all six previous genus-wide molecular phylogenetic studies and support subg. *Chamaesyce* being monophyletic and sister to subg. *Euphorbia* (Steinmann & Porter, 2002; Bruyns & al., 2006, 2011; Park & Jansen, 2007;

Zimmermann & al., 2010; Horn & al., 2012a). Three of these six previous studies supported a single origin of New World taxa from an Old World grade within subg. *Chamaesyce*, with the eastern Brazilian clade sect. *Crossadenia* being sister to the rest of the New World group (Steinmann & Porter, 2002; Zimmermann & al., 2010; Horn & al., 2012a). Our results differ somewhat in that they support an Old World–eastern Brazilian clade sister to a New World clade, and together these are nested in a paraphyletic Old World grade (Fig. 4).

Bruyns & al. (2006) made an attempt to provide a sectional classification of subg. *Chamaesyce* based on molecular data. They recognized four sections within the subgenus: (1) “sect. *Chamaesyce*”, which included the New World clade+Old World–eastern Brazilian clade+sect. *Tenellae*, sharing petaloid cyathial appendages (the “petaloid appendage clade”, Fig. 4; Horn & al., 2012a); (2) sect. *Fronodosae*, a diverse Old World group; (3) sect. *Articulofruticosae*, a group of pencil-stem succulents from southern Africa that is both molecularly and morphologically distinct; and (4) sect. *Espinosa*, a clade of two shrubby or tree-forming species from Africa; they left *E. tannensis* unplaced. Among the four sections that they recognized, we agree with their naming and circumscription for all but the

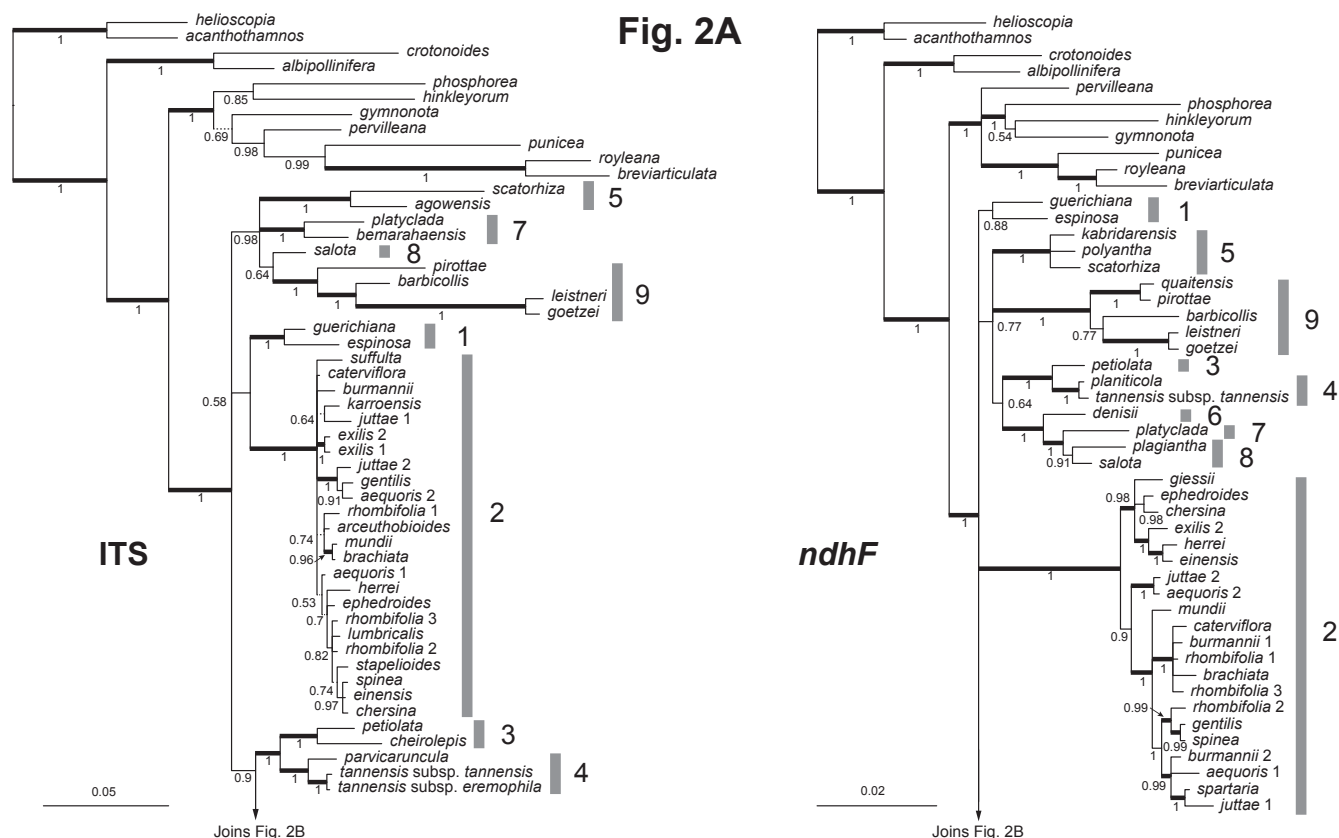


Fig. 2. Majority-rule consensus trees recovered from Bayesian analyses of the nuclear ITS and the chloroplast *ndhF* coding regions. Numbers below the branches indicate Bayesian posterior probabilities (PP). Thick branches indicate maximum likelihood bootstrap percentages (MLB) ≥ 70 and PP ≥ 0.95 , and branches in dashed lines have MLB < 50 and PP < 0.80 . Branch length scale on lower left of each tree. Numbers correspond to numbered sections in Fig. 3 and in the taxonomic treatment. 1 = sect. *Espinosa*; 2 = sect. *Articulofruticosae*; 3 = sect. *Cheirolepidium*; 4 = sect. *Eremophyton*; 5 = sect. *Scatorhiza*; 6 = sect. *Denisiae*; 7 = sect. *Bossieriae*; 8 = sect. *Plagianthae*; 9 = sect. *Fronodosae*; 10 = sect. *Tenellae*; 11 = sect. *Gueinzia*; 12 = sect. *Crossadenia*; 13 = sect. *Anisophyllum*; 14 = sect. *Poinsettia*; 15 = sect. *Alectorocotnum*.

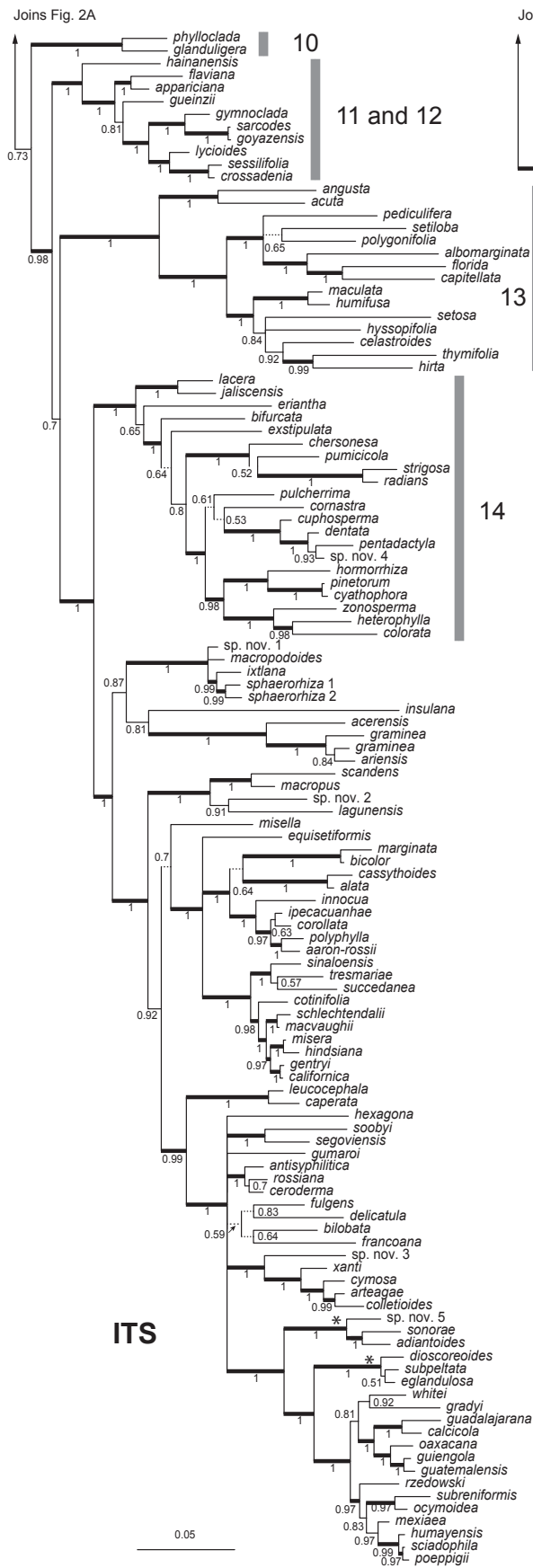
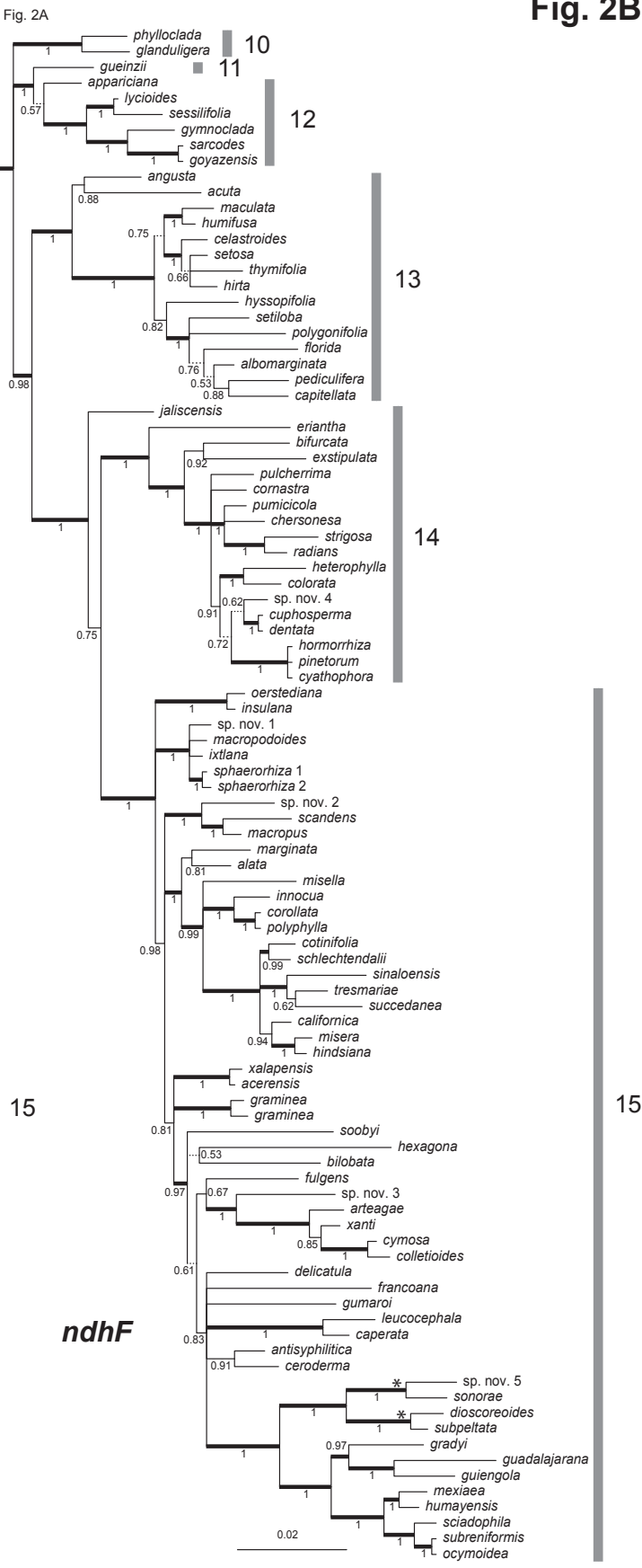


Fig. 2B



first one. In that case, we propose that their “sect. *Chamaesyce*” needs to be divided into six sections: sect. *Tenellae*, sect. *Gueinziae*, sect. *Crossadenia*, sect. *Anisophyllum*, sect. *Poinsettia*, and sect. *Alectrooctonum*. In addition, we designate six additional Old World sections to accommodate species that were either unsampled or unplaced by Bruyns & al. (2006), namely, sect. *Cheirolepidium*, sect. *Eremophyton*, sect. *Scatorhizae*, sect. *Denisiae*, sect. *Bosseriae*, and sect. *Plagianthae*. In the following discussion, we focus on comparing our results to the marker-rich but relatively taxon-poor “backbone” analysis of Horn & al. (2012a).

The Old World grade. — In Fig. 4, clades from sect. *Espinosa* up to sect. *Tenellae* are entirely Old World, forming

the early diverging Old World grade in subg. *Chamaesyce*. Within this group, BI analysis of ITS places sect. *Eremophyton* + sect. *Cheirolepidium* as sister to the petaloid appendage clade, similar to the placement in Bruyns & al. (2006), which was also based on BI of ITS alone (Fig. 2A). However, ML analysis of ITS, and both BI and ML analyses of *ndhF*, all support this clade as sister to the Madagascar clade. The cause of this incongruence between BI and ML is unknown, but it could be because BI is more prone to long-branch attraction (Kolaczowski & Thornton, 2009).

Our results conflict with those of Horn & al. (2012a) as to the earliest branching event within the clade of subg. *Chamaesyce* (Fig. 4). Our combined analysis recovered sect.

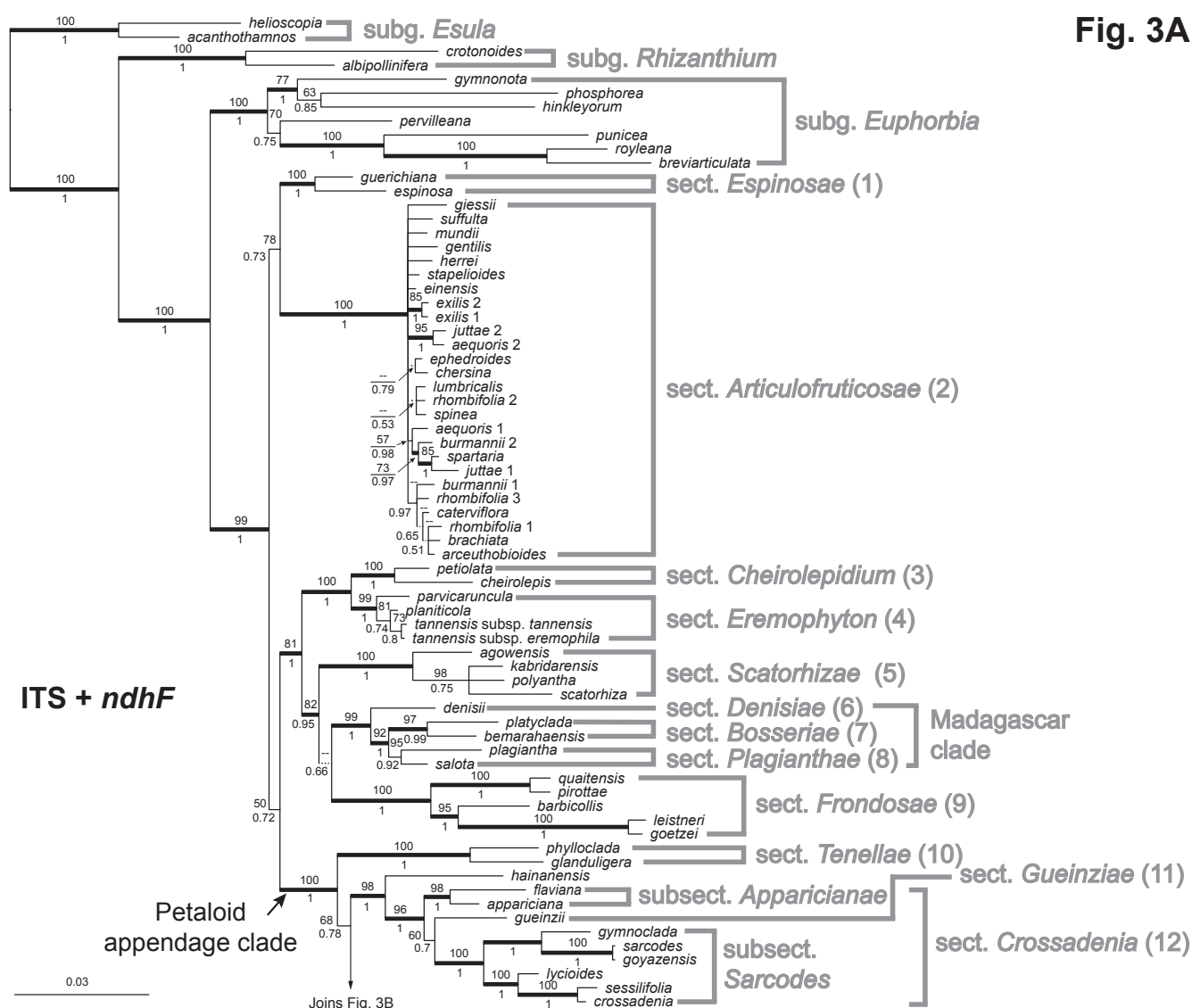


Fig. 3. Majority-rule consensus tree recovered from Bayesian analyses of the combined dataset (ITS + *ndhF*) with designated names of taxonomic units. Numbers above the branches indicate maximum likelihood bootstrap percentages (MLB), and numbers below the branches are Bayesian posterior probabilities (PP). Thick branches indicate MLB ≥ 70 and PP ≥ 0.95, and branches in dashed lines have MLB < 50 and PP < 0.80. Branch length scale on lower left. Numbers next to each section correspond to numbers in Fig. 2 and in the taxonomic treatment. Subgroups within sect. *Alectrooctonum* are indicated with hyphenated numbers.



