Phylogenetic Relationships in Euphorbieae (Euphorbiaceae) Based on ITS and ndhF Sequence Data

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PHYLOGENETIC RELATIONSHIPS IN EUPHORBIEAE (EUPHORBIACEAE) BASED ON ITS AND *ndh*F SEQUENCE DATA[1]

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ABSTRACT

The monophyly and phylogenetic relationships of the tribe Euphorbieae (Euphorbiaceae) were evaluated using separate weighted maximum parsimony analyses of nucleotide sequences of the nrDNA internal transcribed spacer (ITS) region and cpDNA coding region *ndh*F. The study included 223 ingroup species representing nearly all of the previously recognized genera, subgenera, and sections within the Euphorbieae and 4 outgroup taxa from the tribe Hippomaneae (Euphorbiaceae). Both the ITS and *ndh*F analyses support the monophyly of Euphorbieae in addition to the monophyly of its three subtribes, Anthosteminae, Neoguillauminiinae, and Euphorbiinae. Within Euphorbiinae, there are four major clades, only one of which corresponds with a previously recognized taxon; the three remaining clades are conglomerates of various subgenera and sections. The majority of the subtribe is composed of a paraphyletic *Euphorbia*. All other genera currently recognized in the subtribe are nested within *Euphorbia*. In addition, *Synadenium* and *Endadenium* are nested within *Monadenium*. Within *Euphorbia*, the majority of the currently recognized subgenera are either paraphyletic or polyphyletic. Biogeographical patterns examined in light of the molecular evidence suggest that the tribe Euphorbieae arose in Africa, possibly before the breakup of Gondwanaland, at which time the major lineages of subtribe

Euphorbiinae were already present. It is argued that the best solution for *Euphorbia* classification is a broad circumscription of *Euphorbia* that contains all of the about 2000 species of the subtribe Euphorbiinae.

Key words: classification, *Euphorbia*, Euphorbieae, ITS, *ndh*F.

It was only a year after Linnaeus (1753) first circumscribed the genus *Euphorbia* L. (Euphorbiaceae) to include all of the then-known members of the tribe Euphorbieae that other botanists began to divide the genus into several smaller genera (Miller, 1754; Trew, 1754). The controversy has continued since, and almost 250 years later the issue as to whether *Euphorbia* should be recognized in its initial broad sense or be separated into many smaller genera still has not been resolved. *Euphorbia* and Euphorbieae are generally considered taxonomically difficult, and a considerable degree of uncertainty has always existed about the relationships of the groups within them. This problem is due in great part to extreme morphological diversity, a large number of species, and a subcosmopolitan distribution. Few workers have been able to gain a complete understanding of the tribe throughout its immense range, and there has never been a universally accepted classification. This lack of consistency has hindered and to some extent discouraged research within the genus *Euphorbia* as well as the Euphorbieae as a whole. Thus, a clear understanding of relationships within the tribe is of great importance in order to provide subsequent workers with a phylogenetic framework on which to base their studies.

The tribe Euphorbieae is characterized by its synapomorphic pseudanthial inflorescence (termed a cyathium) composed of a gland-bearing involucre of several united bracts and their associated flowers and bracteoles. Each bract subtends a monochasial staminate inflorescence, and these monochasia surround a single pistillate flower. The individual flowers in Euphorbieae are highly reduced and represented by a single stamen or ovary, with or without a perianth. The staminate flowers terminate slender pedicels, and the pistillate flowers can be long-pedicellate or subsessile. This structure is highly complex, and there are still doubts as to its exact nature and evolution (Gilbert, 1994).

According to the most recent synopsis of the Euphorbiaceae (Webster, 1994), the Euphorbieae contain 11 genera placed into three subtribes: Anthosteminae (Baill.) G. L. Webster, Neoguillauminiinae Croizat, and Euphorbiinae. The presence or absence of a perianth (presumably a calyx) on the flowers distinguishes these taxa. In Anthosteminae both the staminate and pistillate flowers possess a

perianth; in Neoguillauminiinae only the pistillate flowers possess a perianth; and in Euphorbiinae neither the pistillate nor the staminate flowers possess a well-developed perianth, although a rudimentary calyx-like structure is present below the pistillate flowers in a few species.

