

Phylogenetics, morphological evolution, and classification of *Euphorbia* subgenus *Euphorbia*

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Abstract *Euphorbia* subg. *Euphorbia* is the largest and most diverse of four recently recognized subgenera within *Euphorbia* and is distributed across the tropics and subtropics. Relationships within this group have been difficult to discern due mainly to homoplasious morphological characters and inadequate taxon sampling in previous phylogenetic studies. Here we present a phylogenetic analysis of *E.* subg. *Euphorbia*, using one nuclear and two plastid regions, for the most complete sampling of molecular sequence data to date. We assign 661 species to the subgenus and show that it is comprised of four highly supported clades, including a single New World clade and multiple independent lineages on Madagascar. Using this phylogenetic framework we discuss patterns of homoplasy in morphological evolution and general patterns of biogeography. Finally, we present a new sectional classification of *E.* subg. *Euphorbia* comprising 21 sections, nine of them newly described here.

Keywords *Euphorbia* subg. *Euphorbia*; Euphorbiaceae; growth forms; ITS; Madagascar; *matK*; *ndhF*; New World; sectional classification

Supplementary Material The Electronic Supplement (Figs. S1–S3, Appendix S1) and the alignment files are available in the Supplementary Data section of the online version of this article (<http://www.ingentaconnect.com/content/iapt/tax>).

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■ INTRODUCTION

Euphorbia L. is one of the largest recognized genera of flowering plants, with about 2000 species. It has a worldwide distribution but is especially diverse in arid or semi-arid regions of the tropics and subtropics. The morphological diversity in this genus includes geophytes, herbs, shrubs, understory and canopy trees, and an array of succulent and xerophytic forms. Despite this vast vegetative variation, the entire genus is united by a distinctive morphological synapomorphy, the cyathium—a pseudanthial inflorescence that looks superficially like a typical dicot flower (Steinmann & Porter, 2002; Horn & al., 2012). This structure is intermediate between a flower and an inflorescence in developmental terms (Prenner & Rudall, 2007) and is comprised of a cup-like involucre that surrounds multiple male flowers (reduced to single stamens) and a single female flower (reduced to a single pistil). From this basic structure various elaborations have evolved, including colorful subtending bracts, cyathial nectary glands with petaloid appendages,

and fusion or addition of cyathial glands. Some of these cyathial traits represent synapomorphies for particular clades within the genus. Despite the information provided by the cyathium and its variations, relationships among species within *Euphorbia* based on morphological characters have been shown to be equivocal in many cases (Steinmann & Porter, 2002).

Previous phylogenetic work based on DNA sequence data suggests that the evolution of characters in *Euphorbia*, including growth form, photosynthetic systems, and cyathial form are highly homoplasious, and that the genus has a complex biogeographic history leading to its nearly worldwide distribution (Steinmann & Porter, 2002; Haevermans & al., 2004; Bruyns & al., 2006, 2011; Park & Jansen, 2007; Horn & al., 2012; Yang & al., 2012). These evolutionary and biogeographic patterns make *Euphorbia* an ideal system for the study of complex character evolution and adaptation of plants to different environments. Establishing a well-resolved phylogenetic framework for the major clades of the genus is a prerequisite to this research.

Over the past decade, molecular phylogenetic studies have made much progress in understanding the broad-scale relationships within *Euphorbia* (Steinmann & Porter, 2002; Bruyns & al., 2006, 2011; Park & Jansen, 2007; Horn & al., 2012; Yang & al., 2012). Steinmann & Porter (2002) circumscribed *Euphorbia* as the clade including all species with cyathia and furthermore established the presence of four major clades within the genus. Bruyns & al. (2006) formally recognized these four clades as subgenera: *E. subg. Esula* Pers., *E. subg. Rhizanthium* (Boiss.) Wheeler, *E. subg. Chamaesyce* Raf., and *E. subg. Euphorbia*. Peirson & al. (in prep.) have since determined that *E. subg. Athymalus* Neck. ex Reichb. is an earlier valid name for *E. subg. Rhizanthium*. Horn & al. (2012) analyzed ten gene regions from all three plant genomes to firmly establish that *E. subg. Esula* is the first clade to diverge, followed by *E. subg. Athymalus*, which is sister in turn to the clade of *E. subg. Chamaesyce* and *E. subg. Euphorbia*. With the relatively sparse taxon sampling in all previous phylogenetic studies, many species in *Euphorbia* had not been placed to their corresponding subgenus, and relationships within the subgenera are still incompletely resolved. From an evolutionary and taxonomic standpoint, there is a need to develop a comprehensive sectional classification for each of the subgenera. In this study we attempt to resolve these issues in *E. subg. Euphorbia*, which is the largest subgenus in *Euphorbia*.

Euphorbia subg. *Euphorbia* contains over 650 species, and it is the most diverse of the four subgenera in terms of cyathial variation, growth form, and habitat (Horn & al., 2012). Variation in cyathial morphology in this subgenus is particularly high and had been the basis for previously recognizing five segregate genera. These segregates include *E. sect. Monadenium* (including the former genera *Monadenium* Pax + *Synadenium* Boiss. + *Endadenium* L.C. Leach) from eastern tropical Africa, *E. sect. Crepidaria* (represented by the former genus *Pedilanthus* Neck.) from Mexico and the Caribbean, and *E. sect. Cubanthus* (the former genus *Cubanthus* (Boiss.) Millspaugh) from the Caribbean. Each of these groups displays a unique variation on the basic cyathial form. The genus *Elaeophorbia* was also previously segregated based on the possession of fleshy fruits, a rare character state in *Euphorbia*. Species of *E. subg. Euphorbia* include herbs, geophytes, woody shrubs, understory and canopy trees, stem succulents that range from dwarf shrubs to candelabrum trees, and the unusual growth form of pencil-stemmed plants (e.g., *E. decorsei*, Fig. 1F). Woody shrubs and trees occur in both xeric and mesic forests of Madagascar and in the New World tropics. Herbaceous species are found in South America, Africa, and Australia. Geophytes have evolved several times in *E. subg. Euphorbia* and are found in Africa, Madagascar, the Arabian Peninsula, and

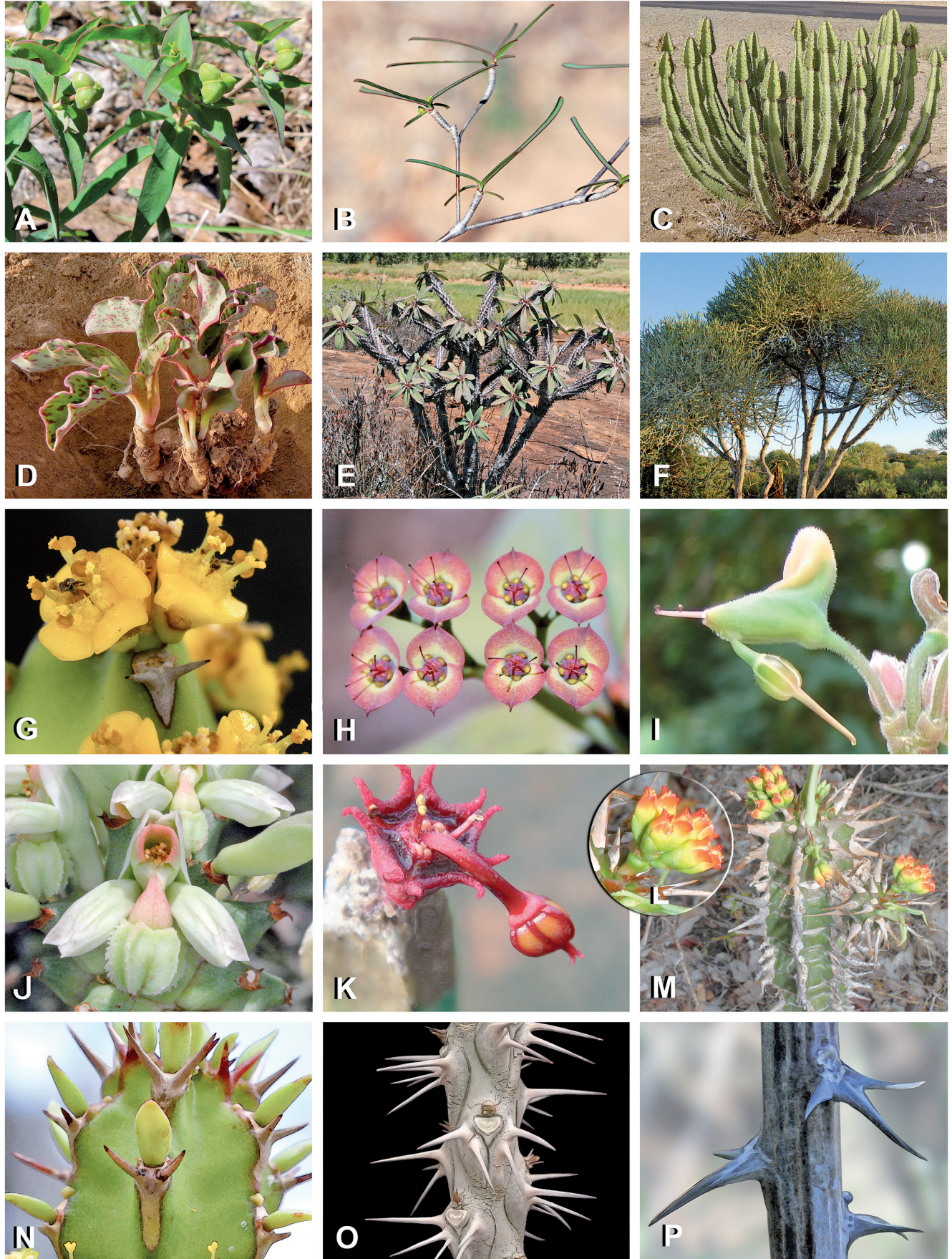
southern Asia. The species of *E. sect. Euphorbia* from Africa and Asia are often compared to the cacti of the New World as a classic example of convergent evolution, and they are the prime representatives of stem succulents in *E. subg. Euphorbia*.

Bruyns & al. (2006) proposed a sectional classification for *E. subg. Euphorbia* based almost entirely on Old World species, but their relatively small taxonomic sampling did not allow for the establishment of a comprehensive phylogenetic hypothesis and classification. Even with an expanded sampling of mostly African and Arabian species from *E. subg. Euphorbia* (Bruyns & al., 2011), important groups from Madagascar and the New World were not well represented in a phylogenetic analysis of *E. subg. Euphorbia*; a much broader sampling of the putative members of *E. subg. Euphorbia* from across the geographic range of the subgenus is required to gain a global understanding of the evolutionary relationships in this complex group.

To date, the relationships and phylogenetic position of the New World species in *E. subg. Euphorbia* have not been suitably resolved (Steinmann & Porter, 2002; Bruyns & al., 2006). The 26 New World species in *E. subg. Euphorbia* included by Zimmerman & al. (2010) formed a grade in their analysis of ITS and *trnL-trnF* chloroplast spacer data, but the eleven species sampled by Horn & al. (2012) for their ten-locus study formed a well-supported clade. The placement of the New World members of *E. subg. Euphorbia* and determining whether they represent a single clade is one of the main aims of this study.

Another key question involves an ecologically and morphologically diverse set of approximately 120 species from Madagascar. In contrast to other well-defined Old World groups, such as *E. sect. Euphorbia* and *E. sect. Monadenium*, the Madagascan species are the least understood group of species in *E. subg. Euphorbia* from a phylogenetic standpoint (Steinmann & Porter, 2002; Haevermans & al., 2004; Bruyns & al., 2006; Park & Jansen, 2007; Zimmermann & al., 2010; Horn & al., 2012). The Madagascan species include, among others, the crown-of-thorns complex (*E. milii* and allies) and coraliform, pencil-stemmed trees such as *E. tirucalli* and *E. alluaudii*. There have been two clades of Madagascan species resolved in all previous phylogenetic studies involving *E. subg. Euphorbia*, but their relationship to each other has not been well resolved. All of the pencil-stemmed species in *Euphorbia* have previously been placed in one group, *E. sect. Tirucalli*, (e.g., Boissier, 1862; Hassall, 1977), but there is ample evidence now that this previous circumscription of *E. sect. Tirucalli* does not represent a monophyletic group (Boissier, 1862; Hassall, 1977; Steinmann & Porter, 2002; Haevermans, 2003; Haevermans & al., 2004; Bruyns & al., 2006; Barres & al., 2011; Horn & al., 2012; Yang & al., 2012). Also, there are

Fig. 1. Examples of morphological diversity in *E. subg. Euphorbia*. **A–F**, Growth forms: **A**, herb, *E. floridana*; **B**, leafy shrub with long- and short-shoots, *E. hedyotoides*; **C**, cactiform succulent, *E. cooperi*; **D**, geophyte, *E. nana*; **E**, spiny, xerophytic shrub, *E. horombensis*; **F**, pencil-stem tree, *E. decorsei*. **G–L**, Cyathial variations: **G**, simple dichasial form of *E. sect. Euphorbia*, *E. inarticulata*; **H**, spreading cyathophylls common in *E. sect. Goniostema*, *E. horombensis*; **I**, zygomorphic cyathium with nectar spur typical of *E. sect. Crepidaria*, *E. calcarata*; **J**, fused glands of *E. sect. Monadenium*, *E. heteropoda*; **K**, horned glands of *E. sect. Brasilienses*, *E. sipolisii*; **L**, cyathophylls forming a pseudofloral tube typical of several members of *E. sect. Goniostema*, *E. viguieri*. **M–P**, Spine structures: **M**, comb-like stipular spines in *E. sect. Goniostema*, *E. viguieri*; **N**, spine-shields in *E. sect. Euphorbia*, *E. zoutpansbergensis*; **O**, stipular spines in *E. sect. Goniostema*, *E. milii*; **P**, spines of *E. neospinescens*, *E. sect. Monadenium*. — Photo credits: A: K. Gulletge, Atlas of Florida Vascular Plants (<http://www.florida.plantatlas.usf.edu/>); D: S. Dutta; I: P. Carillo-Reyes; L, M: B. van Ee; O: F. Vincentz (www.euphorbia.de).



a number of poorly studied leafy species, such as *E. pervilleana* from Madagascar, which have been placed in *E.* sect. *Tirucalli* by Bruyns & al. (2006), but are likely part of a separate clade (Haevermans & Labat, 2004). Because the position of these species within *E.* subg. *Euphorbia* has not been congruent among previous studies, we still do not know if the Madagascan species form a single clade or represent two or more independent radiations on the island.

As part of the worldwide *Euphorbia* Planetary Biodiversity Inventory (PBI; www.euphorbiaceae.org) project, the goals of the present study are to: (1) produce a robust phylogenetic hypothesis of the relationships of all major groups in *E.* subg. *Euphorbia* based on a thorough taxonomic and geographic sampling and utilizing multiple regions of DNA sequence data, (2) establish the phylogenetic position of as many members of *E.* subg. *Euphorbia* as possible, and (3) create a sectional classification system for the subgenus. We plan to use this phylogenetic framework to address the outstanding phylogenetic questions within *E.* subg. *Euphorbia*, as mentioned above. In particular, we aim to determine if the New World species form a monophyletic group and to resolve the relationships of the Madagascan species.

■ MATERIALS AND METHODS

Taxonomic sampling. — A total of 317 accessions representing 226 species of *Euphorbia* were analyzed in this study, including ten outgroup species representing the three other subgenera within the genus. Taxa were selected to obtain a broad and thorough sampling of putative members of *E.* subg. *Euphorbia* across its geographic range based on previous molecular phylogenetic studies and the collective knowledge of the collaborators within the *Euphorbia* PBI project. Material for DNA extraction was collected by the authors and by additional PBI collaborators from live plants in the field or in living collections, as well as from herbarium collections. Live tissue was preserved in silica gel prior to extraction. Vouchers of wild specimens were collected as whole or partial plants and deposited at MICH and/or local herbaria (see Electr. Suppl.: Appendix S1). Greenhouse specimens were documented with digital photographs because destructive sampling was discouraged by collection owners. In this case, photo voucher specimens were made using a set of printed photographs from each sampled specimen and deposited at MICH.

DNA extraction, amplification, and sequencing. — Total genomic DNA was extracted using the DNeasy Plant Mini Kit (Qiagen Inc., Valencia, California, U.S.A.) following the manufacturer's instructions with slight modification for herbarium material. DNA was diluted 10 to 50 times to reduce inhibition of PCR enzymes by secondary compounds. Primer pairs were chosen for this study based on their previous utility in phylogenetic studies of *Euphorbia* or preliminary tests for polymerase chain reaction (PCR) amplification specificity, phylogenetic information content, and absence of long polyA/T regions that may interrupt sequencing reactions (Steinmann & Porter, 2002; Haevermans & al., 2004; Bruyns & al., 2006; Steinmann & al., 2007). The final regions chosen were the cpDNA coding region

matK including the partial *trnK* intron, the cpDNA coding region *ndhF*, and the internal transcribed spacer region of the nuclear ribosomal DNA (ITS). All PCR reactions from genomic DNA were carried out using Ex Taq taq-polymerase and buffer (Takara Bio Inc., Otsu, Shiga, Japan).

The *ndhF* gene was PCR-amplified in two pieces: the 5' half was amplified using primers 536F and 1318R (Olmstead & Sweere, 1994), and the 3' half using primers 972F (Olmstead & Sweere, 1994) and 2110Ri (Steinmann & Porter, 2002). The 15 μ L PCR mixture contained 1.5 μ L 10 \times Ex Taq Buffer, 1.2 μ L dNTP (2.5 mM), 0.4–0.6 μ L of each primer (10 μ M), 0.075 μ L of 5 units/ μ L Ex Taq, 2–2.5 μ L of diluted template DNA and the remainder of ddH₂O. The PCR protocol consisted of an initial denaturing step of 95°C for 2 min followed by 35 cycles of denaturing at 95°C for 45 s, annealing at 53.8°C for 45 s, extension at 65°C for 3 min and then a final extension step at 65°C for 5 min (modified from Shaw & al., 2005). The *matK* region was amplified using the primers *trnK*570F and *matK*1710R (Samuel & al., 2005). The 15 μ L PCR mixture contained 1.5 μ L 10 \times Ex Taq Buffer, 1.2 μ L dNTP (2.5 mM), 0.5 μ L of each primer (10 μ M), 0.12 μ L of 5 units/ μ L Ex Taq, 2 μ L of diluted template DNA and the remainder of ddH₂O. The PCR protocol consisted of an initial denaturing step of 95°C for 2 min followed by 35 cycles of denaturing at 95°C for 45 s, annealing at 57°C for 45 s, extension at 65°C for 5 min and then a final extension step at 65°C for 10 min (modified from Shaw & al., 2005). The ITS region was amplified using the primers ITS-I (Urbatsch & al., 2000) and ITS4 (White & al., 1990). The 15 μ L PCR mixture contained 1.5 μ L 10 \times Ex Taq Buffer, 1.2 μ L dNTP (2.5 mM), 0.5 μ L of 5M Betaine solution (Sigma-Aldrich, Inc., St. Louis, Missouri, U.S.A.), 0.5 μ L of each primer (10 μ M), 0.12 μ L of 5 units/ μ L Ex Taq, 2 μ L of diluted template DNA and the remainder of ddH₂O. A touchdown PCR protocol was used for the ITS region with an initial denaturing step at 95°C for 2 min and a final extension at 72°C for 15 min. The intervening 35 cycles each had a 2 min denaturing step of 30 s at 95°C and an extension step of 45 s at 72°C. The annealing temperature was decreased from 60°C to 50°C as follows: 1 cycle at 60°C, 2 cycles at 59°C, 3 cycles at 58°C, 4 cycles at 57°C, 5 cycles at 55°C, 6 cycles at 52°C, and 14 cycles at 50°C.