Articulofruticosae + sect. *Espinosa* as sister to the rest of the subgenus with moderate support. However, Horn & al. (2012a) recovered sect. *Cheirolepidium* + sect. *Eremophyton* + sect. *Scatorhizae* + the Madagascar clade + sect. *Frondosae* as sister to the rest of subg. *Chamaesyce*. The latter received much stronger statistical support and may be more accurate because of their deeper molecular sampling.

Our results also disagree with Park & Jansen's (2007) placement of *E. cuneata*. The *E. cuneata* sequence retrieved from GenBank (specimen/voucher Park 24023) was nested in our sect. *Scatorhizae* (not shown). However, our own field-collected sample of *E. cuneata* is placed within *Euphorbia* subg. *Rhizanthium* (Riina & al., in prep.), as was another collection sequenced by Bruyns & al. (2011). Park & Jansen's (2007) *E. cuneata* has the same sequence as the *E. polyantha* *ndhF* sequence by Steinmann & Porter (2002), except that Park's *ndhF* sequence has a 9-bp deletion in the middle. Because of this, we believe that Park & Jansen (2007) misidentified *E. polyantha* as *E. cuneata* in their paper.

Among the ten sections we recognize in the Old World grade, sect. *Tenellae* is of particular interest because some of its members share petaloid gland appendages (though they are vestigial or absent in some species—see later descriptions) with the Old World–eastern Brazilian clade+the New World clade. Petaloid appendages (Fig. 11–J) likely evolved in the common ancestor of sect. *Tenellae*+Old World–eastern Brazilian clade+the New World clade, and together they form the “petaloid appendage clade” (Fig. 4; Horn & al., 2012a), which also corresponds to the “*Agaloma* alliance” of Steinmann & Porter (2002).

The Old World–eastern Brazilian clade.— With substantially increased taxon sampling compared to all previous studies, our analyses recovered two Old World species, *E. hainanensis* Croizat and *E. gueinzii* Boiss., that group together with the Brazilian sect. *Crossadenia* rather than with any other Old World group (Figs. 2, 3). However, we still consider the position of *E. hainanensis* to be doubtful. It is a shrub endemic to Hainan Island of southern China, and it is distinctive in having three cyathial glands and has been postulated to be closely related to species from tropical Australasia that belong to *Euphorbia* subg. *Euphorbia* (Croizat, 1940; Dorsey & al.,

subm.). This is a rare island endemic species, and we were only able to obtain a single ITS sequence. On the other hand, the placement of *E. gueinzii* is more reliable, with both ITS and *ndhF* sequences placing it close to sect. *Crossadenia*. The phylogenetic placement of a separate accession of *E. gueinzii*, sequenced for ITS at the Smithsonian Institution, was congruent with our results (K.J. Wurdack, pers. comm.).

Although ITS data places *E. gueinzii* within sect. *Crossadenia* with moderate support, *ndhF* data moderately supports its sister relationship to sect. *Crossadenia*. The combined analysis places it within sect. *Crossadenia*, but the support for this is weak. Because of its distinctive morphology and widely disjunct South African distribution compared to the otherwise entirely Brazilian sect. *Crossadenia*, the *ndhF* placement is more likely to reflect the relationships of *E. gueinzii*. Consequently, we propose a new section for *E. gueinzii*, based on its position as sister to sect. *Crossadenia* in the *ndhF* tree. In the case of the enigmatic *E. hainanensis*, we leave it unplaced until more data are available.

Given the pattern of distribution summarized in Fig. 4 and the postulated age of *Euphorbia* (36 Ma) that would exclude Gondwanan vicariance (Bruyns & al., 2011), a possible biogeographic scenario is that New World groups in subg. *Chamaesyce* did not have a single origin from the Old World, but that sect. *Crossadenia* became established in Brazil first, and then there was a separate introduction accounting for the rest of the New World clade. Alternatively, there could have been a single long-distance dispersal from the Old World to the New World, followed by back-dispersal to the Old World. It is unclear which scenario is more likely until further information on *E. gueinzii*, *E. hainanensis* and their close relatives is available.

The (largely) New World clade.— Sister to the Old World–eastern Brazilian clade is a largely New World clade of more than 500 species. This mainly New World clade consists of three major subclades [1(2,3)]: (1) Section *Anisophyllum* is distinctive in being mostly C_4 and having a specialized growth form with early abortion of the main shoot. It is most prevalent in warm, semi-desert regions and disturbed areas worldwide, with its greatest diversity in the New World. (2) Section *Poinsettia* is characterized by reduction or loss of petaloid



Fig. 4. Cladograms comparing major clades from this study and the “backbone” phylogeny (Horn & al., 2012a). Numbers above the branches indicate maximum likelihood bootstrap percentages (MLB), and numbers below the branches are Bayesian posterior probabilities (PP). Thick branches indicate MLB \geq 70 and PP \geq 0.95, and branches in dashed lines have MLB $<$ 50 and PP $<$ 0.80.

gland appendages and the development of brightly colored leafy bracts subtending congested terminal synflorescences, with the whole structure resembling a large blossom. It occurs mainly in forests and desert scrub of subtropical North America. (3) Section *Alectoroctonum* corresponds largely to the former subg. *Agaloma* (Raf.) House and is predominantly composed of herbs and shrubs, but also has some pencil-stem succulents with CAM photosynthesis. All species in this group have petaloid cyathial gland appendages, and sometimes they are quite showy. This group occurs in desert scrub to moist montane forests and prairies in subtropical to temperate areas throughout the Americas.

Within this New World clade there has been a considerable divergence of classification schemes. Bruyns & al. (2006) opted to lump the entire “petaloid appendage clade” into a single section “*Chamaesyce*”. On the other hand, within the New World clade alone, there are three well-supported clades, each or part of which have been treated previously at the rank of subgenus or even genus (e.g., “*Chamaesyce*”, “*Poinsettia*”, and “*Agaloma*”; see Dressler, 1961; Koutnik, 1984; Ward, 2001). If we were to follow this tendency and recognize genera or subgenera here, we would have to break up groups in the Old World grade into separate genera or subgenera as well in order to preserve monophyly. Instead, we choose to recognize three sections within the New World clade: sect. *Poinsettia*, sect. *Anisophyllum*, and sect. *Alectoroctonum*.

• Section *Poinsettia*. – In view of our molecular results and a re-evaluation of the morphological characters of the group, we propose a broader circumscription of sect. *Poinsettia* compared to the previous treatments by Dressler (1961) and Mayfield (1997). These authors restricted the application of the name “*Poinsettia*” to what we recognize here as subsect. *Stormieae* Croizat, namely those species with deeply cup-shaped involucre glands that lack petaloid appendages and are usually one or few in number (Fig. 1K). Other characteristic features commonly found in these species include colored bracts subtending the congested terminal cymes; pandurately lobed to linear, often heteromorphic leaves with at least some serration on the margins; glandular stipules; and coarsely tuberculate seeds, sometimes with a deeply sunken caruncular facet.

The three other subsections that we recognize in sect. *Poinsettia* are successively sister to subsect. *Stormieae*, beginning with subsect. *Exstipulatae*, followed by subsect. *Erianthae*, and then subsect. *Lacerae* (Fig. 3B). These three subsections all have some kind of involucre gland appendage, but that character is variable within the entire section, and two species nested in subsect. *Stormieae*, *E. chersonesa* and *E. cornastra*, have been reported to have a rudimentary appendage on the outer lip of the glands (Huft, 1984; Mayfield, 1997). In the case of *E. bifurcata*, which is placed here in subsect. *Exstipulatae*, it would be an otherwise indistinguishable member of subsect. *Stormieae* if not for the whitish appendage of its usually single cupular gland. Except for *E. eriantha*, which was placed by Boissier (1862) in sect. *Poinsettia*, the species in the three new subsections proposed here were previously included in sect. *Zygophyllum* (Boissier, 1862; Dressler, 1961; Huft, 1984), which is included within sect. *Alectoroctonum* in our classification.

In addition to the molecular evidence, which strongly supports the monophyly of an expanded sect. *Poinsettia* (PP 1; MLB 100), there are morphological characters that support the inclusion of the additional species in sect. *Poinsettia*, and, conversely, their exclusion from sect. *Alectoroctonum*. First are the serrate leaf margins, which are evident in all species of sect. *Poinsettia*, except *E. pinetorum*, *E. colorata*, *E. restiacea* (all in subsect. *Stormieae*), and *E. eriantha* (subsect. *Erianthae*), although teeth can usually be seen in the latter two species under magnification. These four species all have linear leaves, and their teeth may have become inconspicuous or obsolete as the leaves became narrower. On the other hand, serrate leaves are very rare in sect. *Alectoroctonum*. Both species of subsect. *Lacerae*, which is sister to the other three subsections of sect. *Poinsettia*, have serrate, heteromorphic and/or pandurate leaves, which are usually considered to be hallmarks of sect. *Poinsettia* s.str. The feathery gland appendages of subsect. *Erianthae* (Fig. 1H) are unique in the genus and bear little resemblance to any of those in sect. *Alectoroctonum*. Likewise, the two-horned gland appendages in *E. lacera* are very different from the petaloid appendages in sect. *Alectoroctonum*.

Another factor that may have confounded the recognition of an expanded sect. *Poinsettia* distinct from sect. *Alectoroctonum* in the past was the erroneous placement of *E. bilobata* in sect. *Poinsettia* in the molecular phylogeny of Steinmann & Porter (2002). *Euphorbia bilobata* is a true member of sect. *Alectoroctonum*, as shown by its placement in this study close to *E. hexagona* (the type species of Boissier’s sect. *Zygophyllum*; Fig. 3B); a review of its morphological features shows that they are fully consistent with its placement in sect. *Alectoroctonum*. Thus the position of *E. bilobata* in Steinmann & Porter (2002) was likely due to an error.

In summary, we see no overriding morphological conflicts with sect. *Alectoroctonum* in expanding the circumscription of sect. *Poinsettia* to include the five additional species in three subsections recognized here. Within the context of the “petaloid appendage clade” (Horn & al., 2012a) to which sect. *Poinsettia* belongs, it is not surprising that the earliest diverging subsections in section *Poinsettia* would have petaloid appendages and that these were subsequently lost in subsect. *Stormieae*.

• Section *Anisophyllum*. – Boissier (1862) proposed eight subdivisions within sect. *Anisophyllum*. Since then, due to the relatively homogenous morphology and wide distribution of this group, Boissier’s classification scheme remained largely unchanged except for some minor modifications (Binoj Kumar & Balakrishnan, 2010). Yang & Berry’s (2011) analyses of chloroplast markers strongly supported three major subclades within sect. *Anisophyllum* [1(2,3)]: (1) the Acuta clade, with only three species endemic to southwestern U.S.A. and northern Mexico that have C₂ and C₃ photosynthesis and glandular stipules; (2) the Peplis clade, consisting of mainly glabrous, perennial herbs with entire leaf margins that all have C₄ photosynthesis and mostly endemic to the southwestern U.S.A. and northern Mexico; and (3) the Hypericifolia clade, consisting of annual and perennial herbs to woody perennials, often with toothed leaf margins and usually with some kind of pubescence, distributed worldwide, and which are also all C₄. Since

no character or character sets can readily distinguish species in the latter two clades, and nuclear markers indicate that there has been widespread reticulate evolution among members of these two clades, here we only recognize two subsections in subsect. *Anisophyllum*: the *Acuta* clade constituting subsect. *Acutae*, and all remaining species comprising subsect. *Hypericifoliae*.

• Section *Alectoroctonum*. – Classification within sect. *Alectoroctonum* is difficult due to its diversity of growth forms and the incompletely resolved phylogeny we obtained. Shrubs have evolved several times from herbaceous ancestors (Horn & al., 2012a), and morphologically similar species repeatedly turn out to belong to distinct groups in our molecular phylogeny. In addition, the majority of the deep branches in the section are short and are poorly or only moderately supported (Fig. 3B), and some well-supported branches conflict among markers (Fig. 2B). Between our ITS and *ndhF* results (Fig. 2B), the two clades marked with an asterisk are sister to each other in the *ndhF* analysis but form a grade in the ITS analysis, with each placement being well-supported. Additional gene regions such as nuclear ribosomal ETS, chloroplast *matK*, and the nuclear low-copy coding region exon 9 of *EMB2765* revealed even more extensive conflicts among well-supported clades (data not shown). Therefore, additional markers, expanded taxon sampling, and careful morphological studies are needed to better resolve relationships within sect. *Alectoroctonum* and to formally circumscribe subsections. Here we discuss informal species groups that are well supported by both morphological and molecular data, and then point out ambiguities that will require further investigation.

Clades 15-1 to 15-4 together form the basal grade of sect. *Alectoroctonum* (Fig. 3B). The majority of species in this grade occupy mid-elevation pine-oak forests in Mexico, while clade 15-1 and *E. acerensis* of clade 15-3 occur in the Caribbean and South America. *Euphorbia graminea*, also part of clade 15-3, is a widespread and variable species across warm regions of North and South America. Species in clade 15-1 are distinctive in having only two glands per cyathium (sometimes three in *E. insulana*). Clade 15-2 is endemic to Mexico and has distinctive globose-tuberous roots (Huft, 1979). However, *E. macropus*, which is another Mexican species with globose roots, is placed in clade 15-4 in our analysis, and it indeed shares morphological characters with both clade 15-2 and 15-4. Clade 15-3 is distinctive in having stalked glands and four or five glands per cyathium (sometimes also two or three in *E. graminea*); leaf shape is highly variable, and leaf margins are sometimes sinuate, instead of being entire as in most of sect. *Alectoroctonum*. Both *E. graminea* and *E. ariensis* share white, showy bracts. *Euphorbia graminea* is very similar to both species of clade 15-1 in gross morphology, but it differs from them in having glabrous instead of densely pubescent capsules (Ward, 2001). *Euphorbia graminea* is the type of sect. *Cyttarospermum* Boiss., but other species that were placed in that section by Boissier (1862) are spread over many separate clades within sect. *Alectoroctonum*. Species in clade 15-4 are characterized by opposite leaves and branches, four or five glands per cyathium, green gland appendages, and all are confined to Mexico.

Euphorbia misella appears in an isolated position, sister to clades 15-5 to 15-8 (Fig. 3B). It is a tiny fall annual herb native to high elevation pine-oak forests in Mexico. It is very similar to *E. sinaloensis* and *E. succedanea* of clade 15-5 in morphology, growth form, habitat and distribution. However, these three Mexican annuals do not form a monophyletic group in our analysis. Clade 15-5 contains mostly shrubs. Species from *E. misera* to *E. californica* have alternate branches and spirally arranged leaves on short shoots, and they all occur in desert scrub of the Sonoran Desert. In contrast, species from *E. cotinifolia* to *E. macvaughii* have verticillate leaves and branches and occupy tropical forests from Mexico to South America. Clade 15-6 corresponds to subsect. *Petaloma* Raf. ex Pax; both *E. marginata* and *E. bicolor* are annual herbs that are widely cultivated as ornamentals for their showy, white-margined bracts. Clade 15-7 corresponds to sect. *Arthrothamnus* subsect. (noted as “§” in Boissier, 1862) *Americanae* Boiss., and is characterized by dioecious pencil-stem shrubs, with opposite or whorled, ridged branches; the leaves are scale-like or caducous, and they lack stipules. Both *E. alata* and *E. cassythoides* occur in the Greater Antilles (Cuba and Jamaica, respectively). The closely related Galápagos endemic *E. equisetiformis* is also a leafless opposite-stemmed shrub, yet these three species do not form a monophyletic group in our analyses. *Euphorbia innocua* occurs in an isolated position sister to clade 15-8; it is a prostrate herb with four glands that superficially resembles sect. *Anisophyllum*; it was treated by Webster (1967) as the sole representative of sect. *Tithymalopsis* subsect. *Innocuae* G.L. Webster. Webster (1967) considered it to be intermediate between sect. *Alectoroctonum* and sect. *Anisophyllum*, but such a relationship is not supported by our analyses. Clade 15-8 largely corresponds to sect. *Tithymalopsis* subsect. *Ipecacuanhae* Boiss. (Huft, 1979; Holmgren & Holmgren, 1988). It represents the northernmost distribution for sect. *Alectoroctonum*, extending from the eastern United States north to southern Canada. Species in this group are perennial herbs with leaves that are rounded at the apex and with ovoid seeds that are rounded in cross-section, smooth or shallowly pitted on the surface, and lacking a caruncle (Huft, 1979).

Both species in clade 15-9, *E. leucocephala* and *E. caperata*, are shrubs with verticillate leaves and five involucre glands (Fig. 3B). They differ from other shrubs of sect. *Alectoroctonum* in having showy, entirely white bracts. Both species have carunculate seeds, which is otherwise rare in sect. *Alectoroctonum*. Clade 15-10 includes three species that are densely branched pencil-stem shrubs with a waxy surface, with cyathia in axillary cymes, five involucre glands with well-developed appendages, and seeds that are ovoid with a smooth surface. Between clades 15-10 and 15-11, there are two species that form part of a polytomy and whose exact affinities are unclear. One of these, *E. fulgens* (“scarlet plume”), is cultivated for its large and showy gland appendages. In the weakly supported clade 15-11, *E. bilobata* and *E. hexagona* both have only opposite leaves and branches and were formerly treated as part of sect. *Zygophyllidium* Boiss. The remaining species of sect. *Zygophyllidium* as defined by Boissier (1862) are scattered in other parts of sect. *Alectoroctonum*.

and in sect. *Poinsettia* in our analyses. The other two species of clade 15-11, *E. soobyi* and *E. segoviensis*, are morphologically consistent with clade 15-13 and may prove to belong to that clade with additional data. Clade 15-12 includes shrubs with verticillate leaves and branches, deciduous leaves, and cyathia that are clustered in dense cymes and have five or six cyathial glands. Between clades 15-12 and 15-13, *E. gumaroi* is a small succulent, decumbent species that was compared to *E. antisiphilitica* in its original description (Meyrán García, 2000), but such an affinity is not supported by our molecular data. Cyathia in *E. gumaroi* are single and terminal rather than in axillary cymes as in *E. antisiphilitica*. Finally, clade 15-13 is a group of about 25 species of herbs and shrubs from warm parts of North and South America. Some species in this clade were treated as part of sect. *Cyttarospermum* Boiss. (Boissier, 1862), but the type of that section (*E. graminea*) belongs in clade 15-3. Species in clade 15-13 are characterized by having petioles that are longer than the leaf blades, five cyathial glands, often deeply lobed gland appendages, and ecarunculate seeds that are deeply pitted, with protrusions on distinctive honeycombed ridges (Fig. 1Q).