Anthosteminae consist of two genera of tropical forest trees: *Anthostema* A. Juss. (4 spp. disjunct in west tropical Africa and Madagascar) and *Dichostemma* Pierre (1 sp. in west tropical Africa). This subtribe is considered the least specialized because of the perianth on both the staminate and pistillate flowers. Further, each individual involucral bract closely envelops a cluster of many bracteoles and staminate flowers. The cyathia are bisexual or staminate. In *Anthostema* the cyathia are arranged in condensed axillary cymes. The involucre is made up of four united bracts and is slightly zygomorphic because it is spread in an open half circle. There are five large glands along the involucral bract margins and between the clusters of staminate flowers. The 3-locular pistillate flower is not contained in the involucre but instead lies at the base of the involucre's open side. Based on its open involucral morphology and the possible lateral position of the pistillate flower, this genus probably most closely resembles the ancestral inflorescence morphology of the Euphorbieae. In *Dichostemma* the cyathia are arranged in loose, open, axillary or terminal cymes. In contrast to *Anthostema*, the four monochasia-containing involucral bracts are united in a ring, and the involucre is completely closed and actinomorphic. The four involucral glands are contained within this structure and attached to the inner walls of the bracts and the base of the gynophore. In the center of the inflorescence is either a minute pistillode or a 4-locular pistillate flower.

Like Anthosteminae, the subtribe Neoguillauminiinae also contains two genera: *Calycopeplus* (5 spp. in Australia) and *Neoguillauminia* Croizat (1 sp. in New Caledonia). In contrast to Anthosteminae, the staminate flowers lack a perianth. However, a perianth is present on the pistillate flower, and this combination of features defines the subtribe. In addition, the bracts of the involucre do not tightly envelop the staminate monochasia, although the latter are enclosed within large bracteoles. *Calycopeplus* are xerophytic shrubs with small, oppo-

site leaves and cyathia arranged in axillary clusters. The involucre is distinctly cupular and is made up of four bracts. The glands are located between the lobes and attached to the wall of the cupular involucre. There is a central pistillate flower surrounded by four staminate monochasia that are opposite the involucral lobes. The sole representative of *Neoguillauminia* is a mesic forest tree or shrub with large, spirally arranged leaves. The cyathia are long-pedunculate and arranged in few-cyathiate axillary or subterminal groups. The involucre is composed of four to six bracts that extend into large, petaloid appendages. There are eight to twelve glands arranged in pairs between the four to six staminate monochasia and attached to the base of the involucre and sometimes also to the base of the gynophore. There is a single central pistillate flower. *Neoguillauminia* is noteworthy because the involucres are generally composed of five bracts, and a 5-merous involucre also characterizes Euphorbiinae, discussed below. *Calycopeplus*, as well as *Anthostema* and *Dichostemma*, possess 4-merous involucres.

With about 2000 species and a subcosmopolitan distribution, the largest and most complex subtribe is Euphorbiinae. It is characterized by the lack of a perianth on both the staminate and pistillate flowers, although a rudimentary calyx-like structure is present below the pistillate flowers of a few species. In addition, the involucre is made up of five united bracts, not four as generally are found in the other subtribes of Euphorbieae, and the bracteoles that surround the staminate monochasia are generally reduced. The glands are mostly located along the rim of a cupular involucre. Again following the circumscription of Webster (1994), the subtribe contains seven genera: *Chamaesyce* Gray, *Cubanthus* (Boiss.) Millsp., *Endadenium* Leach, *Euphorbia*, *Monadenium* Pax, *Pedilanthus* Necker ex Poit., and *Synadenium* Boiss. *Poinsettia* Graham and *Elaeophorbia* Stapf are also sometimes recognized as distinct from *Euphorbia*, but their status is not as widely accepted, and most authors treat these as infrageneric taxa of *Euphorbia*. Extreme emphasis is placed on variation in the configuration of the cyathium, and with the exception of *Chamaesyce*, the genera segregated from *Euphorbia* are distinguished on the basis of involucral features.

Euphorbiinae are dominated by *Euphorbia*, which accounts for ca. 80% of the species and occurs throughout the geographic range of the subtribe. The genus is best known for the common Christmas poinsettia (*Euphorbia pulcherrima* Willd. ex Klotzsch) and is popular with horticulturists because of the prevalence of succulents. One of the most fascinating features of the subtribe is its great diversity of growth forms. Large forest trees, shrubs, perennial herbs, geophytes, annuals, and a great diversity of succulents are all well represented. In comparison to most other genera of Euphorbiinae, the cyathial morphology of *Euphorbia* is relatively unspecialized. The cyathia are actinomorphic and generally possess one to five separate glands situated on the rim of the involucre, and this plesiomorphic feature unites the genus.

With about 300 species, *Chamaesyce* is the largest segregate genus from *Euphorbia*. It occurs widely, but most species are confined to the New World. Distinguished on the basis of vegetative morphology, its cyathia are nearly identical to those of many species of *Euphorbia* subg. *Agaloma* (Raf.) House. *Chamaesyce* is characterized by many unusual synapomorphies: apical abortion of the main shoot and subsequent sympodial growth; interpetiolar stipules; opposite, frequently asymmetrical leaves; and C_4 photosynthesis (Koutnik, 1984, 1987). Numerous Euphorbieae specialists (e.g., Carter, 1988a, 1992b; Gilbert, 1987) retain it as a subgenus of *Euphorbia*.