All PCR products were examined by gel electrophoresis on 1% agarose gels. Specific PCR products were purified using ExoSap-IT (USB Corporation, Cleveland, Ohio, U.S.A.). For weak PCR products, or products with primer dimers, the QIAquick PCR Purification Kit was used. All PCR products were sequenced at the University of Michigan DNA Sequencing Core. ITS and *ndhF* PCR products were sequenced using the amplification primers. To maximize bidirectional reads for the entire length of the *matK* region, the *matK*80F primer (Samuel & al., 2005) and three custom primers (*matK*688R [5'-CRA GAT GRA TGG GRT AMG G-3'], *matK*1850R [CGT CCT CTA TAT AAC TTG CGC G], *matK*1387F [CAG TAG GAC ATC CTA TTA GTA AAC CG]) were used in addition to amplification primers for sequencing.

DNA sequence alignment and models of evolution. — All ABI chromatograms from sequencing were edited and assembled using the Staden software package (v.2.0; Staden,

1996). All sequences are deposited in GenBank, and species names, vouchers, and GenBank accession numbers are given in Appendix S1 (Electr. Suppl.). Sequences of each region were aligned using the MUSCLE web server at <http://www.ebi.ac.uk/Tools/msa/muscle> (Edgar, 2004) and adjusted manually using the program BioEdit v.7.1.3 (Hall, 1999) to maximize the similarity among sequences in the relatively few regions in which MUSCLE unnecessarily created multiple gaps when fewer gaps could be inferred (Simmons, 2004). Some regions of the partial *trnK* intron flanking the *matK* gene were difficult to unambiguously align and were excluded from the alignment. In total, seven data matrices were assembled. For the maximum likelihood (ML) analyses all accessions were included to produce matrices for each of the individual regions, the cpDNA regions concatenated, and all regions concatenated (*matK*, *ndhF*, ITS, cpDNA, and 3-gene matrices, respectively). A reduced taxon set that minimized missing data was used to construct concatenated matrices of the cpDNA (cpDNA-min) and of all regions (3-gene-min) for the Bayesian analyses (see below). Indels were coded as binary characters for the *matK* and the *ndhF* regions using the simple coding method of Simmons & Ochoterena (2000) as implemented in the program SeqState v.1.4.1 (Müller, 2005, 2006). ITS indels were not coded because many were part of ambiguously aligned sections that were more common and spread out in the ITS matrix than in the chloroplast datasets. The best-fitting model of sequence evolution for each of the three individual matrices was selected using Modeltest v.3.07 (Posada & Crandall, 1998), employing the Akaike information criterion (AIC). Modeltest chose the GTR+I+ γ model of nucleotide substitution for all regions and concatenated datasets except *matK*, for which the TVR+I+ γ model was chosen. However, because MrBayes does not allow this model to be specified, and to avoid potential parameter interactions by modeling among-site rate variation with two parameters (RAxML manual, v.7.0.4), we used the GTR+ γ model for all analyses.

Phylogenetic inference. — Separate data partitions were defined for each gene region and character type (DNA or indel), and for codon position within the *ndhF* region. In the alignment of the *matK* region, which includes the *trnK* intron and many more gaps across the entire matrix, we were unable to identify a reliable open reading frame across sequences. We therefore decided not to treat codon positions as separate partitions in the analysis. Maximum likelihood estimation (MLE) of phylogeny and model parameters was performed using the program RAxML v.7.2.8 (Stamatakis, 2006). Where applicable, all model parameters except for branch lengths were estimated separately for each partition. Branch lengths were estimated as the average across partitions. Matrices were analyzed using the rapid bootstrap (1000 pseudoreplicates) plus thorough MLE search option [-f a]. Bayesian inference (BI) of phylogeny and model parameters was performed on the cpDNA-min and 3-gene-min matrices using MrBayes v.3.2.1 (Huelsenbeck & Ronquist, 2001; Ronquist & Huelsenbeck, 2003). Six independent MCMC runs of four chains each were run for 14.8×10^7 generations sampling every 10^4 generations. Stationarity and convergence of the MCMC runs was assessed

using the programs Tracer v.1.5 (Rambaut & Drummond, 2007) and online version of AWTY (<http://ceb.csit.fsu.edu/awty>, Wilgenbusch & al., 2004). Preliminary analyses were used to determine the appropriate parameters for the MCMC runs with the following results. To achieve swap frequencies of 20% to 60% between adjacent heated chains, the temperature parameter was set to 0.02. To prevent unrealistically long tree length estimates, the mean of the prior distribution of tree lengths was adjusted as suggested by Marshall (2010) to a final value of 250 [brlenspr = unconstrained: exponential (250)]. Reduced taxa matrices were used because original matrices failed to converge on a single posterior distribution of tree and model parameters. Recent studies have found that Bayesian analyses can be biased by missing data, potentially due to improper branch length estimation (Marshall & al., 2006; Lemmon & al., 2009; Marshall, 2010). These matrices contained approximately 30% missing data due to variation in sequencing success for regions among taxa. In preliminary analyses of both the cpDNA matrix and the 3-gene matrix, each with all taxa included, multiple independent runs appeared to converge on a particular log likelihood (LnL) and tree length (TL) distribution while other runs converged on a markedly different distribution of each parameter. In these cases a higher mean LnL was consistently associated with a lower mean TL. When the proportion of missing data in the matrices was reduced to approximately 10% (including gaps) by removing most taxa without all three regions sequenced, much better performance of the MCMC chains was achieved in terms of chain swap frequencies, mixing of chains, and convergence of all parameters.

Assessment of clade membership. — Morphological and geographic distribution data were compiled from herbarium collections, live collections, field observations, and the literature for all species included in our molecular datasets as well as any that were previously classified as closely related to these species or suspected to belong in *E.* subg. *Euphorbia*. These data were used to determine whether *Euphorbia* species not sampled for molecular sequence datasets belong to *E.* subg. *Euphorbia* and to assign these species to clades within the subgenus.

■ RESULTS

Individual datasets. — Summary statistics for each dataset are given in Table 1. The *matK* data provided the greatest information across all levels of the subgenus, while *ndhF* was less informative, although it did provide support for major clades. The ITS data supported some major clades but provided little resolution regarding relationships among them, and was most informative for closely related groups (Electr. Suppl.: Fig. S1). The ML analyses of the individual *ndhF* and *matK* datasets resulted in trees with some topological incongruence but no instances of well-supported conflict (trees not shown), so these were concatenated for the cpDNA analyses. We found eight instances of topological incongruence between the ITS phylogeny and the concatenated cpDNA phylogeny (Electr. Suppl.: Figs. S1, S2) where both of the alternate topologies had bootstrap support (BS) over 80%. One of these involved the sister

Table 1. Summary statistics of datasets used for phylogenetic inference. cpDNA dataset consisted of concatenated *matK* and *ndhF* sequences and indel data. 3-gene dataset consisted of concatenated cpDNA and ITS sequences.

	<i>matK</i>	<i>ndhF</i>	ITS	cpDNA	3-gene
Number of accessions	177	162	281	232	314
Aligned sequence length	2115	1435	689	3550	4239
Variable DNA sites (%)	810 (39)	545 (38)	456 (66)	–	–
Indels coded	99	38	–	137	137

relationship of two species in *E.* sect. *Monadenium* and the other six the placement of species within *E.* sect. *Euphorbia*. Both of these sections are well-supported clades in all analyses. Notable among these incongruences, however, is the placement of *E. abdelkuri* and *E. lacei*. In the ITS tree, *E. abdelkuri* is sister to the rest of *E.* sect. *Euphorbia* and *E. lacei* is the next to diverge, while in the cpDNA tree these species are nested within the section close to a group of Indian species that includes *E. antiquorum* and *E. lactea*. Given that the few instances of conflict were within a single strongly supported clade, all datasets were concatenated for the 3-gene analysis.

Phylogenetic results. — Figure 2 shows the ML tree from the 3-gene dataset. This phylogeny is largely congruent with the cpDNA and ITS trees; the few exceptions are noted below (Fig. 2; Electr. Suppl.: Figs. S1, S2). The ML tree includes the most complete taxon sampling of *E.* subg. *Euphorbia*, so we chose to use this tree as the best estimate of the phylogeny. All datasets recovered a monophyletic *E.* subg. *Euphorbia* consisting of four major lineages (Fig. 2; Electr. Suppl.: Figs. S1–S3). These clades can be distinguished by their geographic distributions and we refer to them as the Pacific clade, the New World clade, Old World clade I, and Old World clade II (Fig. 2). Support for each of the major lineages is high (BS > 99%, posterior probability [PP] > 0.95) from all datasets, with the exception of the ITS support for the New World clade and Old World clade II (BS 28% and 79%, respectively); however, the relationships among these clades are not well-supported (Fig. 2; Electr. Suppl.: Figs. S1–S3). One species from Madagascar in our sampling, *E. mandravioky*, which represents *E.* sect. *Pachysanthae*, a newly defined section in *E.* subg. *Euphorbia*, is not well supported as part of any of the four major clades by any dataset. It is sister to Old World clade I in the cpDNA (BS 78%) and 3-gene trees (BS < 50%) and sister to Old World clade II in the ITS tree (BS 54%; Fig. 2; Electr. Suppl.: Figs. S1, S2). The position of *E. mandravioky* as sister to Old World clade I has the highest BS and makes the most sense geographically given that Old World clade I is mainly a Madagascan clade.

Two additional topological incongruences exist between the ITS, cpDNA and 3-gene trees. First, *E. abdelkuri* and *E. lacei* are strongly supported as sister to the rest of *E.* sect. *Euphorbia* in the 3-gene tree (BS 93%) or moderately supported as successive sister lineages in the ITS tree (BS 81%). In contrast, their nested position in the cpDNA tree is well-supported (BS 100%), and the relationships at the base of *E.* sect. *Euphorbia* lack strong support. Second, the position of *E.* sect. *Rubellae*, from northeast Africa, is incongruent between the concatenated

datasets. In the 3-gene tree, *E.* sect. *Rubellae* is sister to the rest of Old World clade II with BS 68%. In the cpDNA tree this section is nested within Old World clade II (BS 82%) and sister to the clade of *E.* sect. *Monadenium* and *E.* sect. *Euphorbia* (BS 77%). We note that while we chose the 3-gene tree to represent our best estimate of the phylogeny of *E.* subg. *Euphorbia*, the cpDNA data resolve the relationships within Old World clade II with higher support. However, because the *matK* matrix did not include *E.* sect. *Rubellae*, its position in the cpDNA tree is determined by the *ndhF* data only.

Among the MrBayes runs that had converged on the same posterior probability distribution, we discarded those that likely had not converged on the same distribution of trees, based on their substantially different support for individual clades (determined with the AWTY Compare analysis). However, for each dataset there were two runs from which the AWTY Compare plots of posterior probabilities for clades were very close to the unity line, indicating that they had converged on the same distribution of trees. These runs were used to determine support for clades. The Cumulative analyses in AWTY for both the cpDNA-min and 3-gene-min datasets indicated that runs that had likely converged reached stationarity by generation 1.2×10^7 . All prior trees were discarded as burn-in. Although the difference in taxon sampling among inference methods does not allow for detailed comparisons between the Bayesian and ML trees, the topology of the 50% majority-rule consensus tree from the Bayesian analysis was generally congruent with the ML tree (e.g., the same major clades were recovered). The posterior probabilities of major clades and sections in *E.* subg. *Euphorbia* are summarized in Fig. S3 (Electr. Suppl.).

Taxonomic results. — The phylogenetic hypothesis presented here along with a review of morphological and geographic distribution data allowed us to assign 661 species to *E.* subg. *Euphorbia* and place all of these species to sections. These sections are indicated on Fig. 2 and are detailed below in the taxonomic treatment, where we newly define or significantly recircumscribe 11 sections, resulting in a total of 21 sections within *E.* subg. *Euphorbia*. The new sections are concentrated in the New World and Madagascar clades.

■ DISCUSSION

With our greatly increased sampling effort, we confirmed the results of several previous studies, which found that *Euphorbia* subg. *Euphorbia* is a strongly supported mono-

phyletic group (Steinmann & Porter, 2002; Bruyns & al., 2006; Zimmermann & al., 2010; Horn & al., 2012). Our analyses also show that the subgenus is comprised of four strongly supported clades: the New World clade, the Pacific clade (*E. sect. Pacificae*), Old World clade I, and Old World clade II, although the relationships among them are not well-supported (Fig. 2). The lack of resolution along the backbone of the subgenus in this and all previous studies, and the very short branch lengths at this level of the tree (data not shown), suggest that the lack of

resolution is not an artifact of marker choice but rather a “true” signal, which may be the result of a rapid radiation early in the evolutionary history of the subgenus. In addition, by comparing our results with those of Horn & al. (2012), we do not see an improvement of the support values in this part of the phylogeny through an increase in taxon sampling. Below we discuss significant morphological characters within each major clade and then discuss general patterns of morphological evolution within the subgenus.

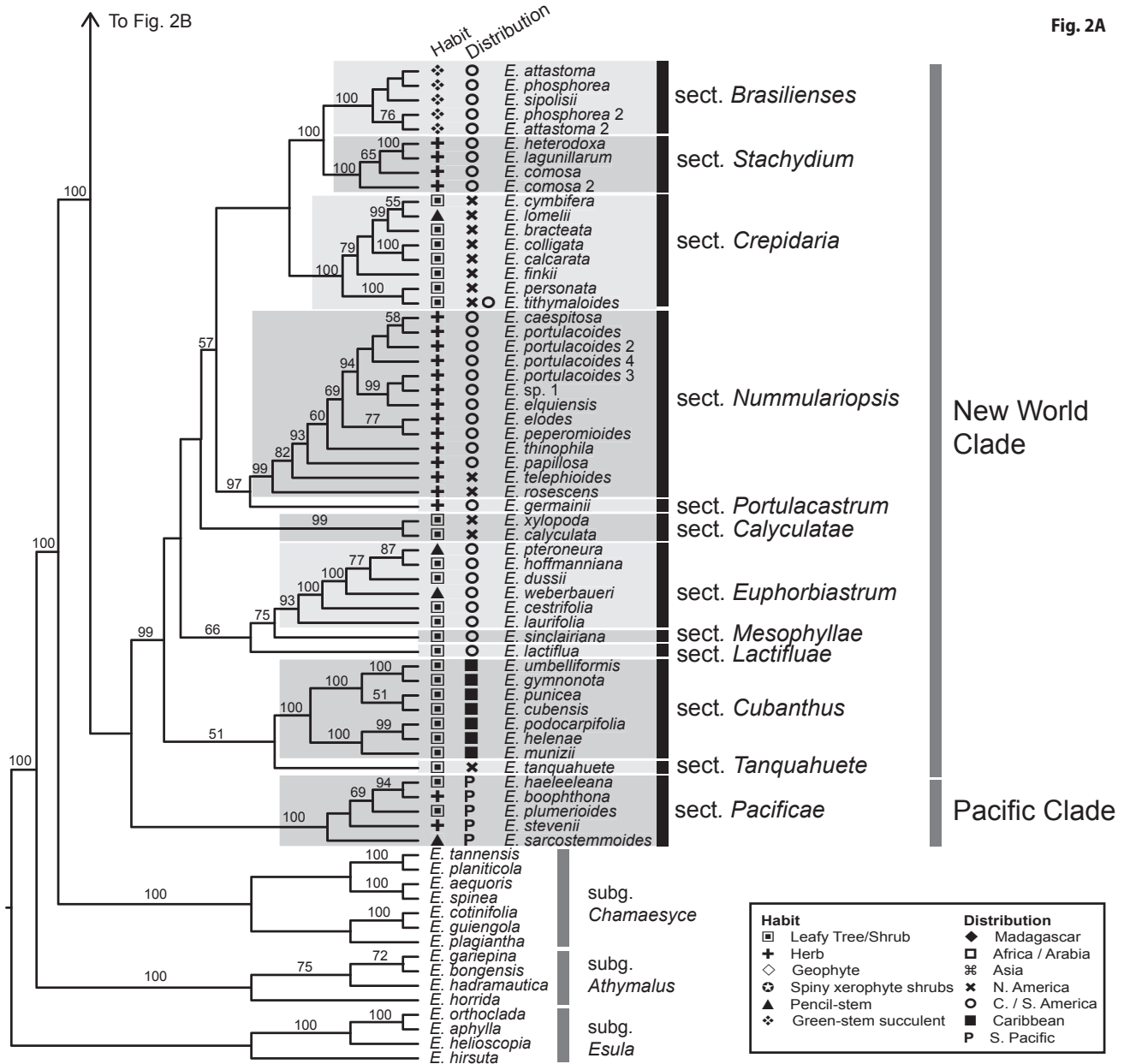
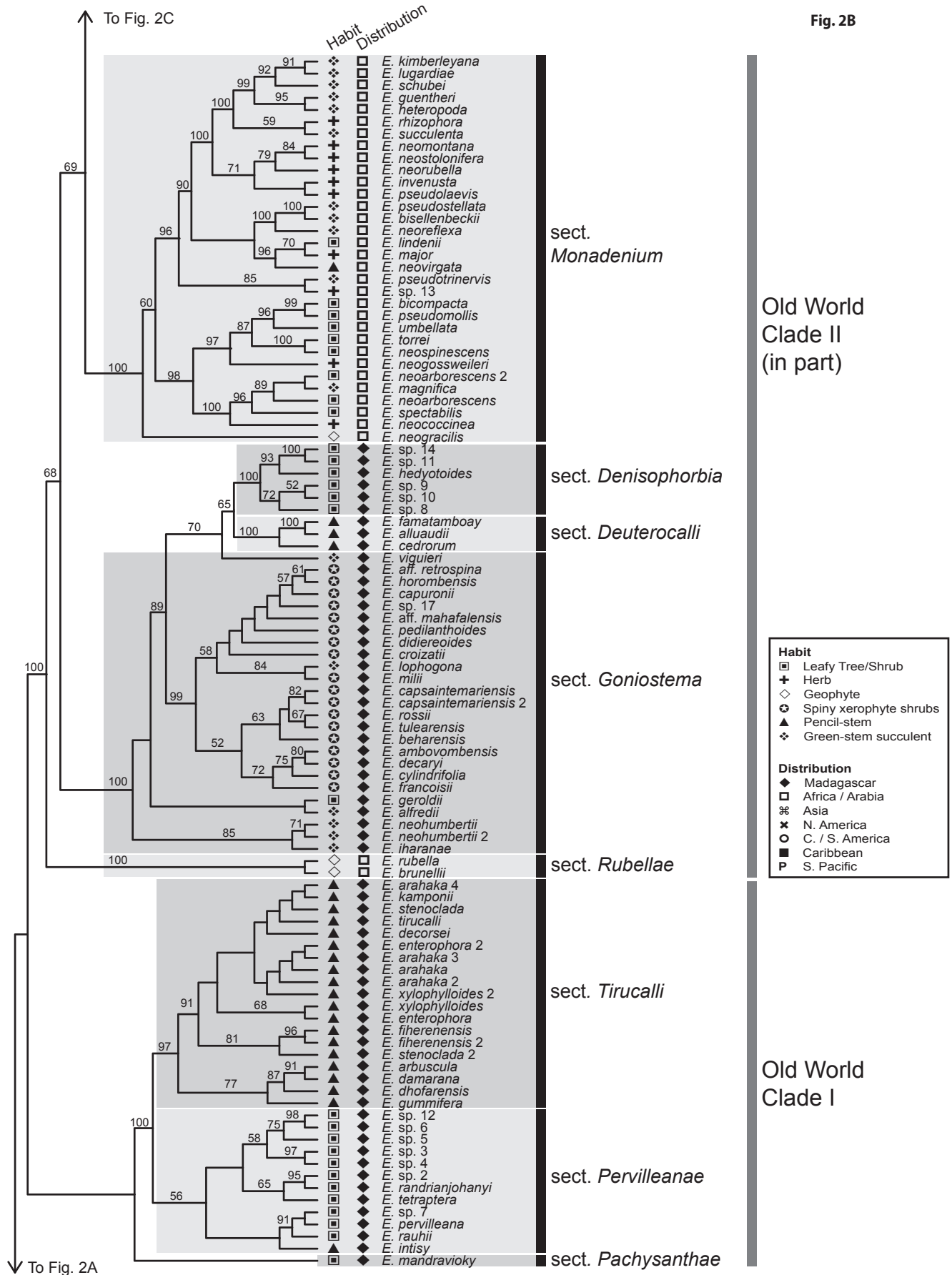
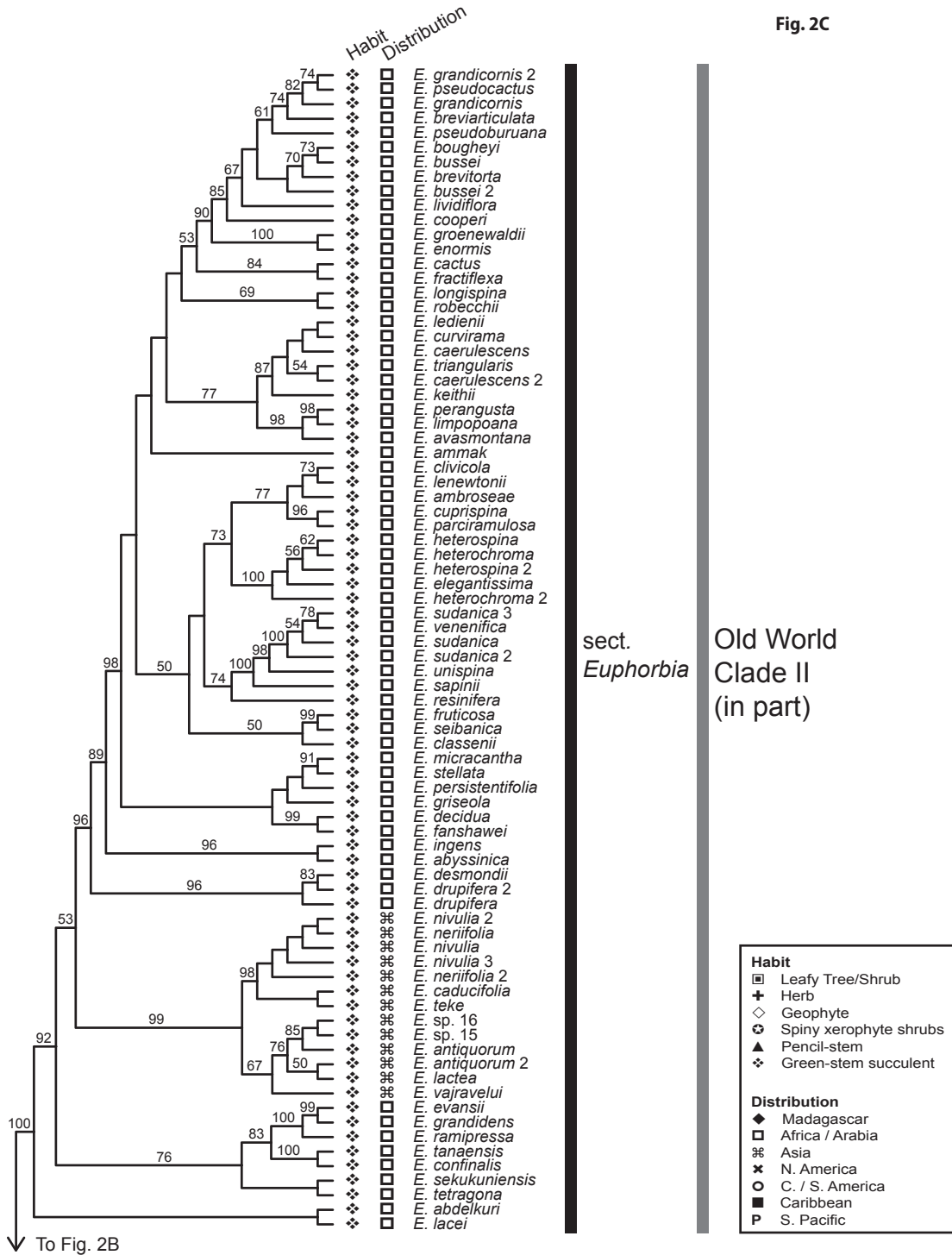