Evolution of growth forms and photosynthetic types.

— The basic structure of a *Euphorbia* plant is shown in Fig. 5A. Annual members of the genus best exemplify this architecture, as various parts of the plant may die back in perennials. Distal to the cotyledonary node, the plant sometimes develops nodes with opposite leaves and side branches. Further up the main shoot, both leaves and branches switch to being alternate. Either, neither, or both of the opposite/alternate vegetative sections can be absent. Later, the main shoot terminates with a whorl of leaves and usually an equal number of branches, concomitant with a switch to reproductive growth, which is typically a pleiochasium of cymes. In this scheme, the synflorescence in *Euphorbia* typically has three levels of organization

(Fig. 5A): (1) the cyathium itself bearing tightly packed male and/or female flowers, (2) the cyathia arranged in cymes, and (3) the cymes arranged in pleiochasia at the point of apical termination of the main stem. Despite various terminologies that have been applied to these three organization levels, here we call the leaves (or bracts when they are not green) that directly subtend a single cyathium “subcyathial bracts”, leaves/bracts at lower nodes of the synflorescence “dichasial bracts”, and the lowest whorl of leaves associated with the synflorescence “pleiochasial bracts” (Fig. 5A; Molero & Rovira, 1992).

One notable modification of the basic plant structure in *Euphorbia* is the lack of apical growth of the main shoot (Figs. 1E, 5B; Hayden, 1988). This growth form is a synapomorphy for sect. *Anisophyllum*, in which essentially the entire plant body resembles a synflorescence. Together with juvenile flowering, copious seed production, and C₄ photosynthesis, sect. *Anisophyllum* has been very successful in colonizing warm and semi-desert areas and disturbed habitats worldwide. However, both *E. remyi* and *E. halemanui*, two ascending shrubs endemic to the Hawaiian Archipelago, develop main shoots with continued apical growth and opposite leaves (Koutnik, 1987). In *E. potentilloides*, and occasionally in *E. angusta* and *E. viscoides*, the annual growth terminates in a whorl of three or more leaves before producing the terminal synflorescence (Simmons & Hayden, 1997).

Another notable example of modification in growth form is the continued elongation of main shoots with alternate or verticillate leaves and branches (Fig. 5C). In this growth form, cyathial cymes are axillary instead of arranged in a terminal whorl. This type is seen in all members of clades 15-12 and most of 15-13 of sect. *Alectoroctonum* (Figs. 1C). A further modification of this growth form occurs when stems become fleshy and photosynthetic, and leaves are deciduous or reduced; then the plants become stem succulents with alternate

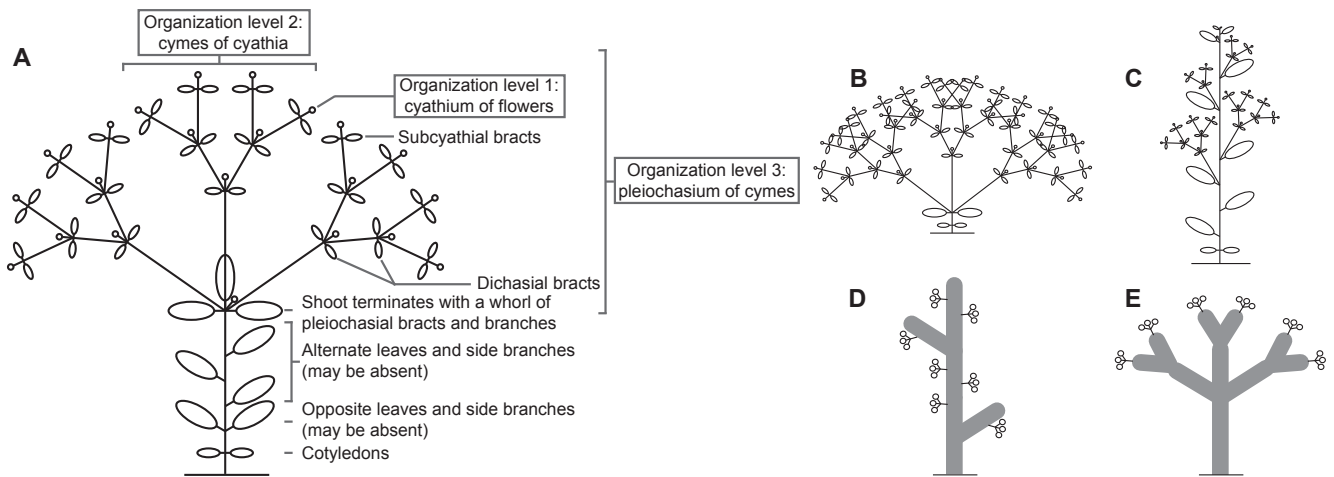


Fig. 5. Diversity of growth forms in *Euphorbia* subg. *Chamaesyce*. **A**, The basic growth form variations in *Euphorbia*, with the three synflorescence organization levels (Wheeler, 1941: pl. 655; Molero & Rovira, 1992). **B–E**, Modifications of the basic growth form: **B**, early termination of the main shoot; **C**, main shoot indeterminate and cymes axillary; **D**, similar to C but stems become succulent; and **E**, stem succulents with terminal cymes.

branching and axillary cyathia or cyathial cymes (Figs. 5D). This type of growth form is seen in sect. *Plagianthae* (*E. plagiantha*, Fig. 1A) and sect. *Alectoroctonum* (all members of clade 15-10, and *E. gradyi* of clade 15-13).

A second type of stem succulence of separate origin occurs when the main shoot terminates with a pleiochasial cyme, and both the vegetative section and the synflorescence (except for the cyathia themselves) become succulent. This way the plants have mostly dichotomous or whorled branching, with terminal cyathia or cyathial cymes (Fig. 5E). This growth form is found in all species of sect. *Articulofruticosae* (Fig. 1B), sect. *Bosseriae*, part of sect. *Crossadenia* (subsect. *Apparicianae* + *E. gymnoclada*), and part of sect. *Alectoroctonum* (clade 15-7 + *E. equisetiformis*). Perhaps a third type of succulent growth form is evident in *Euphorbia gumaroi*, which is a Mexican member of sect. *Alectoroctonum* that is unique in having alternate succulent branches with single, terminal cyathia (Fig. 1D; Meyrán García, 2000).

Euphorbia is extremely diverse in succulent growth forms, and most of the diversity in succulence is found in subg. *Euphorbia* and subg. *Rhizanthium*. Still, in subg. *Chamaesyce*, stem succulence has evolved at least six times, with multiple origins in both the Old World (southern Africa, Madagascar) and the New World (eastern Brazil, North America). Occurrences of stem succulence are usually associated with CAM photosynthesis. Stable isotope ratios ($\delta^{13}\text{C}$) have been tested in sect. *Articulofruticosae*, within which both *E. ephedroides* and *E. rhombifolia* have values typical of CAM plants. In sect. *Bosseriae*, *E. platyclada* was tested for $\delta^{13}\text{C}$ and has a typical CAM value; in sect. *Crossadenia*, *E. apparicana* has a ratio consistent with weak or facultative CAM expression; and in sect. *Alectoroctonum*, *E. ceroderma* (clade 15-10) has a value consistent with CAM photosynthesis (Horn & al., 2012b).

Conclusions. — *Euphorbia* subg. *Chamaesyce* has been recircumscribed here based on molecular data. With taxon sampling covering nearly half of the ingroup species and a well-resolved phylogeny, we can now begin to understand evolutionary trends in a worldwide lineage with diverse growth forms and photosynthetic types. In the following treatment, we circumscribe fifteen sections that are each morphologically and geographically distinctive. This updated sectional and subsectional classification of subg. *Chamaesyce* includes descriptions and lists of accepted species for each section or subsection.

■ TAXONOMIC TREATMENT

Species with molecular sequence data available in GenBank, either published here or previously, are shown in **bold** in the “Included species” lists under each section or subsection. A searchable and downloadable list of accepted names, their synonymies, type information and distribution for *Euphorbia* is available online at <http://app.tolkin.org/projects/72/taxa> (Riina & Berry, 2012).

Euphorbia subg. *Chamaesyce* Raf. in Amer. Monthly Mag. & Crit. Rev. 2: 119. 1817 – Lectotype: *E. supina* Raf.

(= *E. maculata* L.), designated by Wheeler in Contr. Gray Herb. 127: 59. 1939.

Rafinesque did not include *E. chamaesyce* L. in his circumscription of the subgenus, therefore Art. 22.6 of the ICBN does not apply here.

Annual or perennial herbs, shrubs or trees; rarely geophytes. Stems and leaves sometimes more or less fleshy to succulent, but not cactus-like. Taproot slender or variously thickened, cylindrical to globose. Branches few to many, prostrate, decumbent, or upright; alternate, opposite and/or ternate; sometimes the apices become spine-like. Leaves alternate, opposite and/or ternate, glabrous or variously pubescent, sometimes dark green veins visible on species with C_4 photosynthesis; stipules glandular, linear, subulate, triangular, or inconspicuous. Cyathia bisexual, rarely unisexual, solitary or in cymes, axillary or terminal, sometimes subtended by green or brightly colored bracts, actinomorphic or slightly zygomorphic; glands (1–)4–5(–7), often with petaloid appendages, less often appendages horn-like, linear, or missing; ovary glabrous or pubescent; styles 3, connate or free at the base, bifid or entire. Capsules 3-lobed or less often subglobose. Seeds ovoid or oblong, 4-angled, less often 3-angled or rounded in cross-section; surface variously sculptured or smooth, carunculate or ecarunculate.

Discussion. – Within *Euphorbia* subg. *Chamaesyce*, a total of 566–574 (see discussion for sect. *Articulofruticosae*) species are recognized and distributed among 15 sections, with *E. hainanensis* Croizat sampled but left unplaced as to section. There are another 20 or so species in the process of being formally described, and there are still some unplaced species in *Euphorbia* that may prove to belong to this subgenus with further study.

Due to the high level of homoplasy of morphological character states in *Euphorbia* (Horn & al., 2012a), a key to the sections of subg. *Chamaesyce* that is of practical value needs to begin with the entire genus, in which sections can be keyed out directly instead of keying to the subgenera first. Since the taxonomic revisions for the other three subgenera are in different stages of completion, it would be premature to attempt such a key at this point.

1. *Euphorbia* sect. *Espinosa* Pax & K. Hoffm. in Engler, Veg. Erde 9 [Pflanzenw. Afrikas] 3, 2: 149. 1921 = *Euphorbia* subsect. *Espinosa* (Pax & K. Hoffm.) Pax & K. Hoffm. in Engler & Prantl, Nat. Pflanzenfam., ed. 2, 19c: 213. 1931 – Type: *E. spinosa* Pax.

Shrubs to small trees, stems with a shiny or papery bark, the stem apices often drying and becoming spine-like. Leaves alternate, shortly petiolate; stipules glandular, conspicuous. Cyathia bisexual, solitary, axillary, subsessile, or on lateral short shoots, surrounded at the base by a cluster of small leaf-like or scarious bracts; glands 5, entire, yellow-green, exapendiculate (Fig. 1F); ovary subtended by a 3-lobed perianth; styles joined at the base, with spreading, bifid apices. Capsules well-exserted on a reflexed pedicel, deeply 3-lobed, glabrous. Seeds ovoid, slightly dorsiventrally compressed, smooth, with a cap-like caruncle.

Distribution and habitat. – Southern and eastern Africa (Angola, Botswana, Namibia, northern South Africa, Kenya, Malawi, Tanzania, Zambia, Zimbabwe); hilly, deciduous woodlands, 300–1400 m.

Included species (2). – *E. espinosa* Pax and *E. guerichiana* Pax.

Discussion. – There are several other sections that resemble sect. *Espinosa* in their shrubby habit, coppery bark, and sometimes spinose branches. These include *E. sect. Somalica* S. Carter, *E. sect. Lyciopsis* Boiss., the *E. balsamifera* group (all in subg. *Rhizanthium*, also from Africa); and *E. sect. Plagianthae* (subg. *Chamaesyce*, from Madagascar).

2. *Euphorbia* sect. *Articulofrutosae* Bruyns in Taxon 55: 416. 2006 – Type: *E. aequoris* N.E. Br.

Generally dioecious, semi-woody to succulent shrubs; branches dichotomous or opposite, usually much-branched from the base; branches cylindrical or variously ridged, apices drying spine-like in some species. Leaves opposite, small and often scale-like, quickly deciduous leaving a calloused scar; stipules apparently absent or glandular and conspicuous. Cyathia or cyathial cymes terminal (sometimes appearing to be axillary when borne on apex of short shoots); cymes branching few to many times, internodes progressively shorter above; subcyathial bracts and dichasial bracts spatulate or similar to the leaves, deciduous. Cyathia small, usually unisexual, subsessile; glands 5, entire, exappendiculate; styles connate at the base and free above, bifid at the tip. Capsules subsessile or exerted and recurved, glabrous or pubescent. Seeds conical, obtusely 4-angled, surface finely tuberculate, ecarunculate (Fig. 10).

Distribution and habitat. – Most diverse in the arid winter-rainfall region of western South Africa and southern Namibia, extending into southern Angola and Botswana and east to Kwa-Zulu-Natal, South Africa. Growing in sandy soils or on rock outcrops, in low shrublands to deserts and consolidated dunes, from sea level to ca. 2000 m.

Included species (18–26). – *E. aequoris* N.E. Br. [= *E. jutae* sensu Bruyns], *E. angrae* N.E. Br., *E. arceuthoboides* Boiss. [= *E. tenax* sensu Bruyns], *E. brachiata* E. Mey. ex Boiss. [= *E. rhombifolia* sensu Bruyns], *E. burmannii* E. Mey. ex Boiss., *E. caterviflora* N.E. Br. [= *E. rhombifolia* sensu Bruyns], *E. chersina* N.E. Br. [= *E. rhombifolia* sensu Bruyns], *E. einensis* G. Will. [= *E. angrae* sensu Bruyns], *E. ephe-droides* E. Mey. ex Boiss., *E. exilis* L.C. Leach, *E. gentilis* N.E. Br., *E. giessii* L.C. Leach, *E. herrei* A.C. White, R.A. Dyer & B. Sloane, *E. jutae* Dinter, *E. lavranii* L.C. Leach, *E. lumbricalis* L.C. Leach [= *E. stapelioides* sensu Bruyns], *E. mundii* N.E. Br. [= *E. rhombifolia* sensu Bruyns], *E. muricata* Thunb., *E. negromontana* N.E. Br., *E. rhombifolia* Boiss., *E. spartaria* N.E. Br., *E. spinea* N.E. Br., *E. stapelioides* Boiss., *E. suffulta* Bruyns, *E. tenax* Burch., *E. verruculosa* N.E. Br.

Discussion. – This is a very well characterized group of pencil-stemmed succulents with greatly reduced and caducous leaves, and they are readily distinguished by their opposite or dichotomous branching and mostly unisexual cyathia (Fig. 1B). However, species limits in this section are unclear, and the

group is in need of a taxonomic revision. Bruyns & al. (2011) and Bruyns (in press) recognized only 18 species in this section, but we are tentatively including here a number of names that are treated as synonyms in those publications. According to the age estimates of Bruyns & al. (2011), this section diversified in southern Africa during the past 12 Ma.

3. *Euphorbia* sect. *Cheirolepidium* Boiss. in Candolle, Prodr. 15(2): 9, 70. 1862 = *Euphorbia* subsect. *Cheirolepidium* (Boiss.) Pax & K. Hoffm. in Engler, Nat. Pflanzenfam., ed. 2, 19c: 213. 1931 = *Cystidospermum* Prokh., Consp. Syst. Tithymalus Asiae Mediae: 25. 1933 = *Euphorbia* subg. *Cystidospermum* (Prokh.) Prokh. in Komarov & al., Flora U.R.S.S. 14: 480. 1949 – Type: *E. cheirolepis* Fisch. & C.A. Mey.

= *Dematra* Raf., Autik. Bot.: 96. 1840 = *Euphorbia* sect. *Dematra* (Raf.) Prokh. in Komarov & al., Flora U.R.S.S. 14: 476.

1949 – Type: *D. sericea* Raf. (= *E. petiolata* Banks & Sol.).

= *Euphorbia* subsect. *Crotonopsidae* Boiss. in Candolle, Prodr. 15(2): 101. 1862 – Type: *E. petiolata* Banks & Sol.

= *Ctenadenia* Prokh., Consp. Syst. Tithymalus Asiae Mediae: 28. 1933 – Type: *C. lanata* (Sieb.) Prokh. (= *E. petiolata* Banks & Sol.).

Annual erect herbs, well branched. Leaves and branches opposite at the base, alternate in the mid-section before the termination of apical growth and switch to dichotomous branching, with each fork subtended by dichasial bracts; leaves linear-lanceolate to elliptic or ovate, densely villous to subglabrous, margin distinctively spinulose-dentate; stipules subulate. Cyathia solitary between the forks of dichotomous branches, or few-clustered in axillary cymes; both dichasial and subcyathial bracts leaf-like but much reduced in size; glands 4 per cyathium, with deep finger-like to linear lobes, stalked (*E. cheirolepis*) or not (*E. petiolata*), yellow-green, sometimes turning red with age; styles 3, free or connate at the base, tip entire; ovary densely pubescent, 3-lobed. Capsule exerted, pubescent. Seeds 4-angled, surface tuberculate; caruncle large and stipitate in *E. petiolata* (Fig. 1M), or distinctively ligulate with two long flaps in *E. cheirolepis* (Fig. 1N).