The other five segregate genera of *Euphorbia* are also easily identifiable, but their differences, as mentioned above, involve involucral features. Three genera possess zygomorphic cyathia: in *Pedilanthus* (15 spp., primarily Mexico) there are two to six glands enclosed within an adaxial, spurlike extension of the involucre; in *Cubanthus* (3 spp., Cuba and Hispaniola) there are two glands united into a shieldlike structure on the outside of the involucre; and in *Monadenium* (ca. 70 spp., Africa) the glands are united into a single horseshoe-shaped structure. The two remaining segregate genera possess actinomorphic cyathia: in *Synadenium* (20 spp., Africa) the cyathia possess five united glands that form a complete ring around the top, and in *Endadenium* (1 sp., Angola) the closed rim of the cyathium is not a gland but instead an apparently eglandular extension of the involucral wall with a ring of nectar-bearing depressions on the inside of the involucre.

TAXONOMIC HISTORY OF THE TRIBE EUPHORBIEAE

The taxonomic works treating Euphorbieae are numerous, and only a brief overview, focusing on those with broad and significant implications to modern Euphorbieae taxonomy, will be provided here. A more detailed account is found in Steinmann (2001).

One of the first prominent taxonomic treatments of the Euphorbieae was that of Klotzsch and Garcke

(1859, 1860). Although these authors segregated both *Anthostema* and *Pedilanthus* into separate tribes, the Anthostemeae and Pedilantheae, they did concede their close relationship with Euphorbieae. Their Euphorbieae contained 408 species, all members of present-day Euphorbiinae. *Euphorbia* was recognized in a restricted sense, with only 27 species. The remainder were placed in 17 segregate genera, organized in two subtribes: Anisophyllae Klotzsch & Garcke and Tithymalae Klotzsch & Garcke.

The first and last monograph of the entire Euphorbieae, and the basic framework for the classification that is still in use today, was provided by Boissier in 1862 (supplement 1866) for de Candolle's *Prodromus*. Boissier followed Klotzsch and Garcke by recognizing Anthostemeae as distinct, but differed from them by submerging Pedilantheae into Euphorbieae. Euphorbieae contained 740 species. Also in contrast to Klotzsch and Garcke, Boissier recognized *Euphorbia* in a broad sense, and his Euphorbieae contained only three genera, all currently placed in Euphorbiinae: *Pedilanthus* (15 spp.), *Synadenium* (2 spp.), and *Euphorbia* (723 spp.). The taxa of *Euphorbia* were positioned into 27 sections and two "series": Appendiculatae Boiss. (corresponding to Klotzsch and Garcke's subtribe Anisophyllae) and Exappendiculatae Boiss. (corresponding to Klotzsch and Garcke's subtribe Tithymalae). *Calycopeplus* and *Neoguillauminia* were treated in *Euphorbia*, and *Cubanthus* was erected as a section of *Pedilanthus*.

Bentham (1878) expounded greatly on the Euphorbiaceae as a prelude to his treatment of the family in *Genera Plantarum* (Bentham, 1880). He agreed that *Euphorbia* should be recognized in the broad sense and followed Boissier's treatment with only minor modifications. Anthostemae was combined with Euphorbieae. *Calycopeplus*, first described by Planchon in 1861 but subsequently treated as a synonym of *Euphorbia* by Boissier (1862), was resurrected at the rank of genus. Bentham's greatest change concerned the rank of Boissier's sections of *Euphorbia*, and he proposed a system containing only six sections, under which the majority of Boissier's sections were reduced to subsections. Otherwise, Bentham did little to modify Boissier's grouping of species.

Around the turn of the century, Pax (1894a) described *Monadenium* and Pierre (1896) described *Dichostemma*, the second known genus in the modern subtribe Anthosteminae. Nearly two decades later, Millspaugh (1913) first recognized *Cubanthus* as a distinct genus.

The next major treatment of the Euphorbieae was that of Pax and Hoffmann (1931) in Engler's *Die natürlichen Pflanzenfamilien*. They essentially followed Bentham's classification with only minor modifications to accommodate newly described taxa. Again, a single tribe, the Euphorbieae, was recognized without any further divisions. *Anthostema*, *Dichostemma*, and *Calycopeplus* were all treated as distinct. *Euphorbia* continued to be recognized in the broad sense, although the number of segregate genera had increased. In addition to the earlier recognized *Pedilanthus* and *Synadenium*, these authors segregated the genera *Monadenium*, *Stenadenium* Pax, *Elaeophorbia*, and *Diplocyathium* H. Schmidt. The latter two segregates are now treated within *Euphorbia* (Webster, 1994), and *Stenadenium* is currently treated as a synonym of *Monadenium* (Bally, 1959, 1961). *Cubanthus* was relegated back to a section of *Pedilanthus*.