Fig. 2A–C. Maximum-likelihood estimate of the phylogenetic relationships of *E. subg. Euphorbia* based on the combined matrix of ITS, *ndhF*, and *matK* sequences. For clarity, multiple accessions from species shown to be exclusive lineages are excluded from the tree. Bootstrap support for clades >50% is given above branches. Habit (left column) and distribution (right column) are indicated to the left of the taxa—see inset for symbol definitions. Sections circumscribed in this study are indicated by shading and are named to the right of the taxa; the four major clades within *E. subg. Euphorbia* are indicated to the right of the sectional classification. **A**, Outgroups and New World clade; **B**, Pacific clade, Old World clade I and Old World clade II (in part); **C**, Old World clade II (in part).



New World clade. — All species from the New World shown here to belong to *E.* subg. *Euphorbia* are included in a single clade that is highly supported in all but the ITS analysis (Fig. 2; Electr. Suppl.: Figs. S1–S3). The geographic distribution of species in *E.* subg. *Euphorbia* (Fig. 2) suggests that there has been a split between New World and Old World clades early in the history of *E.* subg. *Euphorbia*, although confidence in this interpretation is limited by the low support for the relationships among the Old World clades and the uncertain position

of *E.* sect. *Pachysanthae*. New World species have been placed in *E.* subg. *Euphorbia* in previous studies (Steinmann & Porter, 2002; Bruyns & al., 2006; Zimmermann & al., 2010), but our sampling and sequence data are the first to show the extent of the New World lineage and to demonstrate its monophyly. The New World clade consists of 11 highly supported clades or single species which we treat here as sections. They range in size from a single species in *E.* sect. *Lactifluae* to 36 species in *E.* sect. *Nummulariopsis*. The branches that connect



the New World sections are very short relative to those that subtend each of them, and accordingly there is poor resolution of the sectional relationships within the New World clade. As with the backbone of the subgenus, this pattern is the same as that found by Horn & al. (2012) in their species-poor but marker-intensive phylogeny; thus this pattern is not likely to be an artifact of taxon sampling or marker choice, but rather a reflection of the history of this group. The New World clade is where our results differ most from previous work. Five of the eleven sections that we recognize here have been previously described and remain largely unchanged in our circumscription, but the remaining six are new sections or are significant recircumscriptions of previously named groups reflecting our phylogenetic results.

A notable section we recognize among the New World species is *E. sect. Euphorbiastrum*, which is circumscribed here as an unusually diverse group of species in terms of their growth forms. At the base of this clade are two species, *E. laurifolia* and *E. cestrifolia*, which are both small trees that occur in open, dry scrubland in the northern to central Andes. The next diverging species is *E. weberbaueri*, which is very different from the previous two in being a semi-succulent pencil-stem shrub growing in cactus-scrub vegetation of Peru and Ecuador. This is followed by *E. dussii*, which is a rare shrub from moist forests of Martinique and St. Lucia in the Lesser Antilles. Steinmann & al. (2007) hypothesized that *E. dussii* was part of *E. sect. Cubanthus*, but our data place it instead well nested within *E. sect. Euphorbiastrum*. This indicates that *E. dussii* and *E. sect. Cubanthus* represent two separate introductions of *E. subg. Euphorbia* into the West Indies. *Euphorbia pteroneura* is another semi-succulent species in this clade, with green stems resembling those of *E. weberbaueri*, but it is an herb from southern Mexico with fully developed, drought-deciduous leaves. Sister to *E. pteroneura* is *E. hoffmanniana*, a large shrub from Costa Rica. Despite the heterogeneous morphology of these species, their monophyly is highly supported by our molecular sequence data (BS 93%; Fig. 2A). The relationship of this clade to other species in the New World clade, however, has very little support. This section is a fine-scale example of the lability of growth form evolution in *Euphorbia* and of the potential this group holds for studying the drivers of such evolutionary patterns.

***Euphorbia* sect. *Pacifica* (= Pacific clade).** — This clade was originally recovered by Steinmann and Porter (Steinmann & Porter, 2002), although they only included three species. Based on our results (Fig. 2A) as well as previous treatments (Hassall, 1977; Forster, 1994), *E. sect. Pacifica* consists of twelve species. Nine of these species form a complex related to *E. plumerioides*, and are all shrubs to small trees that grow in highland forests or coastal headlands in the southwestern Pacific area, New Guinea, and tropical Australia. Three other subtropical Australian species are included in *E. sect. Pacifica*, namely *E. boophthona*, *E. stevenii* (both herbs), and *E. sarcostemmoides* (a pencil-stem shrub). Zimmermann & al. (2010) included two accessions of *E. boophthona* in their analysis, one from Steinmann & Porter (2002) and another from their own collection. Their collection was placed in *E. subg. Chamaesyce*,

while the Steinmann collection was placed in *E. sect. Pacifica*. Our own third accession is strongly supported as part of *E. sect. Pacifica* and thus confirms the results of Steinmann & Porter (2002) and Horn & al. (2012). This species is distinct from all other members of *E. sect. Pacifica* in having four cyathial glands and seeds with a pronounced caruncle, while the rest of the species have five glands and ecarunculate seeds. The cpDNA and 3-gene datasets resolve *E. sect. Pacifica* as sister to the New World clade, but the ITS data place it sister to Old World clade I. Both relationships have poor BS ($\leq 55\%$), but the clade itself is highly supported in all analyses regardless of taxon sampling or sequence data used (BS 100%, PP > 95; Fig. 2; Electr. Suppl.: Figs. S1–S3). *Euphorbia* sect. *Pacifica* has a unique geographic distribution within *Euphorbia* (Fig. 2), occurring mainly in Papua New Guinea and Australia but also on islands of Malesia, the Philippines, Melanesia, and Hawaii.

Old World clade I. — The third major clade recovered in our study, which we refer to as Old World clade I, is distributed mainly across Madagascar, but with several species in Africa and the Arabian Peninsula. In the 3-gene and cpDNA analyses (Fig. 2B; Electr. Suppl.: Fig. S2), this clade is sister to the remaining Old World species, although in the ITS tree it is sister to the Pacific clade (Electr. Suppl.: Fig. S1). Neither of these placements is strongly supported, but the geographical distribution of Old World clade I supports the results of our combined analyses (Fig. 2B). The exclusion of this group, with high support (BS 100%), from the rest of the Madagascan species (mostly placed in Old World clade II) suggests that there have been at least two, and possibly three, independent introductions to Madagascar within *E. subg. Euphorbia*.

Old World clade I contains several growth forms and a diversity of cyathium and fruit characters, but it can be distinguished from other clades by the prevalence of dioecy in most species. This reproductive system has not been conclusively documented in all species, but it appears to be a morphological synapomorphy for the clade. We recognize two sections in Old World clade I, the newly described *E. sect. Pervilleanae* and the substantially recircumscribed *E. sect. Tirucalli*. *Euphorbia* sect. *Tirucalli*, as circumscribed here, includes only pencil-stemmed species that have photosynthetic, semi-succulent branches that are typically long relative to their diameter and usually bear rudimentary, caducous leaves (Fig. 1F) (Horn & al., 2012). This growth form is exemplified by *E. tirucalli*, the milkbush tree, which is commonly planted in the tropics but is likely native to southern Africa or Madagascar. *Euphorbia tirucalli* has been the basis for a group at various ranks that has included all or most of the pencil-stemmed species in *Euphorbia*. Previous work has shown that this was an artificial grouping and that the pencil-stemmed habit has evolved independently multiple times, and in each subgenus of *Euphorbia* (Steinmann & Porter, 2002). The true relatives of *E. tirucalli* are a group of 23 species occurring mostly in Madagascar, but with several species in Africa and the Arabian Peninsula (Fig. 2). The various groups of pencil-stemmed species in *Euphorbia* are often difficult to distinguish morphologically. In contrast, the species of *E. sect. Tirucalli* are well-characterized as dioecious shrubs or trees, with alternate branches that can appear

whorled, conspicuous pubescence (especially on the ovaries), female flowers with calyx lobes, and carunculate seeds. This combination of characters can usually serve to tell all species of *E. sect. Tirucalli* from pencil-stemmed species belonging to other clades.

Old World clade II. — The remaining Old World species in *E. subg. Euphorbia* comprise Old World clade II, which is divided into four sections. The size of these sections varies from over 350 species in *E. sect. Euphorbia* to three species in *E. sect. Rubellae*. Species in Old World clade II are distributed in Africa, Asia, and Madagascar, with the majority occurring in warm, arid climates. Spines of various form, but generally considered of stipular origin (White & al., 1941), are quite common in this clade, as are succulent stems (Fig. 1C, G, M–P). Growth forms also vary greatly among the sections of Old World clade II and include geophytes, pencil-stemmed shrubs and trees, leafy shrubs and trees, spiny xerophytic shrubs, and various kinds of stem succulents (Figs. 1B–E, M, 2B, C).

Support for Old World clade II and for each of the four subclades is high (BS 100%, PP 1.0). However, only the cpDNA analysis resolved the relationships among the subclades with good support (BS > 80%; Electr. Suppl.: Fig. S2). Several nodes differ between the ITS tree and the cpDNA tree (though with low BS from ITS), and these are likely the cause of the low BS support in the 3-gene tree. First, *E. sect. Rubellae* is inferred as sister to the rest of Old World clade II in the ITS tree (Electr. Suppl.: Fig. S1), but as sister to *E. sect. Monadenium* + *E. sect. Euphorbia* in the cpDNA tree (Electr. Suppl.: Fig. S2). Second, the sister clade of *E. sect. Euphorbia* is the clade of sections *Denisophorbia*, *Deuterocalli*, and *Goniostema* in the ITS tree, but it is *E. sect. Monadenium* in the cpDNA tree. Horn & al. (2012), who compiled the largest dataset in terms of sequence data, found the same sister relationship for *E. sect. Euphorbia* as in our 3-gene tree (Fig. 2). However, they did not include *E. sect. Rubellae*, so we cannot make comparisons about the overall topology of Old World clade II. For simplicity, we discuss the groups within Old World clade II referring to the topology in Fig. 2.

Euphorbia sect. Rubellae, represented by *E. rubella* and *E. brunellii*, is a group of three species from northeastern Africa and is the only clade in *E. subg. Euphorbia* comprised entirely of geophytic species. Aside from their habit, the most distinctive feature of this group is the 4+2 arrangement of the cyathial glands: four oblong-elliptic glands of equal size and two smaller, orbicular ones that are apparently derived from splitting of the original fifth gland (Gilbert, 1987). These species were formerly included in *E. subg. Lacanthis* (= *E. sect. Goniostema*), but Haevermans & al. (2004) showed that the species of *E. sect. Rubellae* are not part of *E. sect. Goniostema*, which is now an entirely Madagascan group. Our results support their hypothesis of relationships.

Following *E. sect. Rubellae* in Old World clade II is a highly supported clade (BS 100%) consisting of three sections endemic to Madagascar: *E. sect. Goniostema*, *E. sect. Denisophorbia*, and *E. sect. Deuterocalli* (Fig. 2B). In our ITS analysis, these sections form monophyletic groups with 100% BS for *E. sect. Denisophorbia* and sect. *Deuterocalli*, and low support (BS

56%) for *E. sect. Goniostema* (Electr. Suppl.: Fig. S1), but the plastid data does not resolve the relationships of these three groups well (Electr. Suppl.: Fig. S2). Consequently, *E. sect. Goniostema* forms a grade in the 3-gene analysis, although the other two sections are monophyletic and still have 100% BS (Fig. 2B). The grade pattern of *E. sect. Goniostema* in the 3-gene analysis (Fig. 2B) is due to the placement of several species (*E. iharanae*, *E. neohumbertii*, *E. alfredii*, *E. geroldii*, *E. francosii* and *E. viguieri*) outside the core of *E. sect. Goniostema* in the analysis of the plastid dataset (Electr. Suppl.: Fig. S2). Horn & al. (2012) included *E. iharanae* and *E. neohumbertii* in their analysis and also found these two species to form a clade outside the core of *E. sect. Goniostema*. *Euphorbia iharanae* and *E. neohumbertii* represent a group of species from northern Madagascar that share the well-developed, colorful cyathophylls of the rest of *E. sect. Goniostema*. Several species in this northern group are unarmed trees or small shrubs from the rainforest of northeastern Madagascar (e.g., *E. geroldii*), while others are succulent shrubs or monocauls that occur in dry habitats of northern Madagascar. The latter group has bristly spines (e.g., *E. viguieri*, *E. iharanae*) or small glandular combs (e.g., *E. alfredii*) in vertical rows along the stem (Fig. 1M). Some are also distinguished by erect cyathophylls that envelop the cyathia and resemble a floral tube (Fig. 1L). These species have previously been placed in *E. sect. Goniostema* based on morphology and distribution, and despite their placement outside the core of the section in our concatenated analyses, they are part of a monophyletic *E. sect. Goniostema* in our ITS tree (Electr. Suppl.: Fig. S1). Moreover, analyses by Aubriot (2012) of two nuclear and six chloroplast regions, with comprehensive sampling of *E. sect. Deuterocalli*, sect. *Denisophorbia*, and sect. *Goniostema*, produce a well-resolved phylogeny that supports the monophyly of the three sections in Old World clade II and firmly places these species within *E. sect. Goniostema*.

One of the most morphologically distinct groups within Old World clade II is *E. sect. Monadenium*, which is distributed across eastern, central, and southern Africa. This is a highly supported clade (BS 100%, Fig. 2B) of about 90 species that are easily recognized morphologically by the fusion of the cyathial glands into a horseshoe-shaped rim, or less commonly into a complete ring. This unique cyathial morphology was the reason this group was formerly segregated from *Euphorbia*, but our results and those from previous studies have confirmed that this section is well nested within *E. subg. Euphorbia* (Steinmann & Porter, 2002; Bruyns & al., 2006; Zimmermann & al., 2010; Horn & al., 2012). Species of *E. sect. Monadenium* are particularly diverse in terms of growth form and include geophytes, succulent and non-succulent shrubs, as well as trees, vines, and one pencil-stem species (Fig. 2B).

The largest clade in *E. subg. Euphorbia* and perhaps the best known is *E. sect. Euphorbia*—the “spine-shield” euphorbias (Fig. 1C, D, G, N). This group is a well-defined clade of over 340 species distributed mostly in Africa but also across southern and southeast Asia and into Indonesia. The defining character for this clade is the spine-shield—a horny pad of tissue subtending or surrounding each leaf base that typically bears two or four spiny outgrowths (Fig. 1G, N). These

outgrowths are usually interpreted as a pair of stipular spines and a pair of prickles (Carter, 1994). The vast majority of species in *E. sect. Euphorbia* have spine-shields, but they have been lost in a few species, such as *E. abdelkuri* and *E. piscidermis*. Most species in this section are stem succulents that vary in size from prostrate dwarf shrubs to large candelabriform trees, and have angled, winged, or tuberculate stems and minute, caducous leaves. However, there are also geophytes and large trees that have well developed leaves. Several geophytic species from India, including *E. fusiformis*, *E. nana* (Fig. 1D), and *E. meenae*, are now known to belong to *E. sect. Euphorbia*. There are no obvious characters placing them in *E. sect. Euphorbia* because they lack above-ground stems. However, DNA sequence data from previous studies confirm that they are indeed part of this section (Steinmann & Porter, 2002; Bruyns & al., 2006; Zimmermann & al., 2010).