Distribution and habitat. – From northern Africa through Central Asia; fallow fields and dry, open habitats, 500–1500 m.

Included species (2). – *E. cheirolepis* Fisch. & C.A. Mey., *E. petiolata* Banks & Sol.

Discussion. – These two species have been variously treated as members of subg. *Esula*, and they are indeed anomalous geographically among the remaining groups of subg. *Chamaesyce* (excluding sect. *Anisophyllum*). However, the presence of stipules and the pectinate cyathial glands distinguish both species from members of subg. *Esula*. The ligulate caruncle in *E. cheirolepis* is unique in *Euphorbia* (Fig. 1N, Pahlevani & Akhiani, 2011). However, it is caducous, and seeds may appear to be ecarunculate on herbarium sheets.

The pectinate protrusions appear to extend directly from the rim of the glands (Fig. 1G), unlike the petaloid appendages in the “petaloid appendage clade”, which appear to extend from the involucre and emerge from below the glands (Fig. 1I, J).

4. *Euphorbia* sect. *Eremophyton* Boiss. in Candolle, Prodr. 15(2): 9, 70. 1862 ≡ *Euphorbia* subg. *Eremophyton* (Boiss.) L.C. Wheeler in Amer. Midland Naturalist 30: 483. 1943 ≡ *Euphorbia* subsect. *Eueremophyton* (Boiss.) Pax in Engler & Prantl, Nat. Pflanzenfam. 3(5): 107. 1891 ≡ *Euphorbia* sect. *Eremophila* Benth. & F. Mueller, Fl. Austral. 6: 45. 1873, nom. illeg. (Art. 52.1) – Lectotype: *E. eremophila* A. Cunn. (≡ *E. tannensis* subsp. *eremophila* (A. Cunn.) D.C. Hassall), designated by Wheeler in Amer. Midland Naturalist 30: 483. 1943.

Annual or perennial herbs to small shrubs, glabrous to sparsely pubescent. Stems erect, multibranched; leaves and branches opposite at the base, alternate in the mid-section before the termination of apical growth and then switching to dichotomous branching, with each fork subtended by dichasial bracts. Leaves linear-lanceolate to ovate, margins serrate; stipules glandular or subulate. Cyathia solitary between the forks of dichotomous branches or few-clustered in axillary cymes, with dichasial and subcyathial bracts leaf-like but much reduced in size; glands 4, yellow, ovate, margins entire (exappendiculate) or crenate to palmatifid, ovary glabrous; styles 3, connate at the base, bifid at the tips. Capsules exserted, erect, 3-lobed. Seeds more or less 4-angled, surface tuberculate to reticulate; caruncle present, variously shaped.

Distribution and habitat. – Australia, New Caledonia, Vanuatu; coastal sands to inland desert and scrub, sea level to 600 m.

Included species (3). – *E. parvicaruncula* D.C. Hassall, *E. planiticola* D.C. Hassall, *E. tannensis* Spreng.

Discussion. – Boissier (1862) first established sect. *Eremophyton* to include three Old World species, but they now belong to three different sections in subg. *Chamaesyce*. Besides the lectotype of this section, *E. eremophila* A. Cunn., the African *E. agowensis* is placed by our analyses in sect. *Scatorhizae*, while the third species, the South African *E. gueinzii*, is placed in sect. *Gueinziae*. Wheeler (1943) broadened the concept of sect. *Eremophyton* and elevated it to the rank of subgenus, but this was a very heterogeneous assemblage of species that is not supported by molecular data.

Hassall (1977) treated five native Australian *Euphorbia* species as forming a natural group within *Euphorbia* subg. *Eremophyton*. However, our molecular data strongly reject the monophyly of all five species: *E. stevenii* and *E. boophthona* are both nested in *E.* subg. *Euphorbia* (Dorsey & al., subm.), whereas the other three form a monophyletic group in subg. *Chamaesyce*, as treated here in a more restricted sect. *Eremophyton*. The placement of *E. boophthona* in subg. *Chamaesyce* by Zimmermann & al. (2010) was most likely an error.

5. *Euphorbia* sect. *Scatorhizae* Y. Yang & P.E. Berry, **sect. nov.** – Type: *E. scatorhiza* S. Carter.

Annual or perennial herbs, or shrubs; when woody often with peeling bark; with or without tubers. Leaves alternate basally, opposite distally, petiolate, margin entire or undulate, sometimes with gland-tipped marginal teeth at the base; stipules glandular or subulate. Cymes in 2–3-branched umbels or cyathia solitary; subcyathial bracts small to well-developed.

Cyathia sessile or subsessile, glands 4 or 5, elliptic to subcircular, exappendiculate; styles connate at the base, bifid at the tip. Ovary and capsule sessile or exserted on a recurved pedicel, 3-lobed, glabrous or pubescent. Seeds ovoid to oblong, more or less 4-angled in cross-section, dorsal-ventrally flattened, face smooth, wrinkled, or tuberculate; ecarunculate (*E. kabridarensis*) or with a large cap-like caruncle (*E. applanata*, *E. agowensis*, *E. polyantha*, *E. scatorhiza*, *E. trichiocyma*).

Distribution and habitat. – Africa (Angola, Ethiopia, Kenya, Somalia, Tanzania), Arabia (Saudi Arabia, Yemen), India; rocky or sandy scrub or deserts, 200–1850 m.

Included species (7). – *E. agowensis* Hochst. ex Boiss., *E. kabridarensis* Thulin, *E. polyantha* Pax, *E. scatorhiza* S. Carter, *E. trichiocyma* S. Carter. Species that may also belong here: *E. applanata* Thulin & Gifri, *E. suborbicularis* Thulin.

Discussion. – Section *Scatorhizae* is characterized by non-succulent herbs to shrubs, sessile or subsessile cyathia, and flattened, 4-angled seeds. All five carunculate members have been treated in *Euphorbia* subg. *Eremophyton* (Boiss.) L.C. Wheeler (Carter & Radcliffe-Smith, 1988; Thulin & Al-Gifri, 1995), while the ecarunculate *E. kabridarensis* has been treated in sect. *Lyciopsis* Boiss. (Carter, 1992).

6. *Euphorbia* sect. *Denisiae* T. Haevermans & X. Aubriot, **sect. nov.** – Type: *E. denisii* Oudejans.

Nonsucculent, low, densely branched dwarf shrubs to small trees, with rhizomes. Branches numerous, alternate, brownish green with transverse linear darker patches, twigs slightly succulent to ligneous. Leaves arranged spirally on short shoots, deciduous; blade obcordate to rounded, subpeltate with a cylindrical petiole, margin entire; stipules small, deciduous. Cyathia subsessile, bisexual, subterminal, subcyathial bracts present but extremely reduced, pubescent; glands 5, yellow-green, broadly ovate (*E. denisii*) or erect with the upper margin reclined (*E. subpeltatophylla*), exappendiculate; styles connate at base, bifid at the tip; ovary and capsule subsessile, erect, emerging from the cyathium at maturity; 3-lobed, surface smooth and glabrous. Seeds ovoid, more or less 4-angled, apex acute, surface smooth, with a small, reniform caruncle.

Distribution and habitat. – Southern Madagascar, in xerophytic vegetation, sea level to 200 m.

Included species (2). – *E. denisii* Oudejans, *E. subpeltatophylla* Rauh.

Discussion. – Species from southern Madagascar in the *E. tetraptera* clade of subg. *Euphorbia* superficially resemble *E. denisii* and have been incorrectly identified as this species (Haevermans, 2003: 137, 166).

7. *Euphorbia* sect. *Bosseriae* T. Haevermans & X. Aubriot, **sect. nov.** – Type: *E. bosseri* Leandri.

Perennial, creeping to sprawling herbs, stems succulent, with purplish dark blotches; branching monochasial or dichasial. Leaves nonsucculent, rounded and petiolate, or reduced to scales, alternate to subopposite; stipules glandular. Cyathia bisexual, solitary, terminal, pubescent, subcyathial bracts apparently lacking; glands 4 or 5, yellow-green to brown, elliptic to ovate, margin entire, exappendiculate; ovary sparsely

pubescent, subsessile and included in the cyathium cup at maturity (*E. bosseri*, *E. platyclada*) or exerted on a recurved pedicel, impairing the development of the covered gland (*E. bemarahaensis*); styles 3, connate at the base, bifid almost to the base. Capsule 3-lobed, subsessile, sparsely pubescent, surface smooth. Seeds tuberculate and pointed in *E. platyclada*; unknown in the other two species; caruncle unknown in all three species.

Distribution and habitat. – Southwestern and southern Madagascar, in xerophytic vegetation, ca. 50–500 m.

Included species (3). – *E. bemarahaensis* Rauh & R. Mangelsdorff, *E. bosseri* Leandri, *E. platyclada* Rauh.

Discussion. – These three species grow in remote areas of Madagascar and are locally rare endemics. Rauh & Mangelsdorff (1999) placed these three species in their informal “groupe d’*E. bosseri*” but without a clear idea of its affinities. Cremers (1984) believed *E. bosseri* and *E. platyclada* were related to taxa like *E. enterophora* subsp. *enterophora* (subg. *Euphorbia* sect. *Tirucalli*), due to the presence of flattened twigs in both. However, this relationship is not supported by our molecular evidence.

8. *Euphorbia* sect. ***Plagianthae*** T. Haevermans & X. Aubriot, **sect. nov.** – Type: *E. plagiantha* Drake.

Broom-like dioecious shrubs or trees with coppery-shiny bark peeling in papyraceous rings. Branches alternate, densely aggregated. Leaves scale-like and quickly deciduous (*E. plagiantha*) or developed and elongate (*E. salota*), distributed all along the twigs; stipules minute. Pistillate cyathia usually single, staminate cyathia in few-flowered cymes, on axillary branches (reduced in *E. plagiantha*, elongated in *E. salota*); subcyathial bracts green, inconspicuous in *E. plagiantha*, leaf-like in *E. salota*; involucre rounded, with a sunken rim and (4–)5(–6) inconspicuous glands with an entire margin, exap- pendiculate; ovary glabrous; styles connate at the base, bifid at the tip. Capsules 3-lobed, smooth and glabrous, oriented upward; surface smooth, green. Seeds ovoid, apex pointed, surface smooth, ecarunculate.

Distribution and habitat. – Southern Madagascar, in xerophytic and semi-xerophytic vegetation; sea level to 1000 m.

Included species (2). – *E. plagiantha* Drake, *E. salota* Leandri.

Discussion. – *Euphorbia plagiantha* is a striking tree with coppery, peeling bark and leafless, photosynthetic stems (Fig. 1A), whereas *E. salota* is a broom-like shrub. *Euphorbia plagiantha* is widely distributed in semi-xerophytic forests and shrublands, whereas *E. salota* is restricted to a few ridges around Betroka, northwest of Fort Dauphin. Both species share the features of peeling bark, dioecy, and capsules oriented upwards regardless of twig orientation. They also have cyathia with a shrunken rim bearing tiny reduced glands, and the cyathia are borne laterally on the distal part of the twigs, while the vegetative branching occurs on the basal part of the twigs. *Euphorbia plagiantha*, the only Madagascan species featuring $2n = 14$ chromosomes (Schill, 1971), was previously grouped with *E. tirucalli* (Cremers, 1984), but *E. tirucalli* belongs to subg. *Euphorbia* (Bruyns & al., 2006).

9. *Euphorbia* sect. ***Frondosae*** Bruyns in Taxon 55: 416. 2006 – Type: *E. goetzei* Pax.

Annual or perennial herbs, or shrubs, tuberous in perennial species. Stems terete and semi-succulent to succulent, green and photosynthetic. Leaves alternate at base, opposite above, glabrous or pubescent, deciduous, margin entire; stipules glandular, mainly on young growth (or absent). Synflorescence of 3–5-branched terminal umbels of cymes with internodes on primary rays up to 6–12 cm long, bracts similar to leaves in size and shape; cyathial glands 4(5), usually bilobed (sometimes entire), or with 2–4 suberect linear processes (*E. barbicollis*, *E. goetzei*); ovary glabrous or pubescent; styles free or connate at the base, bifid up to half their length. Capsules exerted on a reflexed pedicel; 3-lobed. Seeds ovoid to oblong, apex pointed, 4-angled in cross-section; surface wrinkled to tuberculate, with or without a caruncle; caruncle shape and size varies.

Distribution and habitat. – Eastern to southern Africa (Angola, Botswana, Ethiopia, Kenya, Malawi, Mozambique, Namibia, South Africa, Tanzania, Uganda, Zambia, Zimbabwe) and the Arabian Peninsula (Oman, Saudi Arabia, Yemen); open to dense bushland, forest, 400–2700 m.

Included species (7). – *E. barbicollis* P.R.O. Bally, *E. engleri* Pax, *E. goetzei* Pax, *E. leistneri* R.H. Archer, *E. pirottae* N. Terrac., *E. quaitensis* S. Carter, *E. transvaalensis* Schltr.

Discussion. – This group is characterized by being fleshy, stem photosynthetic herbs and shrubs. The umbellate rays are well-spaced with long internodes. Other species that might belong in this section include *E. dolichoceras* S. Carter and *E. ruficeps* S. Carter. Both have ecarunculate, tuberculate seeds and different kinds of cyathial gland appendages, but their placements need to be further investigated.

10. *Euphorbia* sect. ***Tenellae*** Pax & K. Hoffm. in Engler, Veg. Erde 9, [Pflanzenw. Afrikas] 3, 2: 147. 1921 – Type: *E. glauccella* Pax (= *E. glanduligera* Pax).

= *Euphorbia* subsect. *Capensis* Boiss. in Candolle, Prodr. 15(2): 66. 1862 – Type: *E. phylloclada* Boiss.

Annual or perennial herbs, stems decumbent or erect, branches few to many. Leaves all opposite, narrow to subcordate, glabrous, margin entire or denticulate; stipules subulate or inconspicuous. Cymes forking many times, bracts leaf-like. Cyathial glands 4, with petaloid appendages or exap- pendiculate (they may have a very thin rim on the glands); ovary glabrous or pubescent; styles free or connate at the base, tip bifid, 3-lobed. Capsule exerted on a recurved pedicel. Seeds oblong, 4-angled in cross-section, tuberculate to smooth, with a cap-like caruncle.

Distribution and habitat. – Southern Africa (Angola, Botswana, Namibia, South Africa, Zimbabwe); in open desert areas, exposed gravelly or sandy soils and rocky slopes, ca. 100–1100 m.

Included species (4). – *E. claytonioides* Pax, *E. glanduligera* Pax (incl. *E. pfeilii* Pax), *E. macra* Hiern., *E. phylloclada* Boiss.

Discussion. – This is a small, but very significant section because it is sister to the rest of the mostly New World petaloid appendage clade. Pax (1921: 147) recognized its similarities to sect. *Anisophyllum*, and Koutnik (1984) placed *E. glanduligera*

in *Chamaesyce* S.F. Gray (= sect. *Anisophyllum*) and also wondered whether *E. pfeilii* should belong here as well. *Euphorbia pfeilii* was treated as distinct from *E. glanduligera* by Carter & Leach (2001), but examination of a range of specimens shows that they are all part of a single, distinctive species. We therefore include it under *E. glanduligera*. Apart from its extremely slender leaves, *E. macra* is similar to *E. glanduligera*, but it has a woody, perennial base.

Boissier (1862) placed *E. phylloclada* in *E.* [subg. *Euphorbia*] sect. *Stachydium*, presumably because the subcyathial bracts are so congested, but in sect. *Stachydium* the plants tend to be monochasial and the leaves enclose the cyathia more completely than in *E. phylloclada*. Later, Pax (1921) placed *E. phylloclada* in *E.* sect. *Pseudacalypha* Boiss., presumably because of its axillary cyathia and herbaceous habit, but the rest of sect. *Pseudacalypha* is now placed in subg. *Rhizanthium* (Steinmann & Porter, 2002; Horn & al., 2012a). *Euphorbia claytonioides* has subcordate leaves similar to *E. phylloclada*, but its cyathial features and the glands in the leaf axils closely resemble those of *E. glanduligera*. *Euphorbia macra* appears to be the only perennial species in this group.

11. *Euphorbia* sect. ***Gueinziae*** Riina, sect. nov. – Type: *E. gueinzii* Boiss.

Geophyte with tuberous roots and deciduous leaves, glabrous to densely pubescent; stems simple or multiple, branching dichotomously. Leaves usually alternate on lower portion of stem, opposite at the bifurcations of the upper branches, sessile, lanceolate to ovate-lanceolate; stipules inconspicuous, glanduliform. Cyathia bisexual, sometimes unisexual, in terminal cymes or solitary at the bifurcation of branches; glands 5, trapezoidal or oblong-ovate, the margin entire to crenulate, without petaloid appendages; ovary usually pubescent; styles 3, connate at the base, tips bifid and spreading. Capsule exserted, subglobose, 3-lobed. Seeds oblongoid, more or less 4-angled, obscurely sculptured, pale grayish, ecarunculate.

Distribution and habitat. – South Africa (Mpumalanga, Free State, KwaZulu-Natal, Eastern Cape), Lesotho, and Swaziland; grasslands on rocky slopes and above sandstone cliffs, 200–2000 m.

Included species (1). – *E. gueinzii* Boiss.

Discussion. – In his treatment of *E. gueinzii* in *Flora Capensis*, Brown & al. (1915) characterized this species as dioecious; however, Hargreaves (1992) contended that it is monoecious, sometimes presenting unisexual cyathia as well as bisexual ones. The molecular data indicate that *E. gueinzii* is related to the Brazilian *E.* sect. *Crossadenia* (Figs. 2, 3), which is consistent with its cyathial morphology and five glands, although *E. gueinzii* is quite distinct in its geophytic habit and inconspicuous cyathial glands. In the *Euphorbia* Seed Atlas (Morawetz & al., 2010), the seed shown of *E. gueinzii* was misidentified, and likely belongs to subg. *Rhizanthium*.

12. *Euphorbia* sect. ***Crossadenia*** Boiss. in Candolle, Prodr. 15(2): 9, 64. 1862 – Lectotype: *E. sarcodes* Boiss., designated by Wheeler in Amer. Midland Naturalist 30: 481. 1943. = *Euphorbia* sect. *Ephedropeplus* Müll. Arg. in Martius, Fl.

Bras. 11(2): 668. 1874 = *Euphorbia* subsect. *Ephedropeplus* (Müll. Arg.) Müll. Arg. ex Pax in Engler & Prantl, Nat. Pflanzenfam. 3(5): 106. 1891 – Type: *E. gymnoclada* Boiss.

Perennial herbs, small leafy shrubs, or pencil-stem shrubs, glabrous or pubescent, stems branching dichotomously or verticillately. Leaves opposite to alternate (spiral) on the lower stem, whorled at the base of umbellate rays, and opposite above, either rudimentary, minute, and soon deciduous, or well developed and persistent; stipules inconspicuous, glanduliform, rarely subulate. Cyathia terminal and axillary, arranged in short cymes or umbellate cymose rays, subtended by a pair of scale-like or foliose dichasial bracts. Involucres unisexual or bisexual, with 4 or 5 yellowish to green, appendiculate or exappendiculate glands; when present, gland appendages are short crenulate-dentate or long deeply cleft to fimbriate; ovary glabrous or pubescent; styles 3, basally connate, tips entire or bifid. Capsule well-exserted, subglobose to deeply 3-lobed. Seeds subglobose to ovoid, more or less 4-angled, apex mucronate, surface shallowly to obscurely tuberculate, rarely smooth, tubercles usually rounded (Fig. 1P), covered by a crustaceous, hydrophylic layer, ecarunculate.

Discussion. – The characteristic ornamentation of the seed coat, with low and rounded tubercles, may be a synapomorphy for this group. Boissier (1862) described the seeds of sect. *Crossadenia* as having a crustaceous caruncle, but our observations indicate that the apical part of the seed does not have a true caruncle; rather, the mucronate apex is an extension of the seed coat. The whitish layer on the outside of the seeds is hydrophilic and becomes mucilaginous when wet, much like seeds in sect. *Anisophyllum*. Both molecular data (Figs. 2 & 3) and morphological characters support the division of this group into two subsections.

Key to the subsections of *E.* sect. *Crossadenia*

- 1 Involucral glands 5, lacking appendages or with crenulate to dentate appendages <0.2 mm long 12a. subsect. ***Apparicianae***
- 1 Involucral glands 4 (5 in *E. gymnoclada*), with multiple finger-like appendages 2–4 mm long 12b. subsect. ***Sarcodes***

12a. *Euphorbia* subsect. ***Apparicianae*** Riina, subsect. nov. – Type: *E. appariciana* Rizzini.

Stem leaves rudimentary and soon deciduous. Involucral glands 5, gland appendages crenate to dentate, teeth <0.2 mm long, or appendages lacking (*E. flaviana*).

Distribution and habitat. – Endemic to the state of Bahia, Brazil, growing on granitic domes (inselbergs) or sandstone outcrops, 250–1200 m.

Included species (3). – *E. appariciana* Rizzini, *E. flaviana* Carn.-Torres & Cordeiro (Carneiro-Torres & al., 2012), *E. teres* M. Machado & Hofacker.

12b. *Euphorbia* subsect. ***Sarcodes*** Riina, subsect. nov. – Type: *E. sarcodes* Boiss.

Stem leaves usually well developed and persistent (rudi-

mentary and deciduous in *E. gymnoclada*). Involucral glands 4 (5 in *E. gymnoclada*) with white, finger-like appendages, teeth 2–4 mm long.

Distribution and habitat. – Endemic to eastern-central Brazil (Bahia, Goiás, Minas Gerais, Distrito Federal, Pernambuco, Piauí), in “campo rupestre” vegetation on sandy substrates and coastal “restinga”, sea level to 1400 m.

Included species (6). – *E. crossadenia* Pax & K. Hoffm., *E. goyazensis* Boiss., *E. gymnoclada* Boiss., *E. lycioides* Boiss., *E. sarcodes* Boiss., *E. sessilifolia* Klotzsch ex Boiss.

13. *Euphorbia* sect. *Anisophyllum* Roep. in Duby, Bot. Gall., ed. 2, 1: 412. 1828 ≡ *Anisophyllum* Haw., Syn. Pl. Succ.: 159. 1812, nom. illeg., non Jacq. 1763 ≡ *Chamaesyce* Gray, Nat. Arr. Brit. Pl. 2: 260. 1821 ≡ *Euphorbia* subg. *Chamaesyce* (Gray) Caesalp. ex Rchb., Deut. Bot. Herb.-Buch.: 193. 1841, nom. illeg., non Raf. 1817 – Lectotype: *Euphorbia peplis* L. (≡ *Anisophyllum peplis* (L.) Haw. ≡ *Chamaesyce maritima* Gray, nom. illeg., Art. 52.1) designated by Wheeler in *Rhodora* 43: 111. 1941.

= *Aplarina* Raf., New Fl. 4: 99. 1838 – Lectotype: *A. prostrata* Raf. (= *E. prostrata* Aiton), designated by Wheeler in *Rhodora* 43: 111. 1941.

= *Ditritra* Raf., Sylva Tellur.: 115. 1838 – Lectotype: *D. hirta* (L.) Raf. (≡ *E. hirta* L.), designated by Wheeler in *Amer. Midland Naturalist* 30: 464. 1943.

= *Endoisila* Raf., Sylva Tellur.: 114. 1838 – Type: *Endoisila myrsinites* Raf. (= *E. myrtilifolia* L.). See Wheeler (in *Amer. Midland Naturalist* 30: 465. 1943) for explanation of Rafinesque’s confusion over the specific epithet of the type species.

= *Xamesike* Raf., Fl. Tellur. 4: 115. 1838 – Lectotype: *X. vulgaris* Raf. (= *E. chamaesyce* L.), designated by Wheeler in *Amer. Midland Naturalist* 30: 476. 1943.

Annual or perennial herbs, rarely subshrubs to shrubs. Branches many, dichotomous, prostrate or ascending, rarely erect; main shoot aborts above the cotyledon node (less often continues growing for a few more nodes) and lateral shoots branch dichotomously. Leaves opposite, glabrous or pubescent, base often asymmetrical; sometimes dark green veins are visible on leaf blades; margins entire or serrate; stipules interpetiolar, glandular, linear, or subulate to triangular. Cyathia solitary at the bifurcation of branches or clustered in axillary cymes; glands 4, rarely 5–7; appendages present or absent, petaloid when present; styles 3, free or connate at the base, tip bifid, rarely entire; ovary and capsule glabrous or pubescent. Seed surface with transverse ridges, smooth, or with irregular wrinkles; 4-angled (rarely 3-angled or rounded), ecarunculate. C₂, C₃ or C₄ photosynthesis.

Distribution and habitat. – Warm, arid and semi-arid vegetation or disturbed habitats, and summer annuals of temperate areas; nearly worldwide, sea level to 4000 m.

Discussion. – Section *Anisophyllum* is characterized by its specialized growth form with early abortion of the main shoot and with the lateral shoots producing exclusively opposite leaves. All but three species in the section have C₄ photosynthesis.

Key to the subsections of *E. sect. Anisophyllum*

- 1 Stipules glandular; leaf cross-section without typical Kranz anatomy; cyathial gland appendages crenate and fan-shaped; Texas, New Mexico, and northern Mexico 13a. subsect. *Acutae*
- 1 Stipules subulate, triangular or ciliate, non-glandular; leaf cross-section with Kranz anatomy; cyathial gland appendages absent or present (variously shaped); widespread distribution 13b. subsect. *Hypericifoliae*

13a. *Euphorbia* subsect. *Acutae* Boiss. in Candolle, Prodr. 15(2): 18. 1862 – Type: *E. acuta* Engelm.

Perennial, pubescent herbs with a thickened woody taproot. Stems prostrate, arching, ascending to erect. Leaves opposite, or occasionally annual shoots terminate with a whorl in *E. angusta*; margin entire; stipules glandular. Cyathia solitary at the bifurcation of branches; glands 4, appendages fan-shaped, equal in size; ovary and capsule pubescent, 3-lobed; styles bifid. Seeds ovoid, 4-angled; face smooth, with irregular shallow depressions, or obscurely transversely rugose. C₂ or C₃ photosynthesis.

Distribution and habitat. – U.S.A. (western Texas) and Mexico (Coahuila, Durango, Tamaulipas); grassland to desert scrub in and around the Chihuahuan Desert on sandy or gravelly limestone substrates, 200–1500 m.

Included species (3). – *E. acuta* Engelm., *E. angusta* Engelm., *E. johnstonii* Mayfield.

Discussion. – Subsection *Acutae* is diagnosed within the section by having glandular stipules and lacking C₄ photosynthesis.

13b. *Euphorbia* subsect. *Hypericifoliae* Boiss. in Candolle, Prodr. 15(2): 20. 1862 – Type: *E. hypericifolia* L.

= *Euphorbia* subsect. *Chamaesyce* Boiss. in Candolle, Prodr. 15(2): 27. 1862, nom. illeg. per ICBN Art. 53.4 – Type: *E. chamaesyce* L.

= *Euphorbia* subsect. *Cheloneae* Boiss. in Candolle, Prodr. 15(2): 16. 1862 – Lectotype: *E. nummularia* Hook. f., designated by Wheeler in *Rhodora* 43: 111. 1941.

= *Euphorbia* subsect. *Elegantes* Boiss. in Candolle, Prodr. 15(2): 18. 1862 – Type: *E. elegans* Spreng.

= *Euphorbia* subsect. *Gymnadeniae* Boiss. in Candolle, Prodr. 15(2): 11. 1862 ≡ *Chamaesyce* subsect. *Gymnadeniae* (Boiss.) Koutnik in *Allertonia* 4: 338. 1987 – Lectotype: *E. clusiifolia* Hook. & Arn., designated by Wheeler in *Amer. Midland Naturalist* 30: 480. 1943.

= *Euphorbia* subsect. *Pleiadeniae* Boiss. in Candolle, Prodr. 15(2): 50. 1862 – Lectotype: *E. selloi* (Klotzsch & Garcke) Boiss., designated by Wheeler in *Amer. Midland Naturalist* 30: 480. 1943.

= *Euphorbia* subsect. *Sclerophyllae* Boiss. in Candolle, Prodr. 15(2): 12. 1862 ≡ *Euphorbia* sect. *Sclerophyllae* (Boiss.) Binojk. & N.P. Balakr., *Genus Euphorbia India*: 201. 2010 ≡ *Chamaesyce* Gray sect. *Sclerophyllae* (Boiss.) Hurusawa in *J. Fac. Sci. Univ. Tokyo, Sect. 3, Bot.* 6: 275. 1954 – Lectotype: *E. atoto* G. Forst., designated by Wheeler in *Amer. Midland Naturalist* 30: 480. 1943.

= *Euphorbia* sect. *Longistylae* Binojk. & N.P. Balakr., Genus *Euphorbia* India: 178. 2010 – Type: *E. longistyla* Boiss.

Annual or perennial herbs, rarely subshrubs to shrubs. Branches many, dichotomous, prostrate or ascending, rarely erect; main shoot aborts above the cotyledon node (less often continues elongation) and lateral shoots branch dichotomously. Leaves opposite, glabrous or pubescent, base often asymmetrical; sometimes dark green veins are visible on leaf blades (Kranz anatomy); margins entire or serrate; stipules interpetiolar, linear, subulate to triangular. Cyathia solitary at the bifurcation of branches, or clustered in axillary cymes; glands 4, rarely 5–7; appendages present or absent, petaloid when present, equal or unequal in size; styles 3, free or connate at the base, tip bifid, rarely entire; ovary and capsule glabrous or pubescent. Seed surface with transverse ridges, smooth, or with irregular wrinkles; 4-angled (rarely 3-angled or rounded). C_4 photosynthesis.

Distribution and habitat. – Warm, arid and semi-arid vegetation or disturbed habitats, and summer annuals in temperate areas; worldwide, from sea level to 4000 m.

Included species (365). – *E. abdita* (D.G. Burch) Radcl.-Sm., *E. abdulghafooriana* Abedin, *E. abramsiana* L.C. Wheeler, *E. adenoptera* Bertol., *E. alainii* Oudejans, *E. alato-caulis* V.W. Steinm. & Felger, *E. albomarginata* Torr. & A. Gray, *E. allocarpa* S. Carter, *E. alsiniflora* Baill., *E. alsinifolia* Boiss., *E. amandi* Oudejans, *E. amplexicaulis* Hook. f., *E. anisopetala* (Prokh.) Prokh., *E. anthonyi* Brandegee, *E. anychioides* Boiss., *E. apatzingana* McVaugh, *E. apicata* L.C. Wheeler, *E. arabica* Hochst. & Steud. ex Anderson, *E. arabicoides* N.E. Br., *E. arenarioides* Gagnep., *E. argillosa* Chodat & Hassl., *E. arizonica* Engelm., *E. armstrongiana* Boiss., *E. arnottiana* Endl., *E. articulata* Aubl., *E. astyla* Engelm. ex Boiss., *E. atoto* G. Forst., *E. atrococca* A. Heller, *E. australis* Boiss., *E. austrooccidentalis* Thell., *E. bahiensis* (Klotzsch & Garcke) Boiss., *E. balakrishnanii* Binojk. & Gopalan, *E. bartolomaei* Greene, *E. baueri* Engelm. ex Boiss., *E. berteriana* Balb. ex Spreng., *E. besseri* (Klotzsch & Garcke) Boiss., *E. biconvexa* Domin, *E. bifida* Hook. & Arn., *E. bindloensis* (Stewart) Y. Yang, *E. blodgettii* Engelm. ex Hitchc., *E. boliviana* Rusby, *E. bombensis* Jacq., *E. bracteolaris* Boiss., *E. brandegeei* Millsp., *E. bruntii* (Proctor) Oudejans, *E. burchellii* Müll. Arg., *E. burmanica* Hook. f., *E. calderoniae* V.W. Steinm., *E. camagueyensis* (Millsp.) Urb., *E. capillaries* Gagnep., *E. capitellata* Engelm., *E. carissoides* F.M. Bailey, *E. carunculata* Waterf., *E. catamarcensis* (Croizat) Subils, *E. cayensis* Millsp., *E. celastroides* Boiss., *E. centralis* B.G. Thomson, *E. centunculoides* Kunth, *E. chaetocalyx* (Boiss.) Tidestr., *E. chamaerhodos* Boiss., *E. chamaesyce* L., *E. chamaesycoides* B. Nord., *E. chamberlinii* I.M. Johnst., *E. chamissonis* (Klotzsch & Garcke) Boiss., *E. cinerascens* Engelm., *E. clarkeana* Hook. f., *E. clavidigitata* Gage, *E. clusiifolia* Hook. & Arn., *E. coccinea* B. Heyne ex Roth, *E. coghlanii* F.M. Bailey, *E. compressa* Boiss., *E. concanensis* M.K. Janarth. & S.R. Yadav, *E. conferta* (Small) B.E. Sm., *E. convolvuloides* Hochst. ex Benth., *E. cordifolia* Elliott, *E. corrigioloides* Boiss., *E. cowellii* (Millsp. ex Britton) Oudejans, *E. cozumelensis* Millsp., *E. crassinodis* Urb., *E. crepitata*