Growth form evolution. — *Euphorbia* subg. *Euphorbia* contains the full range of growth form diversity that is present within the genus (Figs. 1A–F, 2). Moreover, our phylogenetic results confirm the conclusion of Horn & al. (2012) that specialized growth forms have evolved independently, and repeatedly, within the subgenus. Horn & al. (2012) inferred the common ancestor of *E. subg. Euphorbia* to be a shrub or tree with alternate leaves and terminal cyathia. This growth form (exclusive of the cyathial position) is mostly retained in *E. sect. Pachysanthae*, sect. *Pervilleanae*, and sect. *Denisophoria* in Madagascar, as well as in most sections of the New World clade. The herbaceous habit has evolved four times in *E. subg. Euphorbia*: in the clade of *E. sect. Portulacastrum* + *E. sect. Nummulariopsis*, in *E. pteroneura* of *E. sect. Euphorbiastrum*, in *E. sect. Monadenium*, and in several members of *E. sect. Pacificae*. Geophytic species are present in all sections of Old World clade II and comprise the entire *E. sect. Rubellae*. The one geophyte from *E. sect. Monadenium* in our study, *E. neogracilis*, is sister to the rest of the section in our cpDNA and 3-gene analyses. The geophytes in *E. sect. Goniostema* and *E. sect. Euphorbia* have been shown to be well nested within those clades. The phylogenetic position of these geophytic species suggests that geophytes have evolved independently multiple times in Old World clade II (Haevermans & al., 2004; Zimmermann & al., 2010; Bruyns & al., 2011). Similarly, the pencil-stem tree/shrub habit appears to have evolved at least eight times in *E. subg. Euphorbia*: four times in the New World clade, twice in Old World clade I, and twice in Old World clade II (Fig. 2).

Highly succulent, photosynthetic stems are present in *E. sect. Euphorbia* and in *E. sect. Monadenium*. While both of these sections contain a range of growth forms, all but a few species in *E. sect. Euphorbia* have spiny, succulent stems. The exceptions include the geophytes mentioned above, and some leafy trees such as *E. drupifera*. Species range from trees up to 25 m tall, such as *E. cussonioides*, to dwarf shrubs only a few centimeters high, such as *E. decidua*. While most species have minute, caducous leaves, some produce quite large, persistent ones (e.g., *E. neriifolia* and *E. royleana* from India). Because these species are nested well within *E. sect. Euphorbia*, the presence of persistent leaves appears to be a reversal to the ancestral state for the subgenus (Horn & al., 2012). Growth

form evolution in *E. sect. Monadenium* involves changes in habits rather than changes in size. This section contains the entire range of growth forms found in the subgenus, and the stem succulent species make up only a few of the total. While the stems of some species are succulent and green, the loss of functional leaves is much less pronounced in *E. sect. Monadenium*, and most species produce large, succulent leaves.

The switch to stem-based photosynthesis, as has happened in *E. sect. Euphorbia* and in all pencil-stemmed species, putatively involves several steps, including an increase in the stem stomatal density, delaying or abandoning bark initiation, increasing the volume of cortex for water storage, and the development of the Crassulacean Acid Metabolism (CAM) photosynthetic system (Nobel, 1988; Edwards & Donoghue, 2006). Given the frequency with which stem-based photosynthesis has evolved in *E. subg. Euphorbia* (Fig. 2), it seems that these are relatively “easy” evolutionary transitions to make in this group. In Cactaceae, Edwards & Donoghue (2006) showed that *Pereskia* Mill. species, which are the closest relatives to the core cacti, have high water use efficiency and some level of CAM photosynthesis. They suggested that this was preadaptive for the transition to the succulent-stemmed cactus life form. CAM has been inferred in most stem photosynthetic species in *E. subg. Euphorbia*, but the close relatives of the pencil-stem species are all C3 plants (Horn & al., 2011), suggesting that CAM is not a prerequisite for the evolution of highly succulent, photosynthetic stems.

Diversity of cyathial morphology. — While most species in *E. subg. Euphorbia* have relatively unspecialized radially symmetric cyathia (with five, usually yellow glands that lack appendages, and with small, inconspicuous cyathophylls), some of the showiest and morphologically most derived forms of cyathia in the genus are also found within this subgenus (Fig. 1G–L). For example, all species in *E. sect. Monadenium* possess cyathia with nectar glands fused either into a horseshoe shape or a full circle, as well as cyathophylls that are more or less fused dorsally, resulting in bilateral symmetry (Fig. 1J).

Euphorbia sect. Crepidaria contains another striking example of fusion of cyathial parts and a shift to bilateral symmetry (Fig. 1I). In this section, the nectar glands are positioned on one side of the involucre and are enveloped in a spur formed by the fusion of petaloid gland appendages. This is perhaps the greatest deviation from the general form of the open, actinomorphic cyathium that resembles a typical dicot flower (Fig. 1G). This cyathial form in *E. sect. Crepidaria* is often associated with hummingbird pollination (Dressler, 1957) and represents a unique syndrome within *Euphorbia*. Cacho & al. (2010) suggested that the nectar spur was a key innovation that led to a rapid radiation in *E. sect. Crepidaria*. They noted that high morphological divergence relative to the low sequence variation among species suggested a rapid radiation after the evolution of nectar spurs, especially when coupled with the long branch leading to the extant members of the clade (found in our study and Bruyns & al., 2006, 2011; Zimmermann & al., 2010). However, they were unable to find unique support for the key innovation hypothesis except when assuming an outgroup of only one species. Our results do not resolve the sister relationship of *E. sect.*

Crepidaria, but place it most closely to clades that would also be unlikely to support the key innovation hypothesis.

Well-developed cyathophylls occur in *E.* sect. *Goniostema*, and this is a morphological synapomorphy for the clade (Fig. 1H). Most species in *E.* sect. *Goniostema* have cyathophylls that become brightly colored (usually red or yellow) and can be spreading, or in a few species (e.g., *E. neohumbertii*, *E. iharanae*) envelop the cyathium completely, mimicking a pseudofloral tube (Fig. 1L). Effects on pollination are unknown, but the change in shape in these “tubular” cyathia presumably affects the mechanism and/or effort required to access the nectar and could be associated with more specialized pollinators.

■ CONCLUSIONS

This study represents the most taxonomically and geographically comprehensive phylogenetic study of *Euphorbia* subg. *Euphorbia* to date. Sequence data from multiple regions representing the nuclear and plastid genomes allowed us to infer phylogenetic relationships across the subgenus, and they support four major lineages within the subgenus that can be characterized by their distributions. Our results clearly establish the monophyly of all New World species in *E.* subg. *Euphorbia*, define the species composition of the New World clade, and suggest a split between the Old World and New World early in the history of the subgenus. Our phylogeny also supports the hypothesis of at least two independent lineages in Madagascar within *E.* subg. *Euphorbia*. Included in these is *E.* sect. *Tirucalli*, which is circumscribed as the clade of pencil-stemmed species within *E.* subg. *Euphorbia* that includes *E. tirucalli*. Also included in these Madagascan clades are three sections of leafy shrubs and trees (*E.* sect. *Denisophorbia*, *E.* sect. *Pervilleanae*, *E.* sect. *Pachysanthae*) that will require more thorough study to better understand their circumscriptions and the delimitations of species within them.

Consistent with the overall evolutionary lability of growth form in *Euphorbia* as a whole, several of the sections in *E.* subg. *Euphorbia* contain a wide range of growth forms for their small size. The pencil-stem growth form is particularly homoplasious within the subgenus, just as it is across the genus as a whole. Utilizing the phylogenetic framework established in this study, future studies will focus on potential drivers of the evolution of the unusual pencil-stem growth form as well as patterns of geographical and morphological differentiation in the large spine-shield clade, *E.* sect. *Euphorbia*.

■ TAXONOMIC TREATMENT

Altogether, 661 species are recognized in the subgenus. For each section listed below, we provide a list of their component species. Those species appearing in **boldface-italics** have been sampled molecularly in this or in previous studies, whereas those appearing only in *italics* are inferred to belong to the section based on their morphology and distribution. A complete

database of names and synonyms with additional information is available online at the Tolkin website (<http://app.tolkin.org/projects/72/taxa>, Riina & Berry, 2012).

Euphorbia L., Sp. Pl.: 450. 1753 – Type (designated by Millspaugh in Publ. Field Columb. Mus., Bot. Ser. 2: 306. 1909): *Euphorbia antiquorum* L.

Euphorbia L. subg. *Euphorbia* ≡ *Euphorbia* subg. *Tithymalus* Pers., Syn. Pl. 2(1): 10. 1806.

As the largest and most diverse of the four subgenera of *Euphorbia*, *E.* subg. *Euphorbia* is probably the most difficult to characterize morphologically. This clade has the greatest number of succulent and spiny species. *Euphorbia* subg. *Athymalus* also has a significant number of spiny, succulent species, but the spines in that group are generally of peduncular origin, whereas in *E.* subg. *Euphorbia* they are either stem enations or more complex “spine-shields” that may be of stipular origin (Fig. 1M–P) (Carter, 1994). Many of the succulent, spiny species are leafless, but members of both *E.* sect. *Euphorbia* and sect. *Goniostema* can also be both leafy and spiny. There are a number of evergreen or deciduous tree species in *E.* subg. *Euphorbia* in both Madagascar and the New World, and there are several lineages or species that show leafless and spineless pencil-stem habits. There are rather few truly herbaceous species in the subgenus, and a limited number of geophytes occur in at least four Old World clades.

Reproductively, *E.* subg. *Euphorbia* is notable for its wide variations of the cyathium, particularly in gland number, shape, and degree of fusion (Fig. 1G–L). The glands generally lack appendages, but there are several small groups with short horns (Fig. 1K), finely divided rims, or even finger-like processes. The bracts immediately subtending the cyathia, as opposed to the dichasial bracts subtending or along the rays of the synflorescence, are showy and diagnostic in several groups (Fig. 1H, L). In our descriptions below we use the term “cyathophylls” to refer to these subcyathial bracts in all groups. The larger sections have bisexual cyathia, but dioecy is characteristic of some of the smaller sections. Similarly, caruncles are present in some groups, but absent in others.

Although certain sections of *E.* subg. *Euphorbia* can be readily distinguished by their specialized cyathial features (e.g., *E.* sect. *Crepidaria* and *E.* sect. *Monadenium*), many sections have a similar, basic cyathium, and habit types have been shown to be particularly homoplasious in the subgenus. This makes construction of a morphologically based key to the sections problematic; however, since major clades in the subgenus are well circumscribed geographically, the most straightforward approach is to first break the subgenus into these more manageable groups.

Key to the sections of *Euphorbia* subg. *Euphorbia*

1	Old World natives	2
1	New World natives	13
2	Madagascar and Indian Ocean islands	3
2	Other Old World and Pacific areas outside of Madagascar and the Indian Ocean	9

- 3 Stipules spiny, papyraceous or comb-like, more or less branched, diversely colored; cyathia always bisexual; cyathophylls well developed (except *E. boissieri*); seeds verrucose; caruncle absent *E. sect. Goniostema* (17)
- 3 Stipules glandular or punctiform, never spiny or papyraceous; cyathia unisexual or bisexual; cyathophylls developed or reduced; seeds smooth; caruncle present or absent 4
- 4 Plants essentially leafless (leaves very small, soon caducous); young stems succulent and photosynthetic 5
- 4 Plants with well-developed leaves, caducous or persistent; young stems not succulent or photosynthetic 7
- 5 Reduced leaves when present more or less lanceolate; petiole base surrounded by a glandular or waxy ring (possibly of stipular origin, but clearly visible after the leaves have fallen off) *E. sect. Deuterocalli* (18)
- 5 Reduced leaves when present variable in shape, but not lanceolate; stipules extremely reduced, located on each side of the leaf insertion (visible or not after the leaves have fallen off) 6
- 6 Twigs glabrous; synflorescences terminal; female flower without a calyx; capsule 1- or 2-locular; seeds wider than long, ecarunculate .. *E. sect. Pervilleanae* (14) (*E. intisy*)
- 6 Young twigs more or less tomentose; synflorescences subterminal; female flower with a rudimentary calyx; capsule 3-locular; seeds longer than wide, with a well-developed caruncle *E. sect. Tirucalli* (in part) (15)
- 7 Shrubs or trees with sympodial branching, the leaves clustered at nodes connected by slender leafless shoots; cyathia unisexual (rarely bisexual); capsule 3-locular, smooth; seeds cylindrical, smooth ... *E. sect. Denisophorbia* (19)
- 7 Shrubs or trees with monopodial growth, the leaves regularly spaced or else clustered at the twig apex; cyathia bisexual; capsule 1- or 2-locular, ornamented or not; seeds globose, smooth or sculptured 8
- 8 Shrubs or trees with thick coriaceous leaves; cyathium shallowly bowl-shaped, with large stipitate glands (>5 mm wide); fascicles of male flowers sheathed by their bracteoles; capsule erect, apparently largely indehiscent, more or less fleshy, the surface smooth or wrinkled, seeds 1 or 2 *E. sect. Pachysanthae* (13)
- 8 Shrubs or trees with soft and thin leaves; cyathium cup-shaped with sessile glands; male flowers not sheathed by their bracteoles; capsule pendulous, dehiscent, winged or with spiny appendages, seeds usually 2 *E. sect. Pervilleanae* (14)
- 9 Natives of Australia and Pacific Islands including New Guinea *E. sect. Pacificae* (1)
- 9 Natives of Africa, Arabia, and Asia 10
- 10 Plants mostly dioecious, essentially leafless (leaves very small, soon caducous), pencil-stemmed shrubs or trees; young stems succulent and photosynthetic, usually terete, more or less tomentose, spines absent *E. sect. Tirucalli* (in part) (15)
- 10 Plants monoecious geophytes, shrubs, or trees either with well developed, caducous or persistent leaves and non-photosynthetic stems, or else leafless and succulent with photosynthetic stems, but then usually with spine-shields or stipular spines 11
- 11 Geophytes with free cyathophylls and cyathia with 4 similar glands and a fifth one divided into two parts; seeds carunculate; northeast Africa *E. sect. Rubellae* (16)
- 11 Plants varied in habit, but if geophytic then with glands fused into a horseshoe shape and with carunculate seeds, or else with highly reduced cyathophylls, 5 similar glands, and ecarunculate seeds; widespread (Africa, southern/eastern Asia) 12
- 12 Stems spineless or with spines of stipular origin, but no spine-shields; cyathophylls usually (partly) fused on one side; cyathia with one large horseshoe-shaped or circular gland; seeds carunculate *E. sect. Monadenium* (20)
- 12 Stems usually succulent, angled or tuberculate, generally with distinctive spine-shields composed of a horny pad and associated spines; cyathophylls reduced, scale-like; cyathia actinomorphic, with 5 similar glands; seeds ecarunculate *E. sect. Euphorbia* (21)
- 13 Cyathia strongly zygomorphic, the glands hidden in a spur-like extension of the cyathial involucre *E. sect. Crepidaria* (10)
- 13 Cyathia actinomorphic, or if slightly zygomorphic, the glands evident on the surface or edge of the involucre . 14
- 14 Leafless stem-succulent shrubs, stems with 4–6 angles or ridges 15
- 14 Leafy herbs, shrubs, or trees (sometimes deciduous), stems terete or rarely angled 16
- 15 Cyathial glands with two horns; eastern Brazil *E. sect. Brasilienses* (12)
- 15 Cyathial glands without horns; Ecuador and Peru *E. sect. Euphorbiastrum* (6) (*E. weberbaueri*)
- 16 Cyathia arranged in a tight synflorescence with the subtending bracts greenish and successively overlapping each other like shrimp scales *E. sect. Stachydium* (11)
- 16 Cyathia laxer and not subtended by overlapping greenish bracts 17
- 17 Herbs 18
- 17 Shrubs or trees 20
- 18 Annuals, the petioles longer than the blades; cyathia solitary and axillary, the glands each with 3–5 digitate appendages *E. sect. Portulacastrum* (8)
- 18 Perennials, the petioles generally shorter than the blades; cyathia in dichasia or pleiochasia, the glands without appendages or else with two horns 19
- 19 Stems terete; pistillate flowers with evident perianth lobes; southern South America and southeastern United States *E. sect. Nummulariopsis* (9)
- 19 Stems ridged; pistillate flowers without evident perianth lobes; Mexico and Guatemala *E. sect. Euphorbiastrum* (*E. pteroneura*)
- 20 Shrubs to small trees of moist evergreen tropical forests; leaves very large, 25–40 × 5–12 cm, persistent *E. sect. Mesophyllae* (5)
- 20 Shrubs or trees of drier, more subtropical habitats; leaves smaller than above, persistent or deciduous 21
- 21 Densely branched bushes; cyathia subtended by numerous

- (4–6) creamy-yellow, leafy cyathophylls; edge of Atacama Desert in northern Chile *E.* sect. *Lactifluae* (4)
- 21 Laxly branched shrubs or single-trunked trees; cyathia usually subtended by 2 or 3 cyathophylls; from Andean Peru north to Mexico and the Caribbean 22
- 22 Cyathophylls red (green in *E. cubensis*); cyathial glands 1–8, on the rim of the involucre or on its outer wall; Caribbean islands (Bahamas, Hispaniola, Cuba, Jamaica)
..... *E.* sect. *Cubanthus* (3)
- 22 Cyathophylls, when present, whitish or yellowish; cyathial glands 4 or 5, on the rim of the involucre; Mexico to Peru (one species, *E. dussii*, from St. Lucia in the Caribbean)
..... 23
- 23 Shrubs or small trees to ca. 5 m tall; cyathia subtended by greenish or inconspicuous cyathophylls; Costa Rica to Peru and St. Lucia (Caribbean)
..... *E.* sect. *Euphorbiastrum* (6)
- 23 Small to large trees 5–25 m tall; cyathia subtended by 2 or 3 whitish or yellowish cyathophylls; Mexico 24
- 24 Trees to 12 m tall with rugose to furrowed bark; capsule exerted from the involucre, seeds carunculate
..... *E.* sect. *Calyculatae* (7)
- 24 Trees to 25 m tall with coppery, exfoliating bark; capsule included within or barely exerted from the involucre, seeds ecarunculate *E.* sect. *Tanquahuete* (2)

1. *Euphorbia* sect. *Pacificae* Dorsey, **sect. nov.** – Type: *Euphorbia plumerioides* Teijsm. ex Hassk.

Monoecious or dioecious herbs, shrubs, or small trees. Stems woody to fleshy, terete, glabrous. Stem leaves alternate, those on fertile branches opposite in *E. boophthona*, persistent to caducous, thin to fleshy, usually petiolate; stipules absent. Synflorescences subterminal, much-branched dichasia or solitary, axillary cyathia; cyathia pedunculate; glands (4)5(–11), green, ovate-elliptic, with short marginal processes. Capsule (sub)globose; seeds oblong to ovoid (cylindrical in *E. boophthona*), carunculate (*E. boophthona*) or ecarunculate.

Species included (11). – *E. boophthona* C.A. Gardner, *E. brassii* P.I. Forst., *E. buxoides* Radcl.-Sm., *E. haeleleana* Herpst., *E. heyligersiana* P.I. Forst., *E. indistincta* P.I. Forst., *E. kanalensis* Boiss., *E. norfolkiana* Boiss., *E. plumerioides* Teijsm. ex Hassk., *E. sarcostemmoides* J.H. Willis, *E. stevenii* F.M. Bailey.

Distribution and habitat. – Australia, Indonesia, New Guinea, Philippines, and Pacific Islands (Norfolk Island, Fiji, Solomon Islands, Hawaiian Islands); the Australian herbaceous or pencil-stemmed species occur in dry interior or coastal habitats, whereas the remaining species occur in tropical or subtropical moist forests or scrub.

Euphorbia sect. *Pacificae* is a novel grouping that has a unique southern Pacific distribution within *Euphorbia*. It contains the *E. plumerioides* complex (Forster, 1994), a group of eight or nine shrubby species, which is most diverse in New Guinea. Whether *E. euonymoclada* Croizat belongs here or not is uncertain and will require obtaining molecular data and more specimens of this rarely collected species; it differs from the other members of the *E. plumerioides* complex

in its well-developed stipules and single-cyathiate synflorescence. Three quite different-looking species that are endemic to Australia are also included in *E.* sect. *Pacificae*, namely *E. boophthona*, *E. stevenii*, and *E. sarcostemmoides*. The first two are herbs, whereas *E. sarcostemmoides* is a leafless pencil-stemmed shrub. *Euphorbia boophthona* is morphologically anomalous here, since it has four cyathial glands and seeds with a pronounced caruncle. An unusual species belonging to this group is *E. haeleleana*, which is endemic to Kauai and Oahu in the Hawaiian Islands; it is a tree with large, woody fruits and cyathia with up to 11 glands.

2. *Euphorbia* sect. *Tanquahuete* V.W. Steinm. & Dorsey, **sect. nov.** – Type: *Euphorbia tanquahuete* Sessé & Moc.

Trees to 25 m tall, trunk to 50 cm d.b.h. Stems round in cross-section, glabrous to pubescent, bark smooth and exfoliating into thin papery sheets. Leaves spirally arranged, drought-deciduous; stipules glandular, minute, lateral at the base of the petiole; petiole well-defined; blade elliptic, base attenuate, apex acute, obtuse, mucronulate or apiculate, margin entire, glabrous to pubescent, pinnately nerved. Synflorescence axillary, originating from leafless nodes of older stems, rays 3–9, dichasia 1-branched; cyathophylls 2, white to yellow; involucre on a thick peduncle that becomes woody in fruit; glands 5, patelliform, situated on the rim of the involucre, without appendages; gynophore terminating in 3 short triangular calyx-like lobes; ovary glabrous, styles connate at the base, shortly swollen-clavate, apex inconspicuously bifid to lobed. Capsule included within or barely exerted from the involucre, dry or with a slightly fleshy mesocarp; seeds broadly ovoid to subglobose, rounded to slightly quadrangular in cross-section, base and apex rounded, smooth, ecarunculate.

Distribution and habitat. – Central-western to southern Mexico; subtropical deciduous forests in montane canyons and lava flows; near sea level to 2100 m.

Species included (2). – *E. lundelliana* Croizat, *E. tanquahuete* Sessé & Moc.

Euphorbia sect. *Tanquahuete* contains two tree species that are by far the largest members of *Euphorbia* in the New World, and among the largest in the genus. *Euphorbia lundelliana* is poorly known, but is placed here because of its arborescent habit, leaves similar to *E. tanquahuete*, large fruits, and smooth, ecarunculate seeds.

3. *Euphorbia* sect. *Cubanthus* (Boiss.) V.W. Steinm. & P.E.

Berry in *Anales Jard. Bot. Madrid* 64: 123–133. 2007 ≡ *Pedilanthus* sect. *Cubanthus* Boiss. in Candolle, *Prodr.* 15(2): 7. 1862 ≡ *Cubanthus* (Boiss.) Millsp. in *Publ. Field Mus. Nat. Hist., Bot. Ser.* 2: 371. 1913 – Type: *Pedilanthus linearifolius* Griseb. (≡ *Euphorbia scutiformis* V.W. Steinm. & P.E. Berry).

= *Adenorima* Raf., *Fl. Tellur.* 4: 112. 1838 (‘1836’) ≡ *Euphorbia* sect. *Adenorima* (Raf.) G.L. Webster in *J. Arnold Arbor.* 48: 407. 1967 – Type: *Adenorima punicea* (Sw.) Raf. (≡ *Euphorbia punicea* Sw.).

Monoecious shrubs to small trees; stems soft-wooded, somewhat fleshy, terete. Leaves alternate, spirally arranged,

clustered toward branch apices, membranaceous to slightly coriaceous, entire, sessile; stipules minute, glanduliform, caducous or apparently absent. Cyathia in terminal dichasia; cyathophylls generally red; glands 1–8, situated on the rim of the involucre or on its outer wall, green, yellow or reddish, appendages lacking; ovary and fruit smooth, glabrous, usually subtended by a three-lobed, calyx-like structure; seeds ecarunculate.

Euphorbia sect. *Cubanthus* is the only section within *E.* subg. *Euphorbia* with a strictly Caribbean distribution. The cyathial glands are distinctive in *E.* subsect. *Moa* in being usually placed on the outer wall of the involucre (rather than on the rim) and in three species, *E. millspaughii*, *E. scutiformis*, and *E. umbelliformis*, reduced to a single gland.

3a. *Euphorbia* subsect. *Cubanthus* V.W. Steinm. & P.E. Berry in *Anales Jard. Bot. Madrid* 64: 123–133. 2007 – Type: *Pedilanthus linearifolius* Griseb. (\equiv *Euphorbia scutiformis* V.W. Steinm. & P.E. Berry).

Leaves narrowly spatulate, clustered at branch apices, those subtending the cyathia not distinct; cyathophylls red but less intensely so than in *E.* subsect. *Moa* (green in *E. cubensis*); glands usually on the outer wall of the involucre.

Distribution and habitat. – Caribbean (Bahamas, Cuba, Jamaica); scrub forest mostly on limestone, sea level to 500 m.

Species included (6). – *E. cubensis* Boiss., *E. gymnonota* Urb., *E. millspaughii* V.M. Steinm. & P.E. Berry, *E. punicea* Sw., *E. scutiformis* V.W. Steinm. & P.E. Berry, *E. umbelliformis* (Urb. & Ekman) V.W. Steinm. & P.E. Berry.

3b. *Euphorbia* subsect. *Moa* V.W. Steinm. & P.E. Berry in *Anales Jard. Bot. Madrid* 64: 123–133. 2007 – Type: *Euphorbia helenae* Urb.

Leaves elliptic to oval, regularly spaced along stems, those subtending the cyathia bright red and distinct in shape. Cyathophylls showy, red; involucre red; glands yellow, situated on involucre rim; male flowers red except for anthers; female flower red.

Distribution and habitat. – Caribbean (eastern Cuba); scrub and forests on serpentine soils, sea level to 800 m.

Species included (3). – *E. helenae* Urb., *E. munizii* Borhidi, *E. podocarpifolia* Urb.

4. *Euphorbia* sect. *Lactifluae* Dorsey & V.W. Steinm., **sect. nov.** – Type: *Euphorbia lactiflua* Phil.

Xerophytic shrubs, to 2.5 m tall, but mostly 1 m or less, soft-wooded and highly branched, bark grayish to red-brown, not exfoliating, drought deciduous; stems rounded in cross-section; whole plant glabrous. Leaves well developed, spirally arranged, loosely arranged on long shoots or highly congested on short shoots; stipules absent or represented by minute punctiform glands less than 0.1 mm in diameter at the base of the petiole; petiole short and inconspicuous; blade linear to narrowly elliptic, base attenuate, apex acute to apiculate, margin entire, secondary venation not evident. Synflorescences terminal on short lateral shoots, sometimes terminal on main branches; rays 3 or 4, dichasial bracts and cyathophylls showy, numerous (3–6), pale yellow; cyathia 2(3), sessile, glands 5(6),

transversely oblong, situated on the rim of the involucre, without appendages; gynophore terminating in 3 inconspicuous, rounded calyx-like lobes; ovary glabrous, styles united into a short column ca. 1/6 their length, apex emarginate to bifid. Capsule barely exerted from the involucre; seeds plumply obloid, rounded in cross-section, base and apex rounded, smooth, with a conspicuous, hooded caruncle.

Distribution and habitat. – Northern Chile, rocky areas of Atacama Desert from the region of Antofagasta south to the vicinity of Copiapó; nearly sea level to 700 m.

Species included (1). – *E. lactiflua* Phil.

Euphorbia lactiflua is distinctive in its swollen branches and showy, yellowish cyathophylls. Although it was previously treated together with a number of leafless Old World succulents in *E.* sect. *Tirucalli* Boiss. (Boissier, 1862), all molecular phylogenetic analyses show that *E.* sect. *Lactifluae* is an isolated lineage within the New World clade of *E.* subg. *Euphorbia*.

5. *Euphorbia* sect. *Mesophyllae* V.W. Steinm. & Dorsey, **sect. nov.** – Type: *Euphorbia sinclairiana* Benth.

Mesophytic shrubs or small trees to 5 m tall, little-branched, bark not exfoliating. Stems thick and fleshy, rounded in cross-section, glabrous. Leaves large (25–40 × 5–12 cm), obovate to oblanceolate, loosely and spirally arranged, pinnately veined, margin entire; stipules well-developed, lateral at the base of the petiole, ovate to triangular, caducous and leaving a conspicuous calloused pad; petiole distinct, less than 1/10 the length of blade. Synflorescence terminal (sometimes appearing axillary), often long-pedunculate; cyathophylls 2, foliaceous or scale-like and highly reduced; cyathia on short peduncles, glands 5, circular to transversely oblong, situated on the rim of the involucre, without appendages; gynophore terminating in 3 triangular calyx-like lobes; ovary glabrous, styles united into a slender column 4/5 to 5/6 their length, apex emarginate to bifid. Capsule included within or barely exerted from the involucre, deeply 3-lobed, smooth or reticulately ridged; seeds globose to ovoid, rounded in cross-section, base truncate with a circular depression, apex mucronulate, smooth, ecarunculate.

Distribution and habitat. – Mexico (Chiapas), Costa Rica, Nicaragua, Panama, Colombia, Ecuador, Peru, Brazil (Acre), Bolivia; understory of wet, lowland forests but also extending to higher elevations in cloud forest, from near sea level to ca. 800 m.

Species included (1). – *E. sinclairiana* Benth.

Bernal & al. (2006) provided a discussion of the morphological variation within this species and concluded that *Euphorbia elata* is best treated as a synonym of *Euphorbia sinclairiana*. Three other species similar to *E. sinclairiana* have been described (*E. capansa* Ducke, *E. tessmannii* Mansf., *E. valerii* Standl.). We treat them here as a single widespread species that varies in characters such as inflorescence length and persistence of the cyathophylls, but is characterized by the extremely distinctive habit and large, oblanceolate leaves, as well as growing in wet forest understoreys.

6. *Euphorbia* sect. *Euphorbiastrum* (Klotzsch & Garcke) Boiss. in Candolle, *Prodr.* 15(2): 10, 98. 1862 \equiv *Euphorbiastrum*

Klotzsch & Garcke in Monatsber. Königl. Preuss. Akad. Wiss. Berlin 1859: 252. 1860 – Type (see Wheeler in Amer. Midl. Naturalist 30: 467. 1943): *Euphorbiastrum hoffmannianum* Klotzsch & Garcke (≡ *Euphorbia hoffmanniana* (Klotzsch & Garcke) Boiss.).

= *Euphorbiadendron* Millsp. in Publ. Field Columb. Mus., Bot. Ser. 2: 305. 1909 – Type (see Wheeler in Amer. Midl. Naturalist 30: 467. 1943): *Euphorbia laurifolia* Juss.

= *Euphorbia* sect. *Pteroneuræ* A. Berger, Sukkul. Euphorb.: 28. 1906 – Type: *Euphorbia pteroneura* A. Berger.

Herbs, shrubs or small trees; branches woody with bark or else green and succulent (then without leaves or with only rudimentary ones, and stems 4–6-ridged). Leaves oblong to rhombic or scale-like and then caducous, stipules present (glandular and surrounding the leaf scar) or absent. Synflorescences axillary or terminal, subsessile to pedunculate; cyathia subsessile to pedunculate; glands 4 or 5, appendages lacking; cyathophylls minute to longer than cyathium; seeds with a tiny caruncle.

Distribution and habitat. – Northern and central Andes of South America (Venezuela, Colombia, Ecuador, Peru), to southern Mexico and West Indies (Windward Islands); montane scrub and forest edges, lowland moist forests.

Species included (6). – *E. cestrifolia* Kunth, *E. dussii* Krug & Urb. ex Duss, *E. hoffmanniana* (Klotzsch & Garcke) Boiss., *E. laurifolia* Juss. ex Lam., *E. pteroneura* A. Berger, *E. weberbaueri* Mansf.

Multiple states from several morphological characters are present in this section, and the group is not easily characterized morphologically. However, as noted in Steinmann & Porter (2002), several morphological characters support the close relationship of these species, including the carunculate seeds and the well-developed, complex glandular stipules in *E. weberbaueri* and *E. cestrifolia*.

7. *Euphorbia* sect. *Calyculatae* V.W. Steinm & Dorsey, sect. nov. – Type: *Euphorbia calyculata* Kunth.

Trees or shrubs to 12 m tall, trunk to 20 cm d.b.h. Stems round in cross-section, glabrous or sparsely pubescent, bark rugose to furrowed. Leaves spirally arranged, loosely so (*E. xylopoda*) or congested at the ends of the branches (*E. calyculata*), drought-deciduous; stipules present, glanduliform-conical, lateral at the base of the petiole; blade elliptic, base attenuate, apex acute or obtuse, margin entire, pinnately veined. Synflorescences subterminal with 3–5 rays and dichasia 2–4 times branched (*E. calyculata*) or cyathia solitary and terminal at the ends of the main branches and subtended by three prominent white cyathophylls (*E. xylopoda*); cyathia pedunculate, glands 5, transversely elliptic to oblong, situated on the rim of the involucre, without appendages; gynophore terminating in 3 triangular calyx-like lobes; ovary glabrous, styles united into a column for 1/5 to 2/3 their length, swollen and emarginate at the apex. Capsule exerted from the involucre; seeds obloid, slightly angled in cross-section, base and apex rounded, smooth, carunculate.

Distribution and habitat. – Mexico (Jalisco, Michoacán, Guanajuato, Guerrero, Mexico, Oaxaca, Puebla); deciduous montane woodlands, oak and pine-oak forest, sometimes on lava flows, 1600–2300 m.

Species included (2). – *E. calyculata* Kunth, *E. xylopoda* Greenm.

Euphorbia sect. *Calyculatae* contains two closely related but morphologically very distinct species. Whereas *E. calyculata* has terminal pseudopleiochasial synflorescences typical of many groups of *Euphorbia*, the cyathia of *E. xylopoda* are solitary and terminal at the tips of the main branches, an uncommon condition in the genus. Steinmann & al. (2007) noted morphological similarities between *E. calyculata* and *E. sect. Cubanthus*, particularly in the leaf arrangement and calyx-like structure, but a close relationship between these sections is not supported by our data.

8. *Euphorbia* sect. *Portulacastrum* Boiss. in Candolle, Prodr. 15(2): 9, 69. 1862 – Type (see Wheeler in Amer. Midl. Naturalist 30: 481. 1943): *Euphorbia pentlandii* Boiss.

Monoecious, annual, procumbent, pubescent herbs. Leaves sparse, entire, ovate to orbicular, petioles as long as blade or longer. Cyathia axillary, solitary, sessile or shortly pedunculate; glands 4, with appendages 3–5-digitate; styles undivided. Capsule depressed ovoid, strongly 3-sulcate; seeds transversely grooved, ecarunculate.

Distribution and habitat. – Bolivia and Chile; montane habitats.

Species included (2). – *E. germainii* Boiss., *E. pentlandii* Boiss.

This is a rarely collected section that differs from its sister clade, *E. sect. Nummulariopsis*, in consisting of annual herbs without pistillate calyces and with digitate cyathial gland appendages.

9. *Euphorbia* sect. *Nummulariopsis* Boiss. in Candolle, Prodr. 15(2): 9, 71. 1862 – Type: *Euphorbia peperomioides* Boiss. = *Euphorbia* subsect. *Inundatae* G.L. Webster in J. Arnold Arbor. 48: 400. 1967 – Type: *Euphorbia inundata* Torr.

Monoecious or dioecious herbs, usually perennial, often with a fleshy rootstock. Stems terete, ascending or prostrate. Leaves alternate or sometimes opposite on vegetative stems, entire to serrate, opposite on fertile rays, stipules glandular, minute to elongate. Cyathia solitary and axillary or in terminal pseudopleiochasia, glands 4–5(7), without appendages or sometimes 2-horned; female flower with well-developed perianth lobes; ovary globose; seeds smooth to variously sculptured, ecarunculate.

Distribution and habitat. – Southeastern U.S.A., southern South America (Argentina, Bolivia, Brazil, Chile, Paraguay, Peru, Uruguay); high montane habitats, grasslands, and sand dunes (South America), pine woodlands and sandy areas (U.S.A.), sea level to ca. 3500 m.

Species included (37). – *E. araucana* Phil., *E. boerhaavioides* Rusby, *E. burkartii* Bacigalupo, *E. caespitosa* Lam., *E. chamaeclada* Ule, *E. copiapina* Phil., *E. cordeiroae* P. Carrillo & V.W. Steinm., *E. correntina* Parodi, *E. cymbiformis* Rusby, *E. duriuscula* Pax & K. Hoffm. ex Herzog, *E. eanophylla* Croizat, *E. elodes* Boiss., *E. elquiensis* Phil., *E. floridana* Chapm., *E. guachanca* Haenke in Azara, *E. guaraniorum* P. Carrillo & V.W. Steinm., *E. hieronymi* Subils, *E. hinkleyorum*

I.M. Johnst., *E. huanchahana* (Klotzsch & Garcke) Boiss., *E. inundata* Torr. ex Chapm., *E. macraulonia* Phil., *E. ovalleana* Phil., *E. pampeana* Speg., *E. papillosa* A. St.-Hil., *E. paransensis* Dusén, *E. pedersenii* Subils, *E. peperomioides* Boiss., *E. porphyrantha* Phil., *E. portulacoides* L., *E. raphanorrhiza* (Millsp.) J.F. Macbr., *E. raphilippii* Oudejans, *E. rhabdodes* Boiss., *E. roscens* E.L. Bridges & Orzell, *E. schickendantzii* Hieron., *E. stenophylla* (Klotzsch & Garcke) Boiss., *E. telephioides* Chapm., *E. thinophila* Phil.

Most species in this section are confined to southern South America, but a group of four species are disjunct to the southeastern United States and was formerly treated as *E.* subsect. *Inundatae* G.L. Webster (Bridges & Orzell, 2002). Here this group is strongly supported as sister to the South American species. Both groups share the uncommon feature of a relatively well-developed calyx on the female flower. The species from the southeastern United States are functionally dioecious, a feature so far shared only with *E. hieronymi* among the South American species (Bridges & Orzell, 2002).

10. *Euphorbia* sect. *Crepidaria* (Haw.) Baill., Étude Euphorb.: 284. 1858 ≡ *Crepidaria* Haw., Syn. Pl. Succ.: 136. 1812 – Type (see Wheeler in Contr. Gray Herb. 124: 44. 1939): *Crepidaria myrtifolia* (Mill.) Haw. (= *Euphorbia tithymaloides* L.) = *Pedilanthus* Neck. ex Poit., Elem. Bot. 2: 354. 1790 ≡ *Tithymaloides* sect. *Pedilanthus* M. Gómez, Fl. Habanera: 154. 1897 ≡ *Tithymalus* Mill., Gard. Dict. ed. 4, 3. 1754, nom. rej. ≡ *Tithymaloides* Ortega, Tab. Bot.: 9. 1773, nom. rej. – Type (Millspaugh in Publ. Field Columb. Mus., Bot. Ser. 2: 300. 1909): *Pedilanthus tithymaloides* (L.) Poiteau (= *Euphorbia tithymaloides* L.) = *Ventenatia* Tratt., Gen. Pl.: 86. 1802 – Type: *Ventenatia bracteata* (Jacq.) Tratt. (= *Euphorbia bracteata* Jacq.) = *Diadenaria* Klotzsch & Garcke in Monatsber. Königl. Preuss. Akad. Wiss. Berlin 1859: 254. 1860 ≡ *Tithymaloides* sect. *Diadenaria* (Klotzsch & Garcke) O. Kuntze in Post & Kuntze, Lex. Gen. Phan.: 562. 1903 – Type (Wheeler in Contr. Gray Herb. 124: 44. 1939): *Diadenaria pavonis* Klotzsch & Garcke (= *Euphorbia bracteata* Jacq.) = *Hexadenia* Klotzsch & Garcke, Monatsber. Königl. Preuss. Akad. Wiss. Berlin 1859: 253. 1860 – Type: *Hexadenia macrocarpa* (Benth.) Klotzsch & Garcke (= *Euphorbia lomelii* V.W. Steinm.).