L.C. Wheeler, *E. crepuscula* (L.C. Wheeler) V.W. Steinm. & Felger, *E. cristata* B. Heyne ex Roth, *E. cumbrae* Boiss., *E. cumlicola* (Small) Oudejans, *E. dallachyana* Baill., *E. deccanensis* V.S. Raju, *E. degeneri* Sherff, *E. delicatissima* S. Carter, *E. deltoidea* Engelm. ex Chapm., *E. densiflora* (Klotzsch and Garcke) Klotzsch, *E. dentosa* I.M. Johnst., *E. deppeana* Boiss., *E. derickii* V.W. Steinm., *E. diminuta* S. Carter, *E. dioeca* Kunth, *E. drummondii* Boiss., *E. duckei* (Croizat) Oudejans, *E. eichleri* Müll. Arg., *E. eleanoriae* (D.H. Lorence & W.L. Wagner) Govaerts, *E. elegans* Spreng., *E. engelmannii* Boiss., *E. erythroclada* Boiss., *E. eylesii* Rendle, *E. feddema* McVaugh, *E. fendleri* Torr. & A. Gray, *E. fischeri* Pax, *E. flindersica* Halford & W.K. Harris, *E. floribunda* Engelm. ex Boiss., *E. florida* Engelm., *E. foliolosa* Boiss., *E. fosbergii* (J. Florence) Govaerts, *E. fruticulosa* Engelm. ex Boiss., *E. galapageia* B.L. Rob. & Greenm., *E. garanbiensis* Hayata, *E. garberi* Engelm. ex Chapm., *E. gaudichaudii* Boiss., *E. geyeri* Engelm. & A. Gray, *E. glyptosperma* Engelm., *E. goliana* Comm. ex Lam., *E. golondrina* L.C. Wheeler, *E. gracillima* S. Watson, *E. grammata* (McVaugh) Oudejans, *E. grandidieri* Baill., *E. granulata* Forssk., *E. guanarensis* Pittier, *E. hajhiensis* Radcl.-Sm., *E. halemanui* Sherff, *E. heleniana* Thell. & Stapf, *E. helwigii* Urb. & Ekman, *E. hepatica* Urb. & Ekman, *E. herbstii* (W.L. Wagner) Oudejans, *E. heyneana* Spreng., *E. hildebrandtii* Baill., *E. hirta* L., *E. hirtella* Boiss., *E. hispida* Boiss., *E. hooveri* L.C. Wheeler, *E. hsinchuensis* (S.C. Lin & S.M. Chaw) C.Y. Wu & J.S. Ma, *E. humbertii* Denis, *E. humifusa* Willd., *E. humistrata* Engelm. ex A. Gray, *E. hunzikeri* Subils, *E. hypericifolia* L., *E. hyssopifolia* L., *E. inaequilatera* Sond., *E. inaguaensis* Oudejans, *E. inappendiculata* Domin, *E. incerta* Brandegee, *E. indica* Lam., *E. indivisa* (Engelm.) Tidestr., *E. infernalis* V.W. Steinm., *Euphorbia inflexa* Urb. & Ekman, *Euphorbia jaegeri* V.W. Steinm. & J. André, *E. jamesonii* Boiss., *E. jejuna* M.C. Johnst. & Warnock, *E. jodhpurensis* Blatt. & Hallb., *E. karibensis* S. Carter, *E. katrajensis* Gage, *E. kerstingii* Pax, *E. kilwana* N.E. Br., *E. kimberleyensis* B.G. Thomson, *E. kischenensis* Vierh., *E. klotzschii* Oudejans, *E. kuriensis* Vierh., *E. kuwaleana* O. Deg. & Sherff, *E. lacinata* Panigrahi, *E. laredana* Millsp., *E. lasiocarpa* Klotzsch, *E. lata* Engelm., *E. lawsonii* Binojkumar & Dwarakan, *E. lecheoides* Millsp., *E. leonardii* (D.G. Burch) Radcl.-Sm., *E. leptoclada* Balf.f., *E. leucantha* (Klotzsch & Garcke) Boiss., *E. leucophylla* Benth., *E. lineata* S. Watson, *E. linguiformis* McVaugh, *E. lissosperma* S. Carter, *E. liukiensis* Hayata, *E. livida* E. Mey. ex Boiss., *E. loandensis* N.E. Br., *E. longin-sulicola* S.R. Hill, *E. longistyla* Boiss., *E. lupatensis* N.E. Br., *E. lutulenta* (Croizat) Oudejans, *E. luzoniensis* Merr., *E. macgillivrayi* Boiss., *E. machrisiae* Steyerl., *E. maconochieana* B.G. Thomson, *E. maculata* L., *E. magdalenae* Benth., *E. makinoidi* Hayata, *E. marayensis* Subils, *E. meganaesos* Featherman, *E. melanadenia* Torr. & A. Gray, *E. mendezii* Boiss., *E. mertonii* Fosberg, *E. mesembryanthemifolia* Jacq., *E. meyeniana* Klotzsch, *E. microcephala* Boiss., *E. micromera* Boiss., *E. minbuensis* Gage, *E. minutula* Boiss., *E. missurica* Raf., *E. mitchelliana* Boiss., *E. mossambicensis* (Klotzsch & Garcke) Boiss., *E. mossamedensis* N.E. Br., *E. muelleri* Boiss., *E. multiformis* Gaudich. ex Hook. & Arn., *E. multinodis* Urb.,

E. myrtillifolia L., *E. neocaledonica* Boiss., *E. neopolycnemoides* Pax & K. Hoffm., *E. nocens* (L.C. Wheeler) V.W. Steinm., *E. nodosa* Houtt., *E. notoptera* Boiss., *E. nummularia* Hook. f., *E. nutans* Lag., *E. obliqua* F.A. Bauer ex Endl., *E. occidentaustralica* Radcl.-Sm. & Govaerts, *E. ocellata* Durand & Hilg., *E. olowaluana* Sherff, *E. ophiolitica* (P.I. Forst.) Y. Yang, *E. ophthalmica* Pers., *E. oranensis* (Croizat) Subils, *E. orbiculata* Kunth, *E. orbifolia* (Alain) Oudejans, *E. originoides* L., *E. oxycoccoides* Boiss., *E. pancheri* Baill., *E. parciflora* Urb., *E. paredonensis* (Millsp.) Oudejans, *E. parishii* Greene, *E. parkeri* Binoj Kumar & N.P. Balakr., *E. parryi* Engelm., *E. parva* N.E. Br., *E. parviflora* L., *E. pediculifera* Engelm., *E. pellegrinii* Leandri, *E. peninsularis* I.M. Johnst., *E. peplis* L., *E. perennans* (Shinners) Warnock & M.C. Johnst., *E. pergamena* Small, *E. pergracilis* P.G. Mey., *E. perlignea* McVaugh, *E. peruviana* L.C. Wheeler, *E. petrina* S. Watson, *E. picachensis* Brandegee, *E. pilosissima* S. Carter, *E. pionsperma* V.W. Steinm. & Felger, *E. platysperma* Engelm. ex S. Watson, *E. podadenia* Boiss., *E. polycarpa* Benth., *E. polycnemoides* Hochst. ex Boiss., *E. polygonifolia* L., *E. pondii* Millsp., *E. porteriana* (Small) Oudejans, *E. portucasadiana* (Croizat) Subils, *E. potentilloides* Boiss., *E. potosina* Fernald, *E. proctori* (D.G. Burch) Correll, *E. prostrata* Aiton, *E. psammogeton* P.S. Green, *E. pueblensis* Brandegee, *E. punctulata* Andersson, *E. pycnostegia* Boiss., *E. quitensis* Boiss., *E. radioloides* Boiss., *E. ramosa* Seaton, *E. rayturneri* V.W. Steinm. & E. Jercinovic, *E. reconciliationis* Radcl.-Sm., *E. recurva* Hook. f., *E. remyi* A. Gray ex Boiss., *E. reniformis* Blume, *E. revoluta* Engelm., *E. rhytisperma* (Klotzsch & Garcke) Boiss., *E. riebeckii* Pax, *E. rivae* Pax, *E. rochaensis* (Croizat) Alonso Paz & Marchesi, *E. rockii* C.N. Forbes, *E. rosea* Retz., *E. rubriflora* N.E. Br., *E. ruiziana* (Klotzsch & Garcke) Boiss., *E. ruizlealii* Subils, *E. rutilis* (Millsp.) Standl. & Steyerl., *E. sabulicola* Boiss., *E. sachetiana* (J. Florence) Govaerts, *E. salsicola* S. Carter, *E. salsuginosa* (McVaugh) Radcl.-Sm. & Govaerts, *E. sanmartensis* Rusby, *E. scabrifolia* Kurz, *E. schizolepis* F. Muell. ex Boiss., *E. schlechteri* Pax, *E. schultzii* Benth., *E. schumannii* Radcl.-Sm., *E. schweinfurthii* Balf.f., *E. scopulorum* Brandegee, *E. scordiifolia* Jacq., *E. sebastinei* Binojk. & N.P. Balakr., *E. seleri* Donn. Sm., *E. selloi* (Klotzsch & Garcke) Boiss., *E. selousiana* S. Carter, *E. senguptae* N.P. Balakr. & Subr., *E. serpens* Kunth, *E. serpyllifolia* Pers., *E. serratifolia* S. Carter, *E. serrula* Engelm., *E. setiloba* Engelm. ex Torr., *E. setosa* (Boiss.) Müll. Arg., *E. sharkoensis* Baill., *E. simulans* (L.C. Wheeler) Warnock & M.C. Johnst., *E. skottsbergii* Sherff, *E. sparrmanii* Boiss., *E. sparsiflora* A. Heller, *E. spellenbergiana* Mayfield & V.W. Steinm., *E. spissiflora* S. Carter, *E. standleyi* (Millsp.) Oudejans, *E. stictospora* Engelm., *E. stoddartii* Fosberg, *E. subterminalis* N.E. Br., *E. sumbawensis* Boiss., *E. taihienensis* (Chaw & Koutnik) Oudejans, *E. taluticola* Wiggins, *E. tamanduana* Boiss., *E. taulipipasana* (Millsp.) Oudejans, *E. tetensis* Klotzsch, *E. theriaca* L.C. Wheeler, *E. thymifolia* L., *E. tinianensis* Hosok., *E. tomentella* Engelm. ex Boiss., *E. tomentulosa* S. Watson, *E. torralbasii* Urb., *E. trachysperma* Engelm., *E. truncapatae* (Croizat) J.F. Macbr., *E. trialata* (Huft) V.W. Steinm., *E. trichophylla* Baker, *E. trinervia*

Schumach. & Thonn., *E. tumistyla* (D.G. Burch) Radcl.-Sm., *E. turpinii* Boiss., *E. umbellulata* Engelm. ex Boiss., *E. vaginulata* Griseb., *E. vallis-mortae* (Millsp.) J.T. Howell, *E. vau-thieriana* Boiss., *E. velleriflora* (Klotzsch & Garcke) Boiss., *E. velligera* Schauer, *E. vermiculata* Raf., *E. vestita* Boiss., *E. vezorum* Leandri, *E. viatilis* Ule, *E. villifera* Scheele, *E. viminea* Hook. f., *E. viridula* Cordem. ex Radcl.-Sm., *E. viscoides* Boiss., *E. wheeleri* Baill., *E. yucatanensis* (Millsp.) Standl., *E. zambesiana* Benth.

Discussion. – Old World species of subsect. *Hypericifoliae* are relatively understudied and there may be additional species to be described as well as others to be placed in synonymy. Currently David Halford (BRI) is revising the group in Australia and has numerous new species he plans to name and publish as part of that revision.

The following combinations are made here to recognize the taxa at the appropriate rank within *Euphorbia*:

Euphorbia bindloensis (Stewart) Y. Yang, **comb. nov.** = *Euphorbia articulata* var. *bindloensis* Stewart in Proc. Calif. Acad. Sci., ser. 4, 1: 91. 1911 = *Chamaesyce bindloensis* (Stewart) D.G. Burch in Ann. Missouri Bot. Gard. 56: 176. 1969 – Type: Ecuador. Galapagos: Bindloe Island, Stewart 1968 (holotype: GH).

Euphorbia deltoidea subsp. *serpyllum* (Small) Y. Yang, **comb. nov.** = *Chamaesyce serpyllum* Small, Fl. Florida Keys: 81. 1913 = *Chamaesyce deltoidea* subsp. *serpyllum* (Small) D.G. Burch in Ann. Missouri Bot. Gard. 53: 99. 1966 = *Euphorbia deltoidea* var. *serpyllum* (Small) Oudejans in Phytologia 67: 45. 1989 – Type: U.S.A. Florida: Big Pine Key, Monroe County, J.K. Small 3811 (holotype: NY). — This new combination is made to be consistent in recognizing four subspecies within the *Euphorbia deltoidea* complex.

Euphorbia ophiolitica (P.I. Forst.) Y. Yang, **comb. nov.** = *Chamaesyce ophiolitica* P.I. Forst. in Austrobaileya 5: 711. 2000 – Type: Australia. Queensland: Port Curtis District, P.I. Forster 15042 (holotype: BRI).

14. *Euphorbia* sect. *Poinsettia* (Graham) Baill., Étude Euphorb.: 284. 1858 = *Poinsettia* Graham in Edinburgh New Philos. J. 20: 412. 1836 = *Euphorbia* subg. *Poinsettia* (Graham) House in Bull. New York State Mus. Nat. Hist. 254: 473. 1924 – Type: *Poinsettia pulcherrima* (Willd.) Graham (= *E. pulcherrima* Willd.).

= *Cyathophora* Raf., Fl. Tellur. 4: 117. 1838 – Type: *C. heterophylla* (Raf.) L. (= *E. heterophylla* L.).

= *Pleuradena* Raf., Atlantic J. 1: 182. 1833 = *Euphorbia* subg. *Pleuradena* (Raf.) Croizat in Revista Sudamer. Bot. 6: 10. 1939 – Type: *Pleuradena coccinea* Raf. (= *E. pulcherrima* Willd.).

Annual or perennial herbs, shrubs, or small trees, from a taproot or tuber. Earliest developing leaves and branches opposite, middle to upper nodes alternate or opposite/whorled, blades usually markedly to finely serrate, rarely entire, sometimes markedly heteromorphic; stipules minute, glanduliform,

often inconspicuous. Cyathia few to many in usually congested, terminal cymes, sometimes appearing corymbiform, leafy bracts sometimes whitish to bright red at the base or on the entire blade; cyathial glands 1–5(–8), slightly concave to deeply cupped, bilabiate, or circular, appendages lacking or present and variously shaped; styles 3, free or connate at the base, tip entire or bifid; ovary and capsule glabrous or pubescent, 3-lobed. Seeds 4-angled to rounded, sharply 4-angled to somewhat rounded in cross-section, usually truncate apically, variously tuberculate, with or without a caruncle.

Discussion. – Species of the first two diverging subsections (subsects. *Lacerae* and *Erianthae*) are distinct in their large caruncles and sharply 4-angled seeds. The seeds of subsect. *Exstipulatae*, in contrast, are similar to many of those in subsect. *Stormieae*, which have a coarsely tuberculate surface, more ovoid shape, and are either carunculate or ecarunculate. See additional discussion in the main text for an expanded justification for the broadened circumscription of sect. *Poinsettia*.

Key to the subsections of *E. sect. Poinsettia*

- 1 Leaves linear, mostly entire; involucre glands densely appressed-pubescent, with lacinate, pubescent appendages that arch upwards and inwards over the gland 14b. subsect. *Erianthae*
- 1 Leaves linear to pandurate and usually toothed (entire in *E. colorata*); involucre glands either lacking appendages or the appendages not covering the glands 2
- 2 Involucre glands 4, appendages either horned or petaloid and green with crenate margins; styles entire; seeds sharply 4-angled, finely tuberculate, with a prominent stipitate caruncle nearly as wide as the seed itself 14a. subsect. *Lacerae*
- 2 Involucre glands 1–5(–8), lacking appendages or, if present, then appendages whitish (green and obsolete in *E. chersonesa*), petaloid and not horned; styles bifid; seeds not sharply 4-angled, apically depressed on the ventral side, coarsely tuberculate, either ecarunculate or with a small caruncle much narrower than the seed 3
- 3 Involucre glands with whitish appendages 14c. subsect. *Exstipulatae*
- 3 Involucre glands without appendages (or obsolete greenish appendages in *E. chersonesa*) ... 14d. subsect. *Stormieae*

14a. *Euphorbia* subsect. *Lacerae* Y. Yang & P.E. Berry, **subsect. nov.** – Type: *Euphorbia lacera* Boiss.

Annual herbs from a taproot. Leaves linear-lanceolate to pandurate, often heteromorphic, noticeably serrate, opposite at lowest nodes, then alternate in the mid-section, the shoot terminating with a whorl of leaves below the fertile branches; stipules absent or glandular. Cyathia in terminal, congested, few-cyathiate cymes, subtended by opposite leaves; glands 4, stipitate, laterally compressed and concave; appendages horned, or petaloid and green with crenate margins; styles entire; ovary and capsule oblong-ovoid. Seeds 4-angled, apically angled, finely tuberculate, with a prominent stipitate caruncle nearly as wide as the seed itself.

Distribution and habitat. – Central and western Mexico; xerophytic scrub, wooded ravines, 900–2500 m.

Included species (2). – *E. jaliscensis* B.L. Rob. & Greenm., *E. lacera* Boiss.

Discussion. – The pandurate, serrate leaves of *E. jaliscensis* are remarkably similar to those found in *E. heterophylla* or *E. cyathophora*, and the leaves of *E. lacera* are also polymorphic. Both species in this section have cupped, stipitate involucre glands. In both cases, the appendages are green and somewhat fleshy, although they are much reduced and almost obsolete in the type of *E. jaliscensis* var. *durangensis* Millsp. *Euphorbia lacera* was initially placed by Boissier (1862) in *E. sect. Zygothylidium*, together with *E. exstipulata* in an undesignated subcategory of § *Carunculatae* Boiss. The rest of Boissier's section consists of § *Ecarunculatae* Boiss., with two species that belong now to sect. *Alectoroxtonum*, *E. bilobata* and *E. hexagona*.

14b. *Euphorbia* subsect. *Erianthae* Y. Yang & P.E. Berry, **subsect. nov.** – Type: *Euphorbia eriantha* Benth.

Annual or short-lived, pubescent, perennial herbs from a taproot. Branches few to many from the base. Leaves linear, appearing entire but usually with a few inconspicuous teeth towards the apex, opposite at basal-most node, alternate in the mid-section; stipules inconspicuous, minute and glanduliform, at the base of the petiole. Cyathia in terminal, congested, few-cyathiate cymes, subtended by opposite or ternate, leaf-like bracts; glands (2–)4–5, protruding from the outer, upper edge of the involucre, shallowly concave; gland appendages elongate, lacinate, densely covered with white, appressed trichomes, arching over and concealing the glands (Fig. 1H); styles free at the base, apex entire, purple; ovary and capsule canescent, obloid or ovoid. Seeds 4-angled, coarsely tuberculate, covered with a white, crustaceous coating, with a circular caruncle about half as wide as the seed.

Distribution and habitat. – Southeastern U.S.A. (Arizona, California, New Mexico, Texas) and northern Mexico (Baja California, Baja California Sur, Chihuahua, Coahuila, Durango, Sonora); desert scrub and thorn scrub on rocky slopes and along washes, sea level to 900 m.

Included species (1). – *E. eriantha* Benth.

Discussion. – This subsection contains a single species that is unique because of its unusual cyathial gland appendages that curl over the gland towards the inside of the cyathium (Fig. 1H).

14c. *Euphorbia* subsect. *Exstipulatae* Y. Yang & P.E. Berry, **subsect. nov.** – Type: *E. exstipulata* Engelm.