Monoecious shrubs to small trees. Stems succulent or not. Leaves alternate, minute and scale-like to large and elliptic, deciduous to persistent, entire; petiole short to absent, stipules small, caducous. Synflorescences terminal or axillary; cyathia zygomorphic, cyathophylls red to green, spreading or not, variously shaped, glands 2–6, appendiculate, situated on dorsal side of involucre and usually enclosed in a spur-like extension of the involucre tube; seeds ecarunculate.

Distribution and habitat. – Mexico, Central America, West Indies, northern South America, southeastern U.S.A. (Florida); desert scrub, as well as dry and wet tropical forests, sea level to ca. 800 m.

Species included (15). – *E. bracteata* Jacq., *E. calcarata* (Schltdl.) V.W. Steinm., *E. coalcomanensis* (Croizat) V.W.

Steinm., *E. colligata* V.W. Steinm., *E. conzattii* V.W. Steinm., *E. cymbifera* (Schltdl.) V.W. Steinm., *E. cyri* V.W. Steinm., *E. diazlanana* (J. Lomeli & Sahagun) V.W. Steinm., *E. dressleri* V.W. Steinm., *E. finkii* (Boiss.) V.W. Steinm., *E. lomelii* V.W. Steinm., *E. peritropoides* (Millsp.) V.W. Steinm., *E. personata* (Croizat) V.W. Steinm., *E. tehuacana* (Brandege) V.W. Steinm., *E. tithymaloides* L.

Euphorbia sect. *Crepidaria* corresponds to the former genus *Pedilanthus* and is a collection of fifteen species from a wide range of habitats. The highly modified, zygomorphic cyathia in which a nectar spur is constructed of both involucre and gland appendage tissue easily distinguish this group (Dressler, 1957).

11. *Euphorbia* sect. *Stachydium* Boiss. in Candolle, Prodr. 15(2): 9, 65. 1862 – Type (see Wheeler in Amer. Midl. Naturalist 30: 481. 1943): *Euphorbia comosa* Vell.

Monoecious herbs or shrubs; stems green, terete, laxly to densely branched. Leaves ovate to linear-lanceolate, petiolate or sessile, drought deciduous (except *E. comosa*); synflorescences monochasial spikes; cyathia sessile, solitary, subtended by a foliaceous bract, which overlaps with those of the other cyathia, glands 4(5), elliptic, green-yellow, appendages lacking. Capsules elongate, glabrous, pedicellate, recurved or erect; seeds tetragonus, tuberculate, carunculate.

Distribution and habitat. – Northern South America to eastern Brazil; low deciduous forest and thorn scrub on sandy or loose stony soils or rocky outcrops; 200–1200 m.

Species included (6). – *E. comosa* Vell., *E. gollmeriana* Klotzsch ex Boiss., *E. heterodoxa* Mull.-Arg., *E. invaginata* Croizat, *E. lagunillarum* Croizat, *E. vervoortii* Subils.

12. *Euphorbia* sect. *Brasilienses* V.W. Steinm. & Dorsey, sect. **nov.** – Type: *Euphorbia phosphorea* Mart.

Monoecious, xerophytic, stem-succulent shrubs to 6 m tall, highly branched. Stems ascending, with a persistent green epidermis, 4–6 angles descending from leaf scars, waxy. Leaves alternate, highly reduced and quickly deciduous, ovate, apex acute, margin entire, secondary venation not evident. Cyathia axillary, solitary or few in dense clusters, subsessile, glands 4–5(–7), transversely oblong, slightly cup-shaped with two horns either spreading or ascending, red or yellow, situated on the rim of the involucre; gynophore terminating in 3 triangular calyx-like lobes; ovary glabrous, styles united most of their length into a slender column, undivided. Capsule exerted from the involucre, green, red, or yellow and red, glabrous, 3-lobed; seeds obloid, rounded to weakly quadrangular in cross-section, base and apex rounded, smooth to minutely papillate, with a minute discoid caruncle.

Distribution and habitat. – Brazil (Espírito Santo, Bahia, Minas Gerais, Paraíba, Pernambuco); rocky uplands (campos rupestres), grasslands, thorn scrub, and tropical deciduous forest; 300–1250 m.

Species included (4). – *E. attastoma* Rizzini, *E. holochlorina* Rizzini, *E. phosphorea* Mart., *E. sipolisii* N.E. Br.

This is the only New World section comprised entirely of stem-succulent species. The group is easily recognized by

this habit and the colorful (dark red or yellow), horned cyathial glands (Fig. 1K). The distinctions among species are mainly of gland color and number of stem angles (Rizzini, 1987; Egli, 1994).

13. *Euphorbia* sect. *Pachysanthae* X. Aubriot & Haev., **sect. nov.** – Type: *Euphorbia pachysantha* Baill.

Shrubs to large trees (2–25 m), “bottle-shaped” and unbranched at the base, mostly monoecious. Stems succulent toward the apices; bark gray, smooth to wrinkled. Leaves spirally arranged, grouped at the apices of the branches, obovate to lanceolate, thick (except in *E. pachysantha*); stipules reduced to two small glands. Synflorescence subterminal, 1 or 2–4 cyathia at the apex of the twigs; cyathophylls 2, well-developed, green-yellow, soon deciduous; glands 5, stipitate, elliptic to reniform, exappendiculate, green-yellow. Capsule indehiscent or tardily dehiscent (dehiscence line present though dehiscence not observed), erect or pendant, 3-locular or more commonly 2-locular or 1-locular by abortion, smooth to slightly wrinkled, green when young, 1.5–4 cm diam.; seeds 1–3, smooth, globular, ecarunculate.

Distribution and habitat. – Madagascar; in a variety of habitats, such as thickets in xeric bush of the southeast, tsingy (karst) formations in the north, remnant forests in the high plateaus in the northwest, and rainforest relicts of the central east.

Species included (4). – *E. mananarensis* Leandri, *E. mandravioky* Baill., *E. pachysantha* Baill., *E. pirahazo* Jum.

The large, uni- or bilocular fruits of this section are quite rare in *Euphorbia* and their presence suggests a close relationship to *E. sect. Pervilleanae*. Although rarely collected, the fruits of *E. pachysantha* are apparently fleshy and indehiscent. There are two additional species from northern Madagascar awaiting publication by Aubriot & al. (in prep.)

14. *Euphorbia* sect. *Pervilleanae* Haev. & X. Aubriot, **sect. nov.** – Type: *Euphorbia pervilleana* Baill.

Usually dioecious shrubs to trees, non-succulent but with a water-storing rootstock; bark smooth to exfoliating. Leaves alternate to subopposite, shape variable (linear, lanceolate, elliptic to obovate, scale-like for *E. intisy*); stipules reduced to black gland-like dots. Synflorescences terminal, male synflorescences bearing a larger number of cyathia; cyathophylls green, inconspicuous, similar to dichasial bracts; glands 4–6, elliptic to bilabiate. Capsule functionally 2(3)-locular, dehiscent or indehiscent, erect, smooth to pubescent, usually bearing ornaments such as wings, spines, or tubercles; seeds 1(2)(3), large (5–10 mm diam.), chestnut-shaped, smooth or tuberculate, ecarunculate.

Distribution and habitat. – Widespread across Madagascar.

Species included (7). – *E. adenopoda* Baill., *E. analamerae* Leandri, *E. intisy* Drake, *E. pervilleana* Baill., *E. randrian-johanyi* Haev. & Labat, *E. rauhii* Haev. & Labat, *E. tetraptera* Baker.

This group was formerly included in *E. sect. Denisophorbia*, to which it is not closely related. The leafless *E. intisy* was previously included in *E. subg. Tirucalli* but was shown to be misplaced there (Haevermans, 2003), and this is confirmed here (Fig. 2B).

15. *Euphorbia* sect. *Tirucalli* Boiss. in Candolle, Prodr. 15(2): 10, 94. 1862 ≡ *Euphorbia* subsect. *Tirucalli* (Boiss.) Benth. & Hook. f., Gen. Pl. 3(1): 260. 1880 ≡ *Euphorbia* subg. *Tirucalli* (Boiss.) S. Carter in Kew Bull. 40: 823. 1985 ≡ *Arthrothamnus* Klotzsch & Garke in Monatsber. Königl. Preuss. Akad. Wiss. Berlin 1859: 251. 1860, non Rupr. 1848 ≡ *Euphorbia* sect. *Arthrothamnus* Boiss. in Candolle, Prodr. 15(2): 10, 74. 1862 – Type: *Euphorbia tirucalli* L. = *Euphorbia* sect. *Armatocalli* Croizat in Webbia 27: 180. 1972 – Type: *Euphorbia stenoclada* Baill.

Usually dioecious shrubs to trees. Stems more or less succulent, with alternate or subverticillate branching (dichotomous in *E. carunculifera*), terete (some species have more or less flattened apices, in *E. stenoclada* sterile twig apices turn into spiny processes), bark much delayed, fissured, detaching in plates (smooth), gray-brown. Leaves alternate, early caducous, variable in size and shape depending on the species but never well-developed; pubescence more or less developed (potentially present on every part of the plant); stipules highly reduced, glandular or absent. Synflorescences subterminal (terminal), composed of one or more lateral dichasia, only the terminal cyathia functional; male synflorescences with many more cyathia than the female ones, cyathophylls green, inconspicuous, similar to dichasial bracts; cyathia usually unisexual, glands 5, orbicular to elliptic, convex or concave, green to red, more or less stipitate; female flower pedicellate, perianth remnants constituting a 3-lobed calyx, styles 3, free to base or united partway down, bifid, recurved. Capsule smooth and sometimes pubescent, pendent or erect, 3(4–6)-locular, green or red, orbicular to acutely 3(4–6)-angled, then more or less deeply lobed; seeds 3(4–6), cylindrical to obtusely 4-angled, testa smooth, carunculate.

Distribution and habitat. – Widespread and most diverse in Madagascar, also native in the Arabian Peninsula (Oman and Yemen, including Socotra) and Africa (Angola, Namibia, Somalia, South Africa). *Euphorbia tirucalli* is widespread across Africa, but it is not clear where the species is native (probably Madagascar and southern Africa). It is widely cultivated in India and in other tropical countries.

Species included (24). – *E. alcornis* Baker, *E. analavensis* Leandri, *E. arahaka* Poiss., *E. arbuscula* Balf. f., *E. bariensis* S. Carter, *E. boinensis* Denis ex Humbert & Leandri, *E. carunculifera* L.C. Leach, *E. congestiflora* L.C. Leach, *E. damarana* L.C. Leach, *E. decorsei* Drake, *E. enterophora* Drake, *E. fiherenensis* Poiss., *E. gregaria* Marloth, *E. gummifera* Boiss., *E. imerina* Cremers, *E. kamponii* Rauh & Pétignat, *E. mainty* (Poiss.) Denis ex Leandri, *E. neochamaeclada* Bruyns, *E. ramofraga* Denis & Humbert ex Leandri, *E. spissa* M. Thulin, *E. stenoclada* Baill., *E. tirucalli* L., *E. uzruk* S. Carter & J.R.I. Wood, *E. xylophyloides* Brongn. ex Lem.

16. *Euphorbia* sect. *Rubellae* Dorsey, **sect. nov.** – Type: *Euphorbia rubella* Pax.

Monoecious geophytes. Root a subglobose to cone-shaped tuber or fibrous. Stems reduced and underground, tuberculate. Leaves elliptic in a rosette at ground level, long petiolate (2–6 cm); stipules threadlike or absent. Synflorescences subapical, produced before leaves emerge or with them, peduncle

2–11 cm long, more or less branched; cyathophylls orbicular-ovate, fused dorsally in *E. cryptocaulis*; cyathia sessile, glands 4+2 due to one being divided, oblong-elliptic, red or yellow; ovary exserted, oblong, smooth. Capsule long-exserted, oblong-ovoid; seeds ovoid, tuberculate, carunculate.

Distribution and habitat. – Northeastern Africa (Sudan, Ethiopia, Kenya, Uganda); open sites in limestone crevices on well-drained soil, or under bushes in evergreen or deciduous bushland.

Species included (3). – *E. brunellii* Chiov., *E. cryptocaulis* M.G. Gilbert, *E. rubella* Pax.

This group of geophytes from northeast Africa is unique in its cyathial gland morphology having 4 equal-sized glands and 2 smaller ones produced by the division of a single gland (Gilbert, 1987). Geophytes are present in several sections of *E.* subg. *Euphorbia*, but this unusual gland structure makes this restricted and small group easily recognizable. Bally (1967) considered *E. brunellii* a variety of *E. rubella*, but Gilbert (1995) treated them as separate species based on distinct root morphology, leaf size, cyathophyll shape, and capsule shape. We follow Gilbert (1995) and note that both the *ndhF* and ITS sequences differ more between these two species than between many other accepted species pairs in *E.* subg. *Euphorbia*.

17. *Euphorbia* sect. *Goniostema* Baill. ex Boiss. in Candolle, Prodr. 15(2): 10, 77. 1862 – Type (Wheeler in Amer. Midl. Naturalist 30: 485. 1943): *Euphorbia lophogona* Lam.

= *Lacanthis* Raf., Fl. Tellur. 2: 94. 1837 ≡ *Euphorbia* subg. *Lacanthis* (Raf.) M.G. Gilbert in Kew Bull. 42: 238. 1987 ≡ *Euphorbia* sect. *Diacanthium* Boiss. in Candolle, Prodr. 15(2): 10, 78. 1862 ≡ *Sterigmanthe* Klotzsch & Garcke in Monatsber. Königl. Preuss. Akad. Wiss. Berlin 1859: 252. 1860 – Type: *Lacanthis splendens* (Bojer) Raf. (= *Euphorbia milii* Des Moul.).

= *Euphorbia* sect. *Rhizanthopsis* Croizat in Webbia 27: 178. 1972 – Type: *Euphorbia francoisii* Leandri.

Monoecious, prostrate geophytes, shrubs, or trees. Stems more or less succulent, branching or not; bark smooth, gray. Leaves alternate, persistent or deciduous; shape highly variable; succulent in some taxa; petiole cylindrical or winged; stipular structures from gland-like to spines, individual or gathered in vertical comb-like structures, some branching, glabrous to pubescent. Synflorescences lateral (subterminal), of a variable number of cyathia (in some taxa, axillary buds can further develop the inflorescence by producing new cyathia); cyathophylls 2 per cyathium, usually well-developed and usually brightly colored, usually distinct from synflorescence bracts, patent or tightly enclosing the cyathia; cyathia bisexual, protandrous or protogynous; glands (4)5(6), shape variable, spreading or enveloping the involucre. Capsule dehiscent, smooth, erect, 3-locular; seeds 3, verrucose, ecarunculate.

Distribution and habitat. – Widespread across Madagascar; in a wide variety of habitats from sea level to upper mountains.

Species included (77). – *E. alfredii* Rauh, *E. ambariva-toensis* Rauh & Bard.-Vauc., *E. ambovombensis* Rauh & Razaf., *E. analavelonensis* Rauh & Mangelsdorff, *E. ankarensis* Boiteau, *E. ankazobensis* Rauh & Hofstätter, *E. annamariae*

Rauh, *E. aureoviridiflora* (Rauh) Rauh, *E. banae* Rauh, *E. beharensis* Leandri, *E. berevoensis* Lawant & Buddens., *E. bero-rohae* Rauh & Hofstätter, *E. beuginii* Rebmann, *E. biaculeata* Denis, *E. boissieri* Baill., *E. boiteaui* Leandri, *E. brachyphylla* Denis, *E. bulbispina* Rauh & Razaf., *E. capmanambatoensis* Rauh, *E. capuronii* Ursch & Leandri, *E. caput-aureum* Denis, *E. cremersii* Rauh & Razaf., *E. croizatii* Leandri, *E. cylindrifolia* Marn.-Lap. & Rauh, *E. decaryi* Guillaumin, *E. delphinensis* Ursch & Leandri, *E. denisiana* Guillaumin, *E. didiereoides* Denis ex Leandri, *E. duranii* Ursch & Leandri, *E. erythrocucullata* Mangelsdorff, *E. fianarantsoae* Ursch & Leandri, *E. francoisii* Leandri, *E. genoudiana* Ursch & Leandri, *E. geroldii* Rauh, *E. gottlebei* Rauh, *E. guillauminiana* Boiteau, *E. hermanschwartzii* Rauh, *E. hexadenia* Denis, *E. hofstaetteri* Rauh, *E. horombensis* Ursch & Leandri, *E. iharanae* Rauh, *E. isalensis* Leandri, *E. itremensis* Kimnach & Lavranos, *E. kondoi* Rauh & Razaf., *E. labatii* Rauh & Bard.-Vauc., *E. leuconeura* Boiss., *E. lophogona* Lam., *E. mahafalensis* Denis, *E. mainiana* Poiss., *E. mangelsdorffii* Rauh, *E. mangokyensis* Denis, *E. maromokotrensis* Rebmann, *E. milii* Des Moul., *E. millotii* Ursch & Leandri, *E. moratii* Rauh, *E. neobosseri* (Rauh) Rauh, *E. neohumbertii* Boiteau, *E. pachypodioides* Boiteau, *E. parvicyathophora* Rauh, *E. paulianii* Ursch & Leandri, *E. pedilanthoides* Denis, *E. perrieri* Drake, *E. primulifolia* Baker, *E. quartzitcola* Leandri, *E. razafindratsirae* Lavranos, *E. razafinjohanyi* Ursch & Leandri, *E. retrospina* Rauh & Gerold, *E. robelonae* Rauh, *E. rossii* Rauh & Buchloh, *E. sakarahaensis* Rauh, *E. suzanae-marnierae* Rauh & Pétignat, *E. tardieuana* Leandri, *E. thuarsiana* Baill., *E. tsimbazazae* Leandri, *E. tulearensis* (Rauh) Rauh, *E. viguieri* Denis, *E. waringiae* Rauh & Gerold.

Bruyns & al. (2006) circumscribed this section to include the entire Old World clade II, but here we limit it to a more restricted clade containing the type, *E. lophogona*, and other species generally characterized by colorful cyathophylls. Section *Goniostema* is the largest clade in *E.* subg. *Euphorbia* on Madagascar and occurs across the island in diverse habitats. It is also a morphologically diverse clade including understory trees and shrubs in moist habitats (e.g., *E. geroldii*), spiny xerophytic or succulent shrubs and dwarfs from more arid habitats (*E. milii* complex), and geophytes in fire-prone regions and unusual substrates (e.g., *E. primulifolia*, *E. quartzitcola*).

18. *Euphorbia* sect. *Deuterocalli* Croizat in Webbia 27: 179. 1972 ≡ *Euphorbia* subsect. *Deuterocalli* (Croizat) Bruyns in Taxon 55: 415. 2006 – Type: *Euphorbia oncoclada* Drake (≡ *Euphorbia alluaudii* subsp. *oncoclada* (Drake) F. Friedmann & Cremers).

Dioecious shrubs or small trees. Stems succulent, terete (sometimes jointed as in a string of sausages because of alternation between long shoot and brachyblast morphology), bark gray, smooth, much delayed. Leaves alternate, soon deciduous, reduced to scales or lanceolate and petiolate; stipules modified as a waxy or glandular ring around the leaf insertion. Synflorescence lateral (subterminal), male cyathia usually more numerous; cyathophylls inconspicuous, green (identical to dichasial bracts); cyathia pedunculate; glands 5, elliptical, green-yellow.

Capsule dehiscent, erect, 3-locular, green, smooth, with ridges tinted with purple; seeds 3, smooth, ecarunculate.

Distribution and habitat. – Widespread in Madagascar, mostly in dry scrub or among rocks in moister habitats, sea level to ca. 500 m.

Species included (3). – *E. alluaudii* Drake, *E. cedrorum* Rauh & Hebding, *E. famatamboay* F. Friedmann & Cremers.

This is a well-supported clade containing three species of trees that were previously grouped with *E. tirucalli* because of their leafless, pencil-stem growth form and dioecy. However, they differ from *E. sect. Tirucalli* in their thicker, more jointed stems, stipules that form glandular or waxy rings around the leaf scars, and ecarunculate seeds. *Euphorbia alluaudii* is treated here to include *E. leucodendron* Drake as well as *E. oncoclada* Drake.

19. *Euphorbia* sect. *Denisophorbia* (Leandri) Croizat in *Webbia* 27: 165. 1972 ≡ *Euphorbia* subsect. *Denisophorbia* Leandri in *Bull. Soc. Bot. France* 104: 500. 1957 – Type: *Euphorbia pyriformis* Lam.

Monoecious or dioecious shrubs or trees, without spines, sometimes with a basal caudex, the upper branching chandelier-like, with plagiotropic branches composed of one or more series of hypopodia (long, leafless internodes) and apical brachyblasts (very short branches with a rosette of leaves), the stems succulent or not, bark smooth, green or reddish-brown. Leaves spirally arranged, shape variable, present only at nodes or extremities of branches, deciduous to persistent, membranaceous to coriaceous (sometimes slightly succulent), petiolate or subsessile; stipules reduced to glandular dots. Synflorescences subterminal on brachyblasts, bearing few to many cyathia; cyathophylls 2, scarious and inconspicuous to well-developed and showy, green to yellow; glands (4)5(6), oval to kidney-shaped, green-yellow or pink. Capsule dehiscent, 3-locular, erect, smooth, round or strongly 3-angled in cross-section; seeds smooth, spherical, ecarunculate.

Distribution and habitat. – Madagascar, Mayotte and Comoro Islands, Seychelles, Mauritius.

Species included (14). – *E. anakaranae* Leandri, *E. aprica* Baill., *E. betacea* Baill., *E. boivinii* Boiss., *E. bongolavensis* Rauh, *E. elliotii* Leandri, *E. hedyotoides* N.E. Br., *E. mahabobokensis* Rauh, *E. mangorensis* Leandri, *E. martiniae* Rauh, *E. physoclada* Boiss., *E. pyriformis* Lam., *E. rangovalensis* Leandri, *E. zakamenae* Leandri.

This section is treated here in a more limited sense than Leandri's original circumscription of *E. subsect. Denisophorbia*. It includes a group of mostly dioecious species from Madagascar and other Indian Ocean islands that have a *Terminalia*-type of sympodial branching, with long arching branches ending in short brachyblasts that bear the leaves and cyathia. The group is currently under revision, and there appear to be at least five new species awaiting description (Haevermans & al., in prep.).

20. *Euphorbia* sect. *Monadenium* (Pax) Bruyns in *Taxon* 55: 411. 2006 ≡ *Monadenium* Pax in *Bot. Jahrb. Syst.* 19: 126. 1894 – Type: *Monadenium coccineum* Pax. (≡ *Euphorbia neococcinea* Bruyns).

= *Synadenium* Boiss. in *Candolle, Prodr.* 15(2): 187. 1862 – Type: *Synadenium arborescens* Boiss. (≡ *Euphorbia cupularis* Boiss.).

= *Stenadenium* Pax in *Bot. Jahrb. Syst.* 30: 343. 1901 – Type: *Stenadenium spinescens* Pax (≡ *Euphorbia spinescens* (Pax) Bruyns).

= *Endadenium* L.C. Leach in *Garcia de Orta, Sér. Bot.* 1: 31. 1973 – Type: *Endadenium gossweileri* (N.E. Br.) L.C. Leach (≡ *Monadenium gossweileri* N.E. Br. ≡ *Euphorbia neogossweileri* Bruyns).

Monoecious geophytes, herbs, shrubs, or trees. Stems terete to angled, ± fleshy to succulent. Leaves fleshy, stipules apparently absent or modified as spines or glands. Synflorescences axillary cymes to single cyathia; cyathophylls conspicuous, persistent, partly united along one edge then partly surrounding the involucre, or free; cyathia sessile; glands united into a horseshoe or ring that surrounds 5 involucre lobes. Capsule 3-lobed, dehiscent, exerted (through notch in gland ring if present); seeds oblong, carunculate.

Distribution and habitat. – Eastern, central, and southeastern tropical Africa; in a variety of mostly arid habitats: thickets, rock outcrops, and other open areas.

Species included (90). – *E. bianoensis* (Malaisse & Lecron) Bruyns, *E. bicompecta* Bruyns, *E. biselegans* Bruyns, *E. bisellenbeckii* Bruyns, *E. bisglobosa* Bruyns, *E. bodenghieniae* (Malaisse & Lecron) Bruyns, *E. catenata* Bruyns, *E. chevalieri* Bruyns, *E. clarae* (Malaisse & Lecron) Bruyns, *E. crenata* (N.E. Br.) Bruyns, *E. cupricola* (Malaisse & Lecron) Bruyns, *E. cupularis* Boiss, *E. descampsii* (Pax) Bruyns, *E. dilunguensis* (Malaisse & Lecron) Bruyns, *E. discoidea* (P.R.O. Bally) Bruyns, *E. echinulata* (Stapf) Bruyns, *E. filiformis* (P.R.O. Bally) Bruyns, *E. friesii* (N.E. Br.) Bruyns, *E. fwambensis* (N.E. Br.) Bruyns, *E. gammaranoi* G. Will., *E. gladiata* (P.R.O. Bally) Bruyns, *E. guentheri* (Pax) Bruyns, *E. hedigeriana* (Malaisse & Lecron) Bruyns, *E. herbacea* (Pax) Bruyns, *E. heteropoda* Pax, *E. iancannellii* Bruyns, *E. invenusta* (N.E. Br.) Bruyns, *E. kimberleyana* (G. Will.) Bruyns, *E. kirkii* (N.E. Br.) Bruyns, *E. kundelunguensis* (Malaisse) Bruyns, *E. letestwana* (Denis) Bruyns, *E. letouzeyana* (Malaisse) Bruyns, *E. lindenii* (S. Carter) Bruyns, *E. lugardiae* (N.E. Br.) Bruyns, *E. mafingensis* (Hargreaves) Bruyns, *E. magnifica* (E.A. Bruce) Bruyns, *E. major* (Pax) Bruyns, *E. mamfwensis* (Malaisse & Lecron) Bruyns, *E. maryrichardsiae* G. Will., *E. neoangolensis* Bruyns, *E. neoarborescens* Bruyns, *E. neocapitata* Bruyns, *E. neococcinea* Bruyns, *E. neocrispa* Bruyns, *E. neocymosa* Bruyns, *E. neogilletii* Bruyns, *E. neoglabrata* Bruyns, *E. neoglaucescens* Bruyns, *E. neogoetzei* Bruyns, *E. neogossweileri* Bruyns, *E. neograxis* Bruyns, *E. neohalipedicola* Bruyns, *E. neokaessneri* Bruyns, *E. neomontana* Bruyns, *E. neoparviflora* Bruyns, *E. neopedunculata* Bruyns, *E. neoreflexa* Bruyns, *E. neorubella* Bruyns, *E. neorugosa* Bruyns, *E. neospinescens* Bruyns, *E. neostolonifera* Bruyns, *E. neovirgata* Bruyns, *E. orobanchoides* (P.R.O. Bally) Bruyns, *E. pereskiiifolia* Houliet ex Baill., *E. pseudohirsuta* Bruyns, *E. pseudolaevis* Bruyns, *E. pseudomollis* Bruyns, *E. pseudonudicaulis* Bruyns, *E. pseudopetiolata* Bruyns, *E. pseudoracemosa* (P.R.O. Bally) Bruyns, *E. pseudosimplex* Bruyns,

E. pseudostellata Bruyns, *E. pseudotrinervis* Bruyns, *E. pseudovolkensii* Bruyns, *E. pudibunda* (P.R.O. Bally) Bruyns, *E. renneyi* (S. Carter) Bruyns, *E. rhizophora* (P.R.O. Bally) Bruyns, *E. ritchei* (P.R.O. Bally) Bruyns, *E. schaijesii* (Malaise) Bruyns, *E. schubei* Pax, *E. shebeliensis* (M.G. Gilbert) Bruyns, *E. spectabilis* (S. Carter) Bruyns, *E. spinulosa* (S. Carter) Bruyns, *E. succulenta* (Schweickerdt) Bruyns, *E. syncalycina* Bruyns, *E. syncameronii* Bruyns, *E. torrei* (L.C. Leach) Bruyns, *E. triangolensis* Bruyns, *E. umbellata* (Pax) Bruyns, *E. yattana* (P.R.O. Bally) Bruyns.

Euphorbia sect. *Monadenium* corresponds to the formerly recognized genera *Monadenium*, *Synadenium*, and *Endadenium*. These were previously segregated from *Euphorbia* based on modifications of the cyathial glands—fused into a ring in *Endadenium* and *Synadenium*, or into a horseshoe shape in *Monadenium*. These modified gland structures continue to be phylogenetically informative, as the former *Synadenium* and *Endadenium* species group closely together within *E. sect. Monadenium*. These species can also be distinguished by their reduced caruncle relative to the distinctive one of most other species in the section. *Euphorbia* sect. *Monadenium* is another example of the lability of growth form evolution in *E. subg. Euphorbia*, since it contains nearly every form present in the subgenus. Many species also bear spine-like structures of various forms that support their close relationship to both *E. sect. Goniostema* and *E. sect. Euphorbia*, although the homology of the “spines” in these three sections is not yet established (Fig. 1N–P).

21. *Euphorbia* sect. *Euphorbia* – Type: *Euphorbia antiquorum* L.

= *Elaeophorbia* Stapf in Johnston, Pl. Liberia 2: 646. 1906 – Type: *Elaeophorbia drupifera* (Thonn.) Stapf (≡ *Euphorbia drupifera* Thonn.).

= *Euphorbia* sect. *Aculeatae* Haw. in Philos. Mag. Ann. Chem. 1: 275. 1827 – Type: *Euphorbia caerulescens* Haw.

= *Euphorbia* sect. *Cereis* Webb & Berthelot, Hist. Nat. Iles Canaries 2(3): 255. 1847 – Type: *Euphorbia canariensis* L.

= *Euphorbia* sect. *Caulanthium* Boiss. in Candolle, Prodr. 15(2): 10, 76. 1862 – Type: *Euphorbia sessiliflora* Roxb.

= *Euphorbia* sect. *Tekeanae* Croizat in Bull. Jard. Bot. État Bruxelles 15: 119. 1938 – Type: *Euphorbia teke* Schweinf.

= *Euphorbia* sect. *Ballyeuphorbia* Croizat in Webbia 27: 181. 1972 – Type: *Euphorbia decidua* P.R.O. Bally & L.C. Leach.

Monoecious geophytes, shrubs or trees. Stems succulent, green, photosynthetic (some species forming bark in older stems), winged, angled or tuberculate. Leaves alternate or spiral, usually strongly reduced and caducous, but large and persistent in some tree or shrub species; stipules apparently modified as spines (rarely fused) and borne on a spine-shield subtending or surrounding the leaf that can also bear a pair of prickles. Synflorescences axillary, simple (compound), dichasia usually of three cyathia; cyathophylls inconspicuous; peduncles usually short; cyathia bisexual; glands 5, entire, typically elliptical, yellow to red; female flower pedicellate. Capsule 3-locular, globose to deeply acutely lobed, in a few

species fleshy and indehiscent; seeds subglobose to ovoid, smooth to minutely tuberculate, ecarunculate.

Distribution and habitat. – Widespread across most of Africa, the Arabian Peninsula, and in southern Asia from Pakistan to Malaysia, Indonesia and Papua New Guinea; in a wide variety of habitats, but especially in arid landscapes, open areas, dry forests, scrub, rock outcrops, with some species occurring in moist forests.

Species included (343). – *E. abdelkuri* Balf. f., *E. abyssinica* J.F. Gmel., *E. acervata* S. Carter, *E. actinoclada* S. Carter, *E. adjurana* P.R.O. Bally & S. Carter, *E. aeruginosa* Schweick., *E. ambacensis* N.E. Br., *E. ambroseae* L.C. Leach, *E. amicorum* S. Carter, *E. ammak* Schweinf., *E. ammophila* S. Carter & Dioli, *E. amphophylla* Pax, *E. angularis* Klotzsch, *E. angustiflora* Pax, *E. antiquorum* L., *E. asthenacantha* S. Carter, *E. atrocarmesina* L.C. Leach, *E. atroflorea* S. Carter, *E. atrox* F.K. Horw. ex S. Carter, *E. avasmontana* Dinter, *E. awashensis* M.G. Gilbert, *E. бага* A. Chev., *E. baioensis* S. Carter, *E. baleensis* M.G. Gilbert, *E. ballyana* Rauh, *E. ballyi* S. Carter, *E. baradii* S. Carter, *E. barnardii* A.C. White, R.A. Dyer & B. Sloane, *E. baylissii* L.C. Leach, *E. beillei* A. Chev., *E. bertemariae* Bissert & Dioli, *E. biharamulensis* S. Carter, *E. bitataensis* M.G. Gilbert, *E. borenensis* M.G. Gilbert, *E. bougheyi* L.C. Leach, *E. breviarticulata* Pax, *E. brevis* N.E. Br., *E. brevitorta* P.R.O. Bally, *E. burgeri* M.G. Gilbert, *E. buruana* Pax, *E. bussei* Pax, *E. bwambensis* S. Carter, *E. cactus* Ehrenb. ex Boiss., *E. caducifolia* Haines, *E. caerulescens* Haw., *E. caloderma* S. Carter, *E. canariensis* L., *E. candelabrum* Trémaux ex Kotschy, *E. cannellii* L.C. Leach, *E. carteriana* P.R.O. Bally, *E. cataractarum* S. Carter, *E. catimandoo* Elliot ex Wight, *E. classenii* P.R.O. Bally & S. Carter, *E. clavigera* N.E. Br., *E. clivicola* R.A. Dyer, *E. coeruleans* Pax, *E. collenetteae* D. Al-Zahrani & El-Karemy, *E. colubrina* P.R.O. Bally & S. Carter, *E. columnaris* P.R.O. Bally, *E. complanata* Warb., *E. complexa* R.A. Dyer, *E. confinalis* R.A. Dyer, *E. conspicua* N.E. Br., *E. contorta* L.C. Leach, *E. cooperi* N.E. Br. ex A. Berger, *E. corniculata* R.A. Dyer, *E. cryptospinosa* P.R.O. Bally, *E. cuneneana* L.C. Leach, *E. cupripina* S. Carter, *E. cupularis* Boiss., *E. curvirama* R.A. Dyer, *E. cussonioides* P.R.O. Bally, *E. dalettiensis* M.G. Gilbert, *E. darbandensis* N.E. Br., *E. dasyacantha* S. Carter, *E. dauana* S. Carter, *E. dawei* N.E. Br., *E. debilis* L.C. Leach, *E. decidua* P.R.O. Bally & L.C. Leach, *E. decliviticola* L.C. Leach, *E. dedzana* L.C. Leach, *E. deightonii* Croizat, *E. dekindtii* Pax, *E. demissa* L.C. Leach, *E. densispina* S. Carter, *E. desmondii* Keay & Milne-Redh., *E. dichroa* S. Carter, *E. discrepans* S. Carter, *E. dispersa* L.C. Leach, *E. dissitispina* L.C. Leach, *E. distinctissima* L.C. Leach, *E. drupifera* Thonn., *E. dumeticola* P.R.O. Bally & S. Carter, *E. eduardoi* L.C. Leach, *E. eilensis* S. Carter, *E. elegantissima* P.R.O. Bally & S. Carter, *E. ellenbeckii* Pax, *E. enormis* N.E. Br., *E. epiphyllodes* Kurz, *E. erigavensis* S. Carter, *E. erlangeri* Pax, *E. evansii* Pax, *E. excelsa* A.C. White, R.A. Dyer & B. Sloane, *E. exilis* L.C. Leach, *E. eyassiana* P.R.O. Bally & S. Carter, *E. fanshawei* L.C. Leach, *E. fascicaulis* S. Carter, *E. faucicola* L.C. Leach, *E. fissispina* P.R.O. Bally & S. Carter, *E. fluminis* S. Carter,

E. forolensis L.E. Newton, *E. fortissima* L.C. Leach, *E. fractiflexa* S. Carter & J.R.I. Wood, *E. franckiana* A. Berger, *E. frankii* Lavranos, *E. fruticosa* Forssk., *E. furcata* N.E. Br., *E. fusiformis* Buch.-Ham. ex D. Don, *E. galgalana* S. Carter, *E. garuana* N.E. Br., *E. geldorensis* S. Carter, *E. gemmea* P.R.O. Bally & S. Carter, *E. gillettii* P.R.O. Bally & S. Carter, *E. glochidiata* Pax, *E. godana* Buddens., Lawant & Lavranos, *E. gracilicaulis* L.C. Leach, *E. graciliramea* Pax, *E. grandialata* R.A. Dyer, *E. grandicornis* Goebel ex N.E. Br., *E. grandidens* Haw., *E. grandifolia* Haw., *E. graniticola* L.C. Leach, *E. greenwayi* P.R.O. Bally & S. Carter, *E. greuteri* N. Kilian, Kürschner & P. Hein, *E. griseola* Pax, *E. groenewaldii* R.A. Dyer, *E. gymnocalycioides* M.G. Gilbert & S. Carter, *E. halipedicola* L.C. Leach, *E. handiensis* Burchard, *E. heterochroma* Pax, *E. heterospina* S. Carter, *E. hiernii* (Croizat) Oudejans, *E. holmesiae* Lavranos, *E. horwoodii* S. Carter & Lavranos, *E. hottentota* Marloth, *E. hubertii* Pax, *E. imitata* N.E. Br., *E. immersa* P.R.O. Bally & S. Carter, *E. imparispina* S. Carter, *E. inaequispina* N.E. Br., *E. inarticulata* Schweinf., *E. inculta* P.R.O. Bally, *E. ingens* E. Mey. ex Boiss., *E. ingenticapsa* L.C. Leach, *E. inundaticola* L.C. Leach, *E. isacantha* Pax, *E. johannis* S. Carter, *E. jubata* L.C. Leach, *E. kalisana* S. Carter, *E. kamerunica* Pax, *E. kaokoensis* (A.C. White, R.A. Dyer, & B. Sloane) L.C. Leach, *E. keithii* R.A. Dyer, *E. khandallensis* Blatt. & Hallb., *E. knobelii* Letty, *E. knuthii* Pax, *E. lacei* Craib, *E. lactea* Haw., *E. laikipiensis* S. Carter, *E. ledienii* A. Berger, *E. lenewtonii* S. Carter, *E. leontopoda* S. Carter, *E. letestui* J. Raynal, *E. limpopoana* L.C. Leach ex S. Carter, *E. lividiflora* L.C. Leach, *E. longispina* Chiov., *E. louwii* L.C. Leach, *E. luapulana* L.C. Leach, *E. lukoseana* S. Carter, *E. lydenburgensis* Schweick. & Letty, *E. madinahensis* Fayed & D. Al-Zahrani, *E. magnicapsula* S. Carter, *E. makallensis* S. Carter, *E. malevola* L.C. Leach, *E. margaretae* S. Carter, *E. marrupana* Bruyns, *E. marsabitensis* S. Carter, *E. mayuranathanii* Croizat, *E. meenae* S. Carter, *E. memorialis* R.A. Dyer, *E. meridionalis* P.R.O. Bally & S. Carter, *E. michaelii* Thulin, *E. micracantha* Boiss., *E. migiurtinorum* Chiov., *E. mitriformis* P.R.O. Bally & S. Carter, *E. mlanjeana* L.C. Leach, *E. momccoyae* Lavranos, *E. monacantha* Pax, *E. monadenioides* M.G. Gilbert, *E. mosaica* P.R.O. Bally & S. Carter, *E. multiclava* P.R.O. Bally & S. Carter, *E. mwiniungensis* L.C. Leach, *E. myrioclada* S. Carter, *E. namuliensis* Bruyns, *E. nana* Royle, *E. neriifolia* L., *E. nicholasii* Oudejans, *E. nigrispina* N.E. Br., *E. nigrispinoides* M.G. Gilbert, *E. nivulia* Buch.-Ham., *E. nubigena* L.C. Leach, *E. nyassae* Pax, *E. nyikae* Pax ex Engl., *E. obconica* Bojer ex N.E. Br., *E. obovalifolia* A. Rich., *E. odontophora* S. Carter, *E. officinarum* L., *E. oligoclada* L.C. Leach, *E. opuntiioides* Welw. ex Hiern, *E. otjingandu* Swanepoel, *E. otjipembana* L.C. Leach, *E. paganorum* A. Chev., *E. parciramulosa* Schweinf., *E. parviceps* L.C. Leach, *E. patentispina* S. Carter, *E. perangusta* R.A. Dyer, *E. perarmata* S. Carter, *E. perplexa* L.C. Leach, *E. persistentifolia* L.C. Leach, *E. pervittata* S. Carter, *E. petraea* S. Carter, *E. petricola* P.R.O. Bally & S. Carter, *E. phillipsiae* N.E. Br., *E. phillipsioides* S. Carter, *E. piceoides* Thulin, *E. piscidermis* M.G. Gilbert, *E. platyrrhiza*