Small, annual herbs from a slender taproot, with opposite, arcuate branching. Leaves linear to ovate, serrate, opposite throughout or with some alternate leaves in the mid-stem section in *E. bifurcata*. Cyathia in terminal, congested few-cyathiate cymes; glands 1–4(–5), oblong to circular, stipitate, laterally compressed and concave, appendages entire, undulate, or divided into triangular segments; styles bifid; ovary and capsule glabrous or pubescent on the keels, 3-lobed. Seeds broadly ovoid, apically depressed on the ventral side, quadrangular to rounded in cross-section, coarsely tuberculate with 2 transverse

ridges and a tiny, reniform caruncle (in *E. exstipulata*), or warty-papillate without an evident caruncle (*E. bifurcata*).

Distribution and habitat. – Southwestern U.S.A. to southern Mexico; desert scrub, grasslands, oak forest, riparian areas, 800–2300 m.

Included species (2). – *E. bifurcata* Engelm., *E. exstipulata* Engelm.

Discussion. – *Euphorbia bifurcata* is very similar to many species in subsect. *Stormieae* in its normally single cupulate gland, some subcyathial bracts that are whitish at the base, and its ecarunculate, verrucose seeds. *Euphorbia exstipulata* was initially placed by Boissier (1862) in *E. sect. Zygomphylidium*, together with *E. lacera* in a subdivision named § *Carunculatae* Boiss.

14d. *Euphorbia* subsect. *Stormieae* Croizat in Revista Sudamer. Bot. 6: 13. 1939 – Type: *Euphorbia stormiae* Croizat (≡ *E. radians* Benth. var. *stormiae* (Croizat) Rzed. & Calderón).

Annual or perennial herbs, shrubs or small trees. Branches opposite; leaves opposite at the epicotyledonary node, leaves and branches often alternate in the mid-section of plant, and then opposite or whorled in the synflorescence; leaves subtending the synflorescence often brightly colored. Cyathia in terminal, usually dense, sometimes monochasial cymes; involucre glands 1–5(–8), deeply to shallowly cupped and stalked, exappendiculate; styles 3, free or connate at the base, bifid to about 1/2 their length from the apex, rarely entire or with only the very apex forked; ovary and capsule glabrous or pubescent, 3-lobed. Seeds ovoid, quadrangular or somewhat rounded in cross-section, usually coarsely and unevenly tuberculate, or the tubercles disposed in one or more transverse, dorsal rows; ecarunculate, or caruncle variously shaped.

Distribution and habitat. – Widespread in the New World, from Canada to Argentina, but with a center of distribution in Mexico; in a wide variety of habitats from desert scrub to moist montane forests, sea level to 2700 m.

Included species (21). – *E. chersonesa* Huft, *E. colorata* Engelm., *E. cornastra* (Dressler) Radcl.-Sm., *E. cuphosperma* (Engelm.) Boiss., *E. cyathophora* Murray, *E. davidii* Subils, *E. dentata* Michx., *E. elliptica* Lam., *E. heterophylla* L., *E. hormorrhiza* Radcl.-Sm., *E. kurtzii* Subils, *E. pentadactyla* Griseb., *E. pinetorum* (Small) G.L. Webster, *E. pulcherrima* Willd., *E. pumicola* Huft, *E. radians* Benth., *E. restiacea* Benth., *E. schiedeana* (Klotzsch & Garcke) Mayfield ex C. Nelson, *E. strigosa* Hook. & Arn., *E. tubadenia* Mayfield ex Y. Yang, *E. zonosperma* Müll. Arg.

Discussion. – This subsection is the most diverse in sect. *Poinsettia* in terms of distribution, habit, and species number. It includes the species that Dressler (1961) included in *Poinsettia*, and those in *Euphorbia* subg. *Poinsettia* sensu Mayfield (1997), with the addition of *E. chersonesa*, which Huft (1984) thought belonged to sect. *Alectoroctonum* because of its vestigial involucre gland appendages and relatively flat glands. Vestigial green gland appendages were reported in *E. chersonesa* and *E. cornastra* (Huft, 1984; Mayfield, 1997), but they are very subtle and difficult for us to see when reexamining

herbarium material of these species. Mayfield (1997) recognized two groups in subg. *Poinsettia*, the *Euphorbia dentata* alliance and “subgenus *Poinsettia* sens.str.” Our combined molecular tree (Fig. 3B) indicates that the *E. dentata* alliance may be monophyletic, but it is nested within the rest of the subsection.

In addition to the species listed above, there are four other species described but not validly published in Mayfield’s (1997) thesis. In addition, Mayfield (1997) proposed a new name and status for another species he recognized in subg. *Poinsettia*. This name is validated below.

***Euphorbia tubadenia* Mayfield ex Y. Yang, nom. & stat. nov.**

≡ *Euphorbia dentata* var. *lasiocarpa* Boiss. in Candolle, Prodr. 15(2): 72. 1862 – Type: Mexico. Nuevo León: Tanquesillos, Jul–Oct 1842, W.F. von Karwinski s.n. (holotype: LE). — Since the epithet *lasiocarpa* is occupied in *Euphorbia* (*E. lasiocarpa* Klotzsch), a new name is required for this taxon when elevated to species.

15. *Euphorbia* sect. *Alectoroctonum* (Schltdl.) Baill., Étude Euphorb.: 284. 1858 ≡ *Alectoroctonum* Schltdl. in Linnaea 19: 252. 1847 – Lectotype: *A. scotatum* (Schltdl.) Schltdl. (≡ *E. scotatum* Schltdl.), designated by Wheeler in Amer. Midland Naturalist 30: 459. 1943.

= *Agaloma* Raf., Fl. Tellur. 4: 116. 1838 ≡ *Euphorbia* subg. *Agaloma* (Raf.) House in Bull. New York State Mus. Nat. Hist. 254: 471. 1924 – Lectotype: *E. corollata* L., designated by Rafinesque in Autik. Bot. 95. 1840.

= *Tithymalopsis* Klotzsch & Garcke in Monatsber. Königl. Preuss. Akad. Wiss. Berlin 1859: 249. 1859 ≡ *Euphorbia* sect. *Tithymalopsis* (Klotzsch & Garcke) Boiss. in Candolle, Prodr. 15(2): 9, 66. 1862 – Lectotype: *E. corollata* L., designated by Small in Britton & Brown, Ill. Fl. N.U.S., ed. 2., 2: 469. 1913.

= *Zalitea* Raf., New Fl. 4: 98. 1838 – Type: *Z. linearis* Raf. (= *E. hexagona* Nutt.).

= *Euphorbia* sect. *Zygomphylidium* Boiss. in Candolle, Prodr. 15(2): 9, 52. 1862 ≡ *Zygomphylidium* (Boiss.) Small in Fl. S.E. U.S.: 714, 1334. 1903 – Lectotype: *Z. hexagonum* (≡ *E. hexagona* Nutt.), designated by Small in Britton & Brown, Ill. Fl. N.U.S., ed. 2., 2: 468. 1913.

Annual or perennial herbs, shrubs, rarely succulent or small trees. Stems erect to decumbent, rarely prostrate. Leaves and branches opposite and/or alternate before the termination of apical growth, which usually produces a 2–8-rayed pseudoumbel and usually equal number of leaves (sometimes there is no apical termination and the main shoots continue elongating), and then switching to dichotomous branching, with each fork subtended by a pair of dichasial bracts. Leaves elliptic, ovate, obovate to linear, margin entire, rarely crenulate; stipules mostly minute and glanduliform, rarely subulate-filiform. Cyathia solitary or in cymes, terminal or axillary; both dichasial and subcyathial bracts leaf-like, sometimes greatly reduced in size, or white and showy; glands 5 per cyathium (rarely 2, 3, 4 or 6), flat or shallowly concave, appendages petaloid; styles free at the base, tip bifid or rarely entire; ovary and capsule

glabrous or pubescent, capsule exerted at maturity; 3-lobed. Seeds ovoid, subglobose, or oblong, more or less 4-angled to rounded; surface smooth or with wart-like protrusions, sometimes distinctively shallowly to deeply pitted, ecarunculate or rarely carunculate.

Distribution and habitat. – Widespread in the New World from Canada to Argentina, with a center of diversity in Mexico and Central America; tropical and subtropical forests, desert scrub, and disturbed areas, sea level to 3000 m.

Included species (115). – *E. aaron-rossii* A.H. Holmgren & N.H. Holmgren, *E. acerensis* Boiss., *E. adiantoides* Lam., *E. alata* Hook., *E. antisiphilitica* Zucc., *E. arenaria* Kunth, *E. ariensis* Kunth, *E. armourii* Millsp., *E. arteagae* W.R. Buck & Huft, *E. barnesii* (Millsp.) Oudejans, *E. bicolor* Engelm. & A. Gray, *E. bilobata* Engelm., *E. calcicola* Fernald, *E. californica* Benth., *E. caperata* McVaugh, *E. cassythoides* Boiss., *E. ceroderma* I.M. Johnst., *E. chenopodiifolia* Boiss., *E. colletioides* Benth., *E. corollata* L., *E. cotinifolia* L., *E. curtisii* Engelm., *E. cymosa* Poir., *E. defoliata* Urb., *E. delicatula* Boiss., *E. dioscoreoides* Boiss., *E. discoidalis* Chapm., *E. du-gandiana* Croizat, *E. dwyeri* D.G. Burch, *E. eglandulosa* V.W. Steinm., *E. ellipsifolia* Gilli, *E. ephedromorpha* Bartlett ex B.L. Rob. & Bartlett, *E. equisetiformis* A. Stewart, *E. estevessii* N. Zimm. & P.J. Braun, *E. exserta* (Small) Coker, *E. francoana* Boiss., *E. fraseri* Boiss., *E. fulgens* Karw. ex Klotzsch, *E. gentryi* V.W. Steinm. & T.F. Daniel, *E. gradyi* V.W. Steinm. & Ram.-Roa, *E. graminea* Jacq., *E. guadalajarana* S. Watson, *E. guatemalensis* Standl. & Steyer., *E. guiengola* W.R. Buck & Huft, *E. gumaroi* J. Meyrán, *E. haematantha* Boiss., *E. henricksonii* M.C. Johnst., *E. hexagona* Nutt. ex Spreng., *E. hexagonoides* S. Watson, *E. hindsiana* Benth., *E. hintonii* L.C. Wheeler, *E. humayensis* Brandegee, *E. innocua* L.C. Wheeler, *E. insulana* Vell., *E. ipecacuanhae* L., *E. ixtlana* Huft, *E. jablonskii* V.W. Steinm., *E. lagunensis* Huft, *E. lancifolia* Schltdl., *E. leucocephala* Lotsy, *E. lottiae* V.W. Steinm., *E. luciismithii* B.L. Rob. & Greenm., *E. macropodoides* B.L. Rob. & Greenm., *E. macropus* (Klotzsch & Garcke) Boiss., *E. macvaughii* Carvajal & Lomeli, *E. marginata* Pursh, *E. mercurialina* Michx., *E. mexiae* Standl., *E. misella* S. Watson, *E. misera* Benth., *E. monantha* C. Wright ex Boiss., *E. montereyana* Millsp., *E. multiseta* Benth., *E. muscicola* Fernald, *E. nayarensis* V.W. Steinm., *E. nephradenia* Barneby, *E. oaxacana* B.L. Rob. & Greenm., *E. ocymoides* L., *E. oerstediana* (Klotzsch & Garcke) Boiss., *E. oppositifolia* McVaugh, *E. petiolaris* Sims, *E. poeppigii* (Klotzsch & Garcke) Boiss., *E. polyphylla* Engelm. ex Holz., *E. pubentissima* Michx., *E. rossiana* Pax, *E. rzadowskii* McVaugh, *E. saccharata* Boiss., *E. scandens* Kunth, *E. schlechtendalii* Boiss., *E. sciadophila* Boiss., *E. scotatum* Schltdl., *E. segoviensis* (Klotzsch & Garcke) Boiss., *E. sinaloensis* Brandegee, *E. sonora* Rose, *E. soobyi* McVaugh, *E. sphaerorhiza* Benth., *E. spruceana* Boiss., *E. strictior* Holz., *E. subpeltata* S. Watson, *E. subreniformis* S. Watson, *E. subtrifoliata* Rusby, *E. succedanea* L.C. Wheeler, *E. surinamensis* Lanj., *E. tresmariae* (Millsp.) Standl., *E. tricolor* Greenm., *E. umbrosa* Bertero ex Spreng., *E. verapazensis* Standl. & Steyer., *E. violacea* Greenm., *E. viridis* (Klotzsch & Garcke) Boiss., *E. whitei* L.C. Wheeler,

E. wrightii Torr. & A. Gray, *E. xalapensis* Kunth, *E. xanti* Engelm. ex Boiss., *E. xbacensis* Millsp., *E. zieroides* Boiss.

Discussion. – Section *Alectoroctonum* is characterized by tiny, mostly glanduliform stipules, petaloid gland appendages, and usually entire leaves. Schlechtendal (1847) coined the genus name *Alectoroctonum* after the Spanish common name for “rooster killer”, presumably referring to the toxicity of the species he assigned to the group.

Due to limited resolution in our analysis, incongruence among markers, and frequent convergence in morphology, additional markers will be required to better resolve relationships within sect. *Alectoroctonum*. Therefore here we are not proposing any formal subsections, but instead some of the distinct subclades were considered in the discussions.

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Appendix. Specimens used in this study.

Taxon, collector, and collection number (herbarium acronym), collection locality, and GenBank accession numbers for ITS and *ndhF* sequences, respectively. Sequences without collection information were downloaded from GenBank.