L.C. Leach, *E. plenispina* S. Carter, *E. poissonii* Pax, *E. polyacantha* Boiss., *E. ponderosa* S. Carter, *E. proballyana* L.C. Leach, *E. prona* S. Carter, *E. pseudoburuana* P.R.O. Bally & S. Carter, *E. pseudocactus* A. Berger, *E. pteroclada* L.C. Leach, *E. qarad* Deflers, *E. quadrangularis* Pax, *E. quadrialata* Pax, *E. quadrilatera* L.C. Leach, *E. quadriispina* S. Carter, *E. quinquecostata* Volken, *E. ramipressa* Croizat, *E. ramulosa* L.C. Leach, *E. reclinata* P.R.O. Bally & S. Carter, *E. reptans* P.R.O. Bally & S. Carter, *E. resinifera* O. Berg, *E. restricta* R.A. Dyer, *E. richardsiae* L.C. Leach, *E. ridleyi* Croizat, *E. robecchii* Pax, *E. rowlandii* R.A. Dyer, *E. royleana* Boiss., *E. rubrispinosa* S. Carter, *E. rubromarginata* L.E. Newton, *E. rugosiflora* L.C. Leach, *E. samburuensis* P.R.O. Bally & S. Carter, *E. santapau* A.N. Henry, *E. sapinii* De Wild., *E. saudiarabica* Fayed & D. Al-Zahrani, *E. saxorum* P.R.O. Bally & S. Carter, *E. scarlatina* S. Carter, *E. schinzii* Pax, *E. schizacantha* Pax, *E. schmitzii* L.C. Leach, *E. scitula* L.C. Leach, *E. sebsebei* M.G. Gilbert, *E. seibanica* Lavranos & Gifri, *E. sekukuniensis* R.A. Dyer, *E. semperflorens* L.C. Leach, *E. septentrionalis* P.R.O. Bally & S. Carter, *E. sepulta* P.R.O. Bally & S. Carter, *E. serendipita* L.E. Newton, *E. seretii* De Wild., *E. sessiliflora* Roxb., *E. setispina* S. Carter, *E. similiramea* S. Carter, *E. songweana* S. Carter, *E. speciosa* L.C. Leach, *E. spiralis* Balf. f., *E. stapfii* A. Berger, *E. stellata* Willd., *E. stenocaulis* Bruyns, *E. strangulata* N.E. Br., *E. subsalsa* Hiern, *E. subscandens* P.R.O. Bally & S. Carter, *E. sudanica* A. Chev., *E. sumati* S. Carter, *E. susan-holmesiae* Binoj Kumar & Gopalan, *E. taifensis* Fayed & D. Al-Zahrani, *E. tanaensis* P.R.O. Bally & S. Carter, *E. taruensis* S. Carter, *E. teixeirae* L.C. Leach, *E. teke* Schweinf. ex Pax, *E. tenuirama* Schweinf. ex A. Berger, *E. tenuispinosa* Gilli, *E. tescorum* S. Carter, *E. tetracantha* Rendle, *E. tetracanthoides* Pax, *E. tetragona* Haw., *E. tholicola* L.C. Leach, *E. tisserantii* A. Chev. & Sillans, *E. torta* Pax & K. Hoffm., *E. tortilis* Rottler ex Ainslie, *E. tortirama* R.A. Dyer, *E. tortistyla* N.E. Br., *E. triaculeata* Forssk., *E. triangularis* Desf. ex A. Berger, *E. trigona* Mill., *E. turbiniformis* Chiov., *E. turkanensis* S. Carter, *E. uhligiana* Pax, *E. umbonata* S. Carter, *E. umfoloziensis* Peckover, *E. undulatifolia* Janse, *E. unicornis* R.A. Dyer, *E. unispina* N.E. Br., *E. vajravelui* Binojk. & N.P. Balakr., *E. vallis* L.C. Leach, *E. vandermere* R.A. Dyer, *E. venenata* Marloth, *E. venenifera* Tremaux ex Kotschy, *E. venterii* L.C. Leach ex R.H. Archer & S. Carter, *E. viduiflora* L.C. Leach, *E. virosa* Willd., *E. vittata* S. Carter, *E. volkmanniae* Dinter, *E. vulcanorum* S. Carter, *E. wakefieldii* N.E. Br., *E. waterbergensis* R.A. Dyer, *E. whelanii* L.C. Leach, *E. williamsonii* L.C. Leach, *E. xylacantha* Pax, *E. zoutpansbergensis* R.A. Dyer.

Euphorbia sect. *Euphorbia* is the largest and one of the most distinctive groups in *E.* subg. *Euphorbia*. The defining character for this clade is the spine-shield—a horny pad of tissue subtending or surrounding each leaf base that typically bears two or four spiny outgrowths. These outgrowths are usually interpreted as a pair of stipular spines and a pair of prickles (Carter, 1994). The vast majority of species in *E.* sect. *Euphorbia* have spine-shields, but in a few species they have been lost (e.g., *E. piscidermis* and geophytes like *E. meenae*).

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■ LITERATURE CITED

- Aubriot, X.** 2012. Radiations évolutives, “innovations clés” et notions d’espèces dans le genre *Euphorbia* L. à Madagascar. Ph.D. Dissertation, Muséum National d’Histoire Naturelle, Paris, France.
- Bally, P.R.O.** 1967. Miscellaneous notes on the flora of Tropical East Africa including description of new taxa, 35–37. *Candollea* 22: 255–263.
- Barres, L., Vilatersana, R., Molero, J., Susanna, A. & Galbany-Casals, M.** 2011. Molecular phylogeny of *Euphorbia* subg. *Esula* sect. *Aphyllis* (Euphorbiaceae) inferred from nrDNA and cpDNA markers with biogeographic insights. *Taxon* 60: 705–720.
- Bernal, R., Mora, F. & Murillo, J.** 2006. *Euphorbia sinclairiana*, an older name for the widespread *Euphorbia elata*. *Caldasia* 28: 217–220.
- Boissier, E.** 1862. Euphorbieae. Pp. 3–188 in: Candolle, A.P. de (ed.), *Prodromus systematis naturalis regni vegetabilis*, vol. 15(2). Paris: Victor Mason and Fils.
- Bridges, E.L. & Orzell, S.L.** 2002. *Euphorbia* (Euphorbiaceae) section *Tithymalus* subsection *Inundatae* in the southeastern United States. *Lundellia* 5: 59–78.
- Bruyns, P.V., Mapaya, R.J. & Hedderson, T.** 2006. A new subgeneric classification for *Euphorbia* (Euphorbiaceae) in southern Africa based on ITS and *psbA-trnH* sequence data. *Taxon* 55: 397–420. <http://dx.doi.org/10.2307/25065587>
- Bruyns, P.V., Klak, C. & Hanacek, P.** 2011. Age and diversity in Old World succulent species of *Euphorbia* (Euphorbiaceae). *Taxon* 60: 1717–1733.
- Cacho, N.I., Berry, P.E., Olson, M.E., Steinmann, V.W. & Baum, D.A.** 2010. Are spurred cyathia a key innovation? Molecular systematics and trait evolution in the slipper spurge (Pedilanthus clade: *Euphorbia*, Euphorbiaceae). *Amer. J. Bot.* 97: 493–510. <http://dx.doi.org/10.3732/ajb.0900090>
- Carter, S.** 1994. A preliminary classification of *Euphorbia* subgenus *Euphorbia*. *Ann. Missouri Bot. Gard.* 81: 368–379. <http://dx.doi.org/10.2307/2992103>
- Dressler, R.L.** 1957. The genus *Pedilanthus*. *Contr. Gray Herb.* 182: 1–188.
- Edgar, R.C.** 2004. MUSCLE: Multiple sequence alignment with high accuracy and high throughput. *Nucl. Acids Res.* 32: 1792–1797. <http://dx.doi.org/10.1093/nar/gkh340>
- Edwards, E.J. & Donoghue, M.J.** 2006. *Pereskia* and the origin of the cactus life-form. *Amer. Naturalist* 167: 777–793. <http://dx.doi.org/10.1086/504605>
- Eggl, U.** 1994. Xerophytic euphorbias from Brazil. *Euphorbia J.* 9: 11–23.
- Forster, P.I.** 1994. Revision of *Euphorbia plumerioides* Tejasm. ex Hassk. (Euphorbiaceae) and allies. *Austrobaileya* 4: 245–264.
- Gilbert, M.G.** 1987. Two new geophytic species of *Euphorbia* with comments on the subgeneric groupings of its African members. *Kew Bull.* 42: 231–244. <http://dx.doi.org/10.2307/4109908>
- Gilbert, M.G.** 1995. Euphorbiaceae. Pp. 265–380 in: Edwards, S., Mesfin Tadesse & Hedberg, I. (eds.), *Flora of Ethiopia and Eritrea*. Uppsala: Uppsala University; Addis Ababa: Addis Ababa University.
- Haevermans, T.** 2003. *Le genre Euphorbia à Madagascar: Phylogénie moléculaire et systématique*. Ph.D. Dissertation, Muséum National d’Histoire Naturelle, Paris, France.
- Haevermans, T. & Labat, J.-N.I.** 2004. A synoptic revision of the Malagasy endemic *Euphorbia pervilleana* group. *Syst. Bot.* 29: 118–124. <http://dx.doi.org/10.1600/036364404772974266>
- Haevermans, T., Hoffmann, P., Lowry, P.P., Labat, J.N. & Randrianjohany, E.** 2004. Phylogenetic analysis of the Madagascan *Euphorbia* subgenus *Lacanthis* based on ITS sequence data. *Ann. Missouri Bot. Gard.* 91: 247–259.
- Hall, T.A.** 1999. BioEdit: A user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. *Nucl. Acids. Symp. Ser.* 41: 95–98.
- Hassall, D.C.** 1977. The genus *Euphorbia* in Australia. *Austral. J. Bot.* 25: 429–453. <http://dx.doi.org/10.1071/BT9770429>
- Horn, J.W., Van Ee, B.W. & Wurdack, K.J.** 2011. The giant genus *Euphorbia* (Euphorbiaceae): Deep phylogenetics and major evolutionary patterns. Symposium talk, International Botanical Conference, Melbourne, Australia.
- Horn, J.W., Van Ee, B.W., Morawetz, J.J., Riina, R., Steinmann, V.W., Berry, P.E. & Wurdack, K.J.** 2012. Phylogenetics and the evolution of major structural characters in the giant genus *Euphorbia* L. (Euphorbiaceae). *Molec. Phylogen. Evol.* 63: 305–326. <http://dx.doi.org/10.1016/j.ympev.2011.12.022>
- Huelsenbeck, J.P. & Ronquist, F.** 2001. MRBAYES: Bayesian inference of phylogenetic trees. *Bioinformatics* 17: 754–755. <http://dx.doi.org/10.1093/bioinformatics/17.8.754>
- Lemmon, A.R.J.M.B., Stanger-Hall, K. & Lemmon, E.M.** 2009. The effect of missing data on phylogenetic estimates obtained by maximum-likelihood and Bayesian inference. *Syst. Biol.* 58: 130–145. <http://dx.doi.org/10.1093/sysbio/syp017>
- Marshall, D.C.** 2010. Cryptic failure of partitioned Bayesian phylogenetic analyses: Lost in the land of long trees. *Syst. Biol.* 59: 108–117. <http://dx.doi.org/10.1093/sysbio/syp080>
- Marshall, D.C., Simon, C. & Buckley, T.R.** 2006. Accurate branch length estimation in partitioned Bayesian analyses requires accommodation of among-partition rate variation and attention to branch length priors. *Syst. Biol.* 55: 993–1003. <http://dx.doi.org/10.1080/10635150601087641>
- Müller, K.** 2005. The efficiency of different search strategies in estimating parsimony jackknife, bootstrap, and Bremer support. *B. M. C. Evol. Biol.* 5: 58. <http://dx.doi.org/10.1186/1471-2148-5-58>
- Müller, K.** 2006. Incorporating information from length-mutational events into phylogenetic analysis. *Molec. Phylogen. Evol.* 38: 667–676. <http://dx.doi.org/10.1016/j.ympev.2005.07.011>
- Nobel, P.S.** 1988. *Environmental biology of agaves and cacti*. Cambridge: Cambridge University Press.
- Olmstead, R.G. & Sweere, J.A.** 1994. Combining data in phylogenetic

- systematics: An empirical approach using three molecular data sets in the Solanaceae. *Syst. Biol.* 43: 467–481.
<http://dx.doi.org/10.1093/sysbio/43.4.467>
- Park, K.R. & Jansen, R.K.** 2007. A phylogeny of Euphorbiae subtribe Euphorbiinae (Euphorbiaceae) based on molecular data. *J. Pl. Biol.* 50: 644–649. <http://dx.doi.org/10.1007/BF03030608>
- Posada, D. & Crandall, K.A.** 1998. MODELTEST: Testing the model of DNA substitution. *Bioinformatics* 14: 817–818.
<http://dx.doi.org/10.1093/bioinformatics/14.9.817>
- Prenner, G. & Rudall, P.J.** 2007. Comparative ontogeny of the cyathium in *Euphorbia* (Euphorbiaceae) and its allies: Exploring the organ-flower-inflorescence boundary. *Amer. J. Bot.* 94: 1612–1629.
<http://dx.doi.org/10.3732/ajb.94.10.1612>
- Rambaut, A. & Drummond, A.** 2007. Tracer, version 1.5. Institute of Evolutionary Biology, University of Edinburgh. <http://beast.bio.ed.ac.uk/Tracer>
- Riina, R. & Berry, P.E. (coord.)** 2012. Euphorbia planetary biodiversity inventory database. <http://app.tolkin.org/projects/72/taxa>
- Rizzini, C.T.** 1987. Cactiform species of *Euphorbia* from Brazil (Euphorbiaceae). *Revista Brasil. Biol.* 49: 979–997.
- Ronquist, F. & Huelsenbeck, J.P.** 2003. MrBayes 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics* 19: 1572–1574.
<http://dx.doi.org/10.1093/bioinformatics/btg180>
- Samuel, R., Kathriarachchi, H., Hoffmann, P., Barfuss, M.H.J., Wurdack, K.J., Davis, C.C. & Chase, M.W.** 2005. Molecular phylogenetics of Phyllanthaceae: Evidence from plastid *matK* and nuclear *phyC* sequences. *Amer. J. Bot.* 92: 132–141.
<http://dx.doi.org/10.3732/ajb.92.1.132>
- Shaw, J., Lickey, E.B., Beck, J.T., Farmer, S.B., Liu, W., Miller, J., Siripun, K.C., Winder, C.T., Schilling, E.E. & Small, R.L.** 2005. The tortoise and the hare II: Relative utility of 21 noncoding chloroplast DNA sequences for phylogenetic analysis. *Amer. J. Bot.* 92: 142–166. <http://dx.doi.org/10.3732/ajb.92.1.142>
- Simmons, M.P. & Ochoterena, H.** 2000. Gaps as characters in sequence-based phylogenetic analyses. *Syst. Biol.* 49: 369–381.
<http://dx.doi.org/10.1093/sysbio/49.2.369>
- Staden, R.** 1996. The Staden sequence analysis package. *Molec. Bio-technol.* 5: 233–241. <http://dx.doi.org/10.1007/BF02900361>
- Stamatakis, A.** 2006. RAxML-VI-HPC: Maximum likelihood-based phylogenetic analyses with thousands of taxa and mixed models. *Bioinformatics* 22: 2688–2690.
<http://dx.doi.org/10.1093/bioinformatics/btl446>
- Steinmann, V.W. & Porter, J.M.** 2002. Phylogenetic relationships in Euphorbiae (Euphorbiaceae) based on ITS and *ndhF* sequence data. *Ann. Missouri Bot. Gard.* 89: 453–490.
<http://dx.doi.org/10.2307/3298591>
- Steinmann, V.W., Van Ee, B., Berry, P.E. & Gutierrez, J.** 2007. The systematic position of *Cubanthus* and other shrubby endemic species of *Euphorbia* (Euphorbiaceae) in Cuba. *Anales Jard. Bot. Madrid* 64: 123–133.
- Urbatsch, L.E., Baldwin, B.G. & Donoghue, M.J.** 2000. Phylogeny of the coneflowers and relatives (Heliantheae: Asteraceae) based on nuclear rDNA internal transcribed spacer (ITS) sequences and chloroplast DNA restriction site data. *Syst. Bot.* 25: 539–565.
<http://dx.doi.org/10.2307/2666695>
- White, A.C., Dyer, R.A. & Sloan, B.** 1941. *The succulent Euphorbiae*, 2 vols. Padasena: Abbey Gardens Press.
- White, T.J., Bruns, T., Lee, S. & Taylor, J.W.** 1990. Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. Pp. 315–324 in: Innis, M.A., Gelfand, D.H., Sninsky, J.J. & White, T.J. (eds.), *PCR protocols: A guide to methods and applications*. San Diego: Academic Press.
- Wilgenbusch, J.C., Warren, D.L. & Swofford, D.L.** 2004. AWTY: A system for graphical exploration of MCMC convergence in Bayesian phylogenetic inference. School of Computation Sciences, Florida State University. <http://ceb.csit.fsu.edu/awty>
- Yang, Y., Riina, R., Morawetz, J.J., Haevermans, T., Aubriot, X. & Berry, P.E.** 2012. Molecular phylogenetics and classification of *Euphorbia* subgenus *Chamaesyce* (Euphorbiaceae). *Taxon* 61: 764–789.
- Zimmermann, N.F.A., Ritz, C.M. & Hellwig, F.H.** 2010. Further support for the phylogenetic relationships within *Euphorbia* L. (Euphorbiaceae) from nrITS and *trnL-trnF* IGS sequence data. *Pl. Syst. Evol.* 286: 39–58.
<http://dx.doi.org/10.1007/s00606-010-0272-7>