Euphorbia aaron-rossii A.H. Holmgren & N.H. Holmgren, AF537396, –; *Euphorbia acanthothamnus* Heldr. & Sart. ex Boiss., *Riina* 1563 (MICH), Greece: Crete, JQ750879, JQ750756; *Euphorbia acerensis* Boiss., *Van Ee* 648 (MICH, SI, US), Argentina: Córdoba, JQ750872, JQ750757; *Euphorbia acuta* Engelm., AF537450, AF538176; *Euphorbia adiantoides* Lam., AF537395, –; *Euphorbia aequoris* N.E. Br. 1, *Becker* 1167 (MICH, PRE, UNIN), South Africa: Western Cape, JQ750873, JQ750758; *Euphorbia aequoris* N.E. Br. 2, *Becker* 1277 (MICH, PRE, UNIN), South Africa: Northern Cape, JQ750874, JQ750759; *Euphorbia agowensis* Hochst. ex Boiss., AF537419, –; *Euphorbia alata* Hook., *Campbell s.n.* (FTG), U.S.A.: cultivated at Fairchild Tropical Botanical Garden, #2009-0138, originally from Jamaica: Cockpit country, JQ750875, JQ750760; *Euphorbia albipollinifera* L.C. Leach, *Marx* 209 (from the field, MA) and *Riina* 1611 (from living collection, MICH), Netherlands: private living collection of R. van Veldhuisen, originally from South Africa: Eastern Cape, JQ750870, JQ750761; *Euphorbia albomarginata* Torr. & A. Gray, *Reina-G.* 2006-389 (MICH), Mexico: Sonora, HQ645221, JQ750762; *Euphorbia angusta* Engelm., *Yang* 41 (MICH), U.S.A.: Texas, HQ645222, JQ750763; *Euphorbia antisiphilitica* Zucc., *Yang* 8 (MICH), U.S.A.: Texas, JQ750876, JQ750764; *Euphorbia apparicana* Rizzini, *Caruzo* 138 (HUEFS), Brazil: Bahia, JQ750877, JQ750765; *Euphorbia arceuthoboides* Boiss., AM040758, –; *Euphorbia ariensis* Kunth, AF537409, –; *Euphorbia artemesia* W.R. Buck & Huft, *Steinmann* 2354 (MICH), Mexico, JQ750878, JQ750766; *Euphorbia barbicollis* P.R.O. Bally, *Horn s.n.* (Arid Lands Nursery), U.S.A.: Cultivated at Arid Lands Nursery, Tucson, Arizona, originally from Somalia, JQ750881, JQ750767; *Euphorbia beharensis* Leandri, *Yang* 188 (MICH), U.S.A.: Cultivated at Fairchild Tropical Botanical Garden, #2006-1173*A, originally from Madagascar, JQ750890, JQ750768; *Euphorbia bemarkhaensis* Rauh & R. Mangelsdorff, AJ508984, –; *Euphorbia bicolor* Engelm. & A. Gray, AF537386, –; *Euphorbia bifurcata* Engelm., AF537434, AF538173; *Euphorbia bilobata* Engelm., *Van Devender* 2007-1036 (MICH), Mexico: Sonora, JQ750882, JQ750769; *Euphorbia brachiata* (E. Mey ex Klotzsch & Garcke) Boiss., *Morawetz* 280 (MICH), South Africa: Western Cape, JQ750883, JQ750770; *Euphorbia breviarticulata* Pax, *Morawetz* 375 (EA, MICH, MO), Kenya, JQ750885, JQ750771; *Euphorbia burmannii* (Klotzsch & Garcke) E. Mey. ex Boiss. 1, *Morawetz* 266 (MICH, NBG), South Africa: Eastern Cape, JQ750884, JQ750772; *Euphorbia burmannii* (Klotzsch & Garcke) E. Mey. ex Boiss. 2, *Becker* 873 (PRE, UNIN), South Africa: Western Cape, JQ750933, JQ750823; *Euphorbia calcicola* Fernald, AF537385, –; *Euphorbia californica* Benth., *Sanchez* 06-050 (MICH), Mexico: Sonora, JQ750892, JQ750773; *Euphorbia caperata* McVaugh, *Steinmann* 5891 (IEB), Mexico, JQ750893, JQ750774; *Euphorbia capitellata* Engelm., *Reina-G.* 2006-539 (MICH), Mexico: Sonora, HQ645237, JQ750775; *Euphorbia cassythoides* Boiss., AF537387, –; *Euphorbia caterviflora* N.E. Br., *Becker* 1126 (MICH, PRE, UNIN), South Africa: Northern Cape, JQ750894, JQ750776; *Euphorbia celastroides* Boiss., *Berry* 7864 (MICH), U.S.A.: cultivated at the Huntington Botanical Gardens, California, originally from U.S.A.: Hawaii, JQ750895, JQ750777; *Euphorbia ceroderma* I.M. Johnston, AF537389, AF538153; *Euphorbia cheirolepis* Fisch. & C.A. Mey. ex Karelín, AF537424, –; *Euphorbia chersina* N.E. Br., *Becker* 903 (PRE, UNIN), South Africa: Northern Cape, JQ750896, JQ750778; *Euphorbia chersonesa* Huft, AF537436, AF538174; *Euphorbia colletioides* Benth., *Reina-G.* 2006-1314 (MICH), Mexico: Sonora, JQ750897, JQ750779; *Euphorbia colorata* Engelm., *Van Devender* 2006-1031 (MICH), Mexico: Sonora, JQ750898, JQ750780; *Euphorbia cornastra* (Dressler) Radcl.-Sm., *Berry* 7840 (MICH), U.S.A.: cultivated at the Ecke Ranch, Encinitas, California, JQ750899, JQ750781; *Euphorbia corollata* L., *Berry* 7764 (MICH), U.S.A.: Indiana, JQ750900, JQ750782; *Euphorbia cotinifolia* L., *Riina* 1587 (VEN), Venezuela: Edo Vargas, JQ750901, JQ750783; *Euphorbia crossandena* Pax & K. Hoffm., *Giulietti* 2417 (HUEFS), Brazil: Bahia, JQ750902, –; *Euphorbia crotonoides* subsp. *crotonoides* Boiss., *Morawetz* 456 (DSM, K, MICH, MO, NHT), Tanzania: Rukwa Region, JQ750871, JQ750784; *Euphorbia cuphosperma* (Engelm.) Boiss., *Yang* 44 (MICH, IEB), Mexico: Guanajuato, JQ750903, JQ750785; *Euphorbia cyathophora* Murray, *Yang* 129 (MICH), U.S.A.: Florida, JQ750904, JQ750786; *Euphorbia cymosa* Poir., *Van Ee* 761 (MICH), Jamaica: St. Andrew, JQ750905, JQ750787; *Euphorbia delicatula* Boiss., AF537393, AF538152; *Euphorbia denisii* Oudejans, *Dorsey* 184 (MICH, TAN, MO), Madagascar: Toliara, –, JQ750788; *Euphorbia dentata* Michx., *Van Ee* 627 (MICH, SI, US), Argentina: Córdoba, JQ750906, JQ750789; *Euphorbia dioscoreoides* subsp. *attenuata* V.W. Steinm., *Reina-G.* 2006-562 (MICH), Mexico: Sonora, JQ750907, JQ750790; *Euphorbia eglandulosa* V.W. Steinm., AF537394, –; *Euphorbia einensis* G. Will., *Becker* 911 (PRE, UNIN), South Africa: Northern Cape, JQ750908, JQ750791; *Euphorbia ephedroides* E. Mey. ex Boiss., *Becker* 908 (PRE, UNIN), South Africa: Northern Cape, JQ750909, JQ750792; *Euphorbia equisetiformis* A. Stewart, AF537388, –; *Euphorbia eriantha* Benth., AF537440, AF538167; *Euphorbia espinosa* Pax, AF537416, AF538190; *Euphorbia exilis* L.C. Leach 1, AM040767, –; *Euphorbia exilis* L.C. Leach 2, *Becker* 894 (PRE, UNIN), South Africa: Northern Cape, JQ750913, JQ750798; *Euphorbia exstipulata* Engelm., *Reina-G.* 2006-674 (MICH), Mexico: Sonora, JQ750910, JQ750793; *Euphorbia flaviana* Carneiro-Torres & Cordeiro, AF537457, –; *Euphorbia florida* Engelm., *Reina-G.* 2006-476 (MICH), Mexico: Sonora, HQ645268, JQ750794; *Euphorbia francoana* Boiss., *Steinmann* 2083 (MICH), Mexico: Michoacán, JQ750911, JQ750795; *Euphorbia fulgens* Karw. ex Klotzsch, AF537404, AF538154; *Euphorbia gentilis* N.E. Br., *Becker* 1188 (MICH, PRE, UNIN), South Africa: Western Cape, JQ750912, JQ750796; *Euphorbia gentryi* V.W. Steinm. & T.F. Daniel, AF537406, –; *Euphorbia giessii* L.C. Leach, *Becker* 1366 (WIND, MICH, PRE, UNIN), Namibia: Erongo, –, JQ750797; *Euphorbia glanduligera* Pax, AF537426, AF538178; *Euphorbia goetzei* Pax, AF537413, AF538185; *Euphorbia goyazensis* Boiss., *Caruzo* 139 (HUEFS), Brazil: Bahia, JQ750914, JQ750799; *Euphorbia gradyi* V.W. Steinm. & Ram.-Roa, AF537407, AF538151; *Euphorbia graminea* Jacq. 1, *Berry* 7843 (MICH), U.S.A.: cultivated at the Ecke Ranch, Encinitas, California, JQ750915, JQ750800; *Euphorbia graminea* Jacq. 2, *Christenhusz* 3297 (MICH), Jamaica, JQ750945, JQ750801; *Euphorbia guadalajara* S. Watson, *Carrillo-Reyes* 5902 (IEB), Mexico: Jalisco, JQ750916, JQ750802; *Euphorbia guatemalensis* Standl. & Steyererm., AF537408, –; *Euphorbia gueinzii* Boiss., *Hobson* 2141 (PRE), Swaziland, JQ750917, JQ750803; *Euphorbia guerichiana* Pax, *Becker* 929 (PRE, UNIN), South Africa: Northern Cape, JQ750918, JQ750804; *Euphorbia guingola* W.R. Buck & Huft, *Berry* 7753 (MICH), U.S.A.: cultivated at the green house of UC-Davis, California, #B76.047, JQ750919, JQ750805; *Euphorbia gumaroi* J. Meyrán, *Steinmann* 5813 (MICH, IEB), Mexico: Hidalgo, JQ750920, JQ750806; *Euphorbia gymnoclada* Boiss., *Caruzo* 130 (HUEFS), Brazil: Bahia, JQ750921, JQ750807; *Euphorbia gymnonota* Boiss., *Yang* 185 (MICH), U.S.A.: Cultivated, JQ750886, JQ750808; *Euphorbia hainanensis* Croizat, *Gilbert* 501 (MO, K), China: Hainan, JQ750922, –; *Euphorbia helioscopia* L., *Riina* 1607 (MICH), Spain: Castilla y León, JQ750880, JQ750809; *Euphorbia herrei* A.C. White, R.A. Dyer & B. Sloane, *Becker* 937 (PRE, UNIN), South Africa: Northern Cape, JQ750923, JQ750810; *Euphorbia heterophylla* L., *Riina* 1596 (VEN), Venezuela: Barinas, JQ750924, JQ750811; *Euphorbia hexagona* Nutt. ex Spreng., *Clark* 1793 (COLO), U.S.A.: Colorado, JQ750925, JQ750812; *Euphorbia hindsiana* Benth., *Steinmann* 6438 (IEB, MICH), Mexico: Baja California Sur, JQ750926, JQ750813; *Euphorbia hinkleyorum* I.M. Johnston, *Carrillo-Reyes* 5963 (CORD), Argentina: Jujuy, JQ750887, JQ750814; *Euphorbia hirta* L., *Reina-G.* 2006-470 (MICH), Mexico: Sonora, HQ645278, JQ750815; *Euphorbia hormorrhiza* Radcl.-Sm., AF537431, AF538165; *Euphorbia humayensis* Brandegee, *Steinmann* 1153 (MICH), Mexico: Sinaloa, JQ750927, JQ750816; *Euphorbia humifusa* Willd., *Schuhwerk* 06/511 (MICH), Germany: Oberpfalz, JQ750928, JQ750817;

Appendix. Continued.

Euphorbia hyssopifolia L., *Van Devender 2006-463* (MICH), Mexico: Sonora, HQ645283, JQ750818; *Euphorbia innocua* L.C. Wheeler, AF537380, AF538161; *Euphorbia insulana* Vell., *Riina 1586* (VEN), Venezuela: Dtto. Federal, JQ750930, JQ750819; *Euphorbia ipecacuanhae* L., AF537397, –; *Euphorbia ixtlana* Huft., *Carrillo-Reyes 5555* (IEB, MICH), Mexico: Oaxaca, JQ750931, JQ750820; *Euphorbia jaliscensis* B.L. Rob. & Greenm., AF537442, AF538166; *Euphorbia juttiae* Dinter 1, AF537418, AF538188; *Euphorbia juttiae* Dinter 2, *Becker 1402* (WIND, MICH, PRE, UNIN), Namibia: Karas, JQ750932, JQ750821; *Euphorbia kabridarensis* Thulin, *Thulin 11585* (UPS), Ethiopia: Somali National Regional State, –, JQ750822; *Euphorbia lacera* Boiss., AF537441, –; *Euphorbia lagunensis* Huft., AF537379, –; *Euphorbia leistneri* R.H. Archer, *Morawetz 303* (MICH), South Africa, JQ750934, JQ750824; *Euphorbia leucocephala* Lott., *Yang 125* (MICH), U.S.A.: Florida, JQ750935, JQ750825; *Euphorbia lumbricalis* L.C. Leach, AM040779, –; *Euphorbia lycioides* Boiss., *Farias Castro 2030* (EAC), Brazil: Piauí, JQ750936, JQ750826; *Euphorbia macropodoides* B.L. Rob. & Greenm., *Anderson 4840* (MICH), Mexico: Oaxaca, JQ750937, JQ750827; *Euphorbia macropus* (Klotzsch & Garcke) Boiss., *Van Devender 2006-1033* (MICH), Mexico: Sonora, JQ750938, JQ750828; *Euphorbia maculata* L., *Schuhwerk 6/598* (M), JQ750939, JQ750829; *Euphorbia macvaughii* Carvajal & Lomeli, AF537382, –; *Euphorbia marginata* Pursh, AJ534787, AJ534788, EU022037; *Euphorbia mexiae* Standl., *Carrillo-Reyes 5800* (MICH), Mexico: Jalisco, JQ750942, JQ750831; *Euphorbia misella* S. Watson, AF537384, AF538160; *Euphorbia misera* Benth., AF537383, EU022036; *Euphorbia mundii* N.E. Br., *Becker 1147* (MICH, PRE, UNIN), South Africa: Western Cape, JQ750943, JQ750832; *Euphorbia oaxacana* B.L. Rob. & Greenm., AF537373, –; *Euphorbia ocymioidea* L., *Van Devender 2007-1346* (MICH), Mexico, JQ750944, JQ750833; *Euphorbia oerstediana* Klotzsch & Garcke Boiss., –, AF538159; *Euphorbia parvicaruncula* D.C. Hassall, AJ534809+AJ534810, –; *Euphorbia pediculifera* Engelm., *Reina-G. 2006-483* (MICH), Mexico: Sonora, JQ750946, JQ750834; *Euphorbia pentadactyla* Griseb., AF537428, –; *Euphorbia pervilleana* Baill., *Dorsey 188* (MICH, TAN, MO), Madagascar: Toliara, JQ750888, JQ750835; *Euphorbia petiolata* Banks & Sol., AF537422, AF538180; *Euphorbia phosphorea* Mart., *Caruzo 145* (HUEFS), Brazil: Bahia, JQ750889, JQ750836; *Euphorbia phylloclada* Boiss., AF537427, AF538179; *Euphorbia pinetorum* (Small) G.L. Webster, *Yang 168* (MICH), U.S.A.: Florida, JQ750947, JQ750837; *Euphorbia pirottae* N. Terrac., AF537417, AF538186; *Euphorbia plagiantha* Drake, *Dorsey 164* (MICH, TAN, MO), Madagascar: Toliara, –, JQ750838; *Euphorbia planiticola* D.C. Hassall, *Gillespie 7324* (MICH), Australia: New South Wales, –, JQ750839; *Euphorbia platyclada* Rauh, AF537421, AF538187; *Euphorbia poeppigii* (Klotzsch & Garcke) Boiss., AJ534793+AJ534794, –; *Euphorbia polyantha* Pax, –, EU022107; *Euphorbia polygonifolia* L., *Berry 7765* (MICH), Canada: Ontario, JQ750948, JQ750840; *Euphorbia polyphylla* Engelm. ex Holz., *Yang 0158* (MICH), U.S.A.: Florida, JQ750949, JQ750841; *Euphorbia pulcherrima* Willd. ex Klotzsch, *Van Devender 2007-1177* (MICH), Mexico, JQ750950, JQ750842; *Euphorbia pumicicola* Huft., AF537437, AF538164; *Euphorbia quaitensis* S. Carter, –, EU022061; *Euphorbia radians* Benth., AF537438, AF538169; *Euphorbia rhombifolia* Boiss. 1, AF537414, AF538183; *Euphorbia rhombifolia* Boiss. 2, *Becker 864* (PRE, UNIN), South Africa: Western Cape, JQ750929, JQ750843; *Euphorbia rhombifolia* Boiss. 3, *Becker 1105* (MICH, PRE, UNIN), South Africa: Eastern Cape, JQ750951, JQ750844; *Euphorbia rossiana* Pax, AF537374, –; *Euphorbia royleana* Boiss., *Berry 7739* (MICH), U.S.A.: Cultivated, JQ750891, JQ750845; *Euphorbia rzadowskii* McVaugh, AF537399, –; *Euphorbia salota* Leandri, *Aubriot 28* (P, MICH), Madagascar: Androy, JQ750952, JQ750846; *Euphorbia sarcodes* Boiss., *Caruzo 141* (HUEFS), Brazil: Bahia, JQ750953, JQ750847; *Euphorbia scandens* Kunth, *Carrillo-Reyes 5146* (IEB, MICH), Mexico: Chiapas, JQ750954, JQ750848; *Euphorbia scatorhiza* S. Carter, AF537420, AF538181; *Euphorbia schlechtendalii* Boiss., *Steinmann 2172* (MICH, IEB), Mexico: Michoacán, JQ750955, JQ750849; *Euphorbia sciadophila* Boiss., *Van Ee 650* (MICH, SI, US), Argentina: Córdoba, JQ750956, JQ750850; *Euphorbia segoviensis* (Klotzsch & Garcke) Boiss., AF537400, –; *Euphorbia sessilifolia* Klotzsch ex Boiss., *Caruzo 133* (HUEFS), Brazil: Bahia, JQ750957, JQ750851; *Euphorbia setiloba* Engelm. ex Torr., *Reina-G. 2006-478* (MICH), Mexico: Sonora, HQ645345, JQ750852; *Euphorbia setosa* (Boiss.) Müll.Arg., *Cordeiro 3025* (SP), Brazil: Minas Gerais, HQ645346, JQ750853; *Euphorbia sinaloensis* Brandegee, AF537401, AF538156; *Euphorbia sonorae* Rose, *Reina-G. 2006-830* (MICH), Mexico: Sonora, JQ750958, JQ750854; *Euphorbia soobyi* McVaugh, *Carrillo-Reyes 5895* (MICH), Mexico: Jalisco, JQ750959, JQ750855; *Euphorbia* sp. nov. 1, *Ramírez-Amezcu 1428* (MICH, IEB), Mexico: Michoacán, JQ750962, JQ750856; *Euphorbia* sp. nov. 2, *Steinmann 6586* (IEB), Mexico: Michoacán, JQ750960, JQ750857; *Euphorbia* sp. nov. 3, *Van Devender 2006-1030* (MICH), Mexico: Sonora, JQ750961, JQ750858; *Euphorbia* sp. nov. 4, *Linneo 1053* (MO), Bolivia: Santa Cruz, JQ750940, JQ750830; *Euphorbia* sp. nov. 5, *Steinmann 5833* (IEB), Mexico: Querétaro, JQ750970, JQ750869; *Euphorbia spartaria* N.E. Br., *Becker 1370* (WIND, MICH, PRE, UNIN), Namibia: Khomas, –, JQ750859; *Euphorbia sphaerorrhiza* Benth. 1, *Yang 110* (MICH, IEB), Mexico: Michoacán, JQ750963, JQ750860; *Euphorbia sphaerorrhiza* Benth. 2, *Breedlove 63154* (MICH), Mexico: Durango, JQ750941, JQ750861; *Euphorbia spinea* N.E. Br., *Becker 967* (PRE, UNIN), South Africa: Northern Cape, JQ750964, JQ750862; *Euphorbia stapelioides* Boiss., AM040790, –; *Euphorbia strigosa* Hook. & Arn., AF537439, AF538163; *Euphorbia subpeltata* S. Watson, *Ramírez-Amezcu 1129* (IEB), Mexico, JQ750965, JQ750863; *Euphorbia subreniformis* S. Watson, *Van Devender 2006-1003* (MICH), Mexico: Sonora, JQ750966, JQ750864; *Euphorbia succedanea* L.C. Wheeler, AF537403, AF538162; *Euphorbia suffulta* Bruyns, AM040794, –; *Euphorbia tannensis* subsp. *tannensis* Spreng., AF537425, AF538184; *Euphorbia tannensis* subsp. *eremophila* (A. Cunn. ex Hook.) D.C. Hassall, AF537423, –; *Euphorbia thymifolia* L., *Van Devender 2006-628* (MICH), Mexico: Sonora, JQ750967, JQ750865; *Euphorbia tresmariae* (Millsp.) Standl., *Steinmann 1089* (MICH, RSA), Mexico: Jalisco, JQ750968, JQ750866; *Euphorbia whitei* L.C. Wheeler, AF537391, –; *Euphorbia xalapensis* Kunth, *Steinmann 4221* (MICH, IEB), Mexico: Michoacán, –, JQ750867; *Euphorbia xanti* Engelm. ex Boiss., *Yang 0199* (IEB, MICH), Mexico: Baja California Sur, JQ750969, JQ750868; *Euphorbia zonosperma* Müll. Arg., AF537430, –.