In 1937, Croizat described the genus *Neoguillauminia* and the subtribe Neoguillauminiinae to accommodate it. The type, *N. cleopatra*, was first described by Baillon (1861) as a species of *Euphorbia* and placed in his monotypic *E.* sect. *Decadenia* Baill. Boissier (1862) treated this species within *E.* sect. *Tithymalus*.

Shortly after Croizat's contribution, Wheeler (1943) published a broad classification of the entire Euphorbieae. This was the first major conspectus to advocate the use of subgenus as the primary division of *Euphorbia*, and it is this rank that predominates in current Euphorbiinae classification. Wheeler recognized a single Euphorbieae but abandoned Croizat's subtribes. The genera that he included were the same as those of Pax and Hoffmann (1931) except that *Diplocyathium* was relegated to synonymy within *Euphorbia*, and Croizat's newly described *Neoguillauminia* was recognized. *Euphorbia* consisted of eight subgenera, and in general, these corresponded to the sections recognized by Pax and Hoffmann (1931).

Dressler (1957) provided a monograph of *Pedilanthus* in which he convincingly demonstrated that the species of *Cubanthus* do not belong within *Pedilanthus* and should be treated separately. Dressler is also noteworthy because he advocated that *Euphorbia* should be recognized in the narrow sense and restricted to Old World succulents.

In the years after Dressler's treatment, Webster made important contributions to Euphorbieae taxonomy. He suggested the recognition of *Chamaesyce* as a genus and at the same time strongly suggested that *Elaeophorbia* should be treated within *Euphorbia* (Webster, 1967). Eight years later, Webster (1975) circumscribed the tribe to its present, generally accepted configuration. He created the

subtribe Anthosteminae to accommodate *Anthostema* and *Dichostemma* and resurrected Neoguillauminiinae to include *Calycopeplus* and *Neoguillauminia*. In his third subtribe Euphorbiinae, he recognized seven genera: *Euphorbia, Chamaesyce, Cubanthus, Endadenium, Monadenium, Pedilanthus,* and *Synadenium*.

Gilbert (1987) and Carter (1985, 1988a) have made the most recent modifications in Euphorbiinae classification. Their changes primarily involve African members and the elevation of various previously recognized sections of *Euphorbia* to subgeneric rank.

In summary, at the time of this writing most authors agree that Euphorbieae is a single tribe with three subtribes: the Anthosteminae, the Neoguillauminiinae, and the Euphorbiinae. Within Anthosteminae there are two genera, *Anthostema* and *Dichostemma*. Within Neoguillauminiinae there are also two genera, *Calycopeplus* and *Neoguillauminia*. The subtribe Euphorbiinae contains about seven genera. Those that are universally accepted are *Euphorbia, Endadenium, Monadenium, Synadenium, Pedilanthus,* and *Cubanthus*. Genera that are less frequently accepted are *Chamaescye, Elaeophorbia,* and *Poinsettia*. Other segregate genera have not even gained minor acceptance. Within *Euphorbia*, the common primary division employed is the rank of subgenus, and there are 9 to 11 generally recognized subgenera: *Agaloma, Chamaesyce* Raf. (when not treated as a genus), *Poinsettia* (Graham) House (when not treated as a genus), *Esula* Pers., *Eremophyton* (Boiss.) L. C. Wheeler, *Euphorbia, Lacanthis* (Raf.) M. G. Gilbert, *Tirucalli* (Boiss.) S. Carter, *Trichadenia* (Pax) S. Carter, *Rhizanthium* (Boiss.) L. C. Wheeler, and *Lyciopsis* (Boiss.) L. C. Wheeler. However, a modern, global, coherent classification of the genus is lacking, and some proposed sections of *Euphorbia* have not been adequately accommodated within a currently recognized subgenus (e.g., *E.* sects. *Arthrothamnus* (Klotzsch & Garcke) Boiss., *Denisophorbia* (Leandri) Croizat, and *Deuterocalli* Croizat). Detailed accounts of the currently recognized infrageneric taxa of *Euphorbia* and their taxonomic histories are presented in the discussion section.

MATERIALS AND METHODS

In total, 227 species were sampled (Appendix 1), including 4 outgroup and 223 ingroup species. Outgroups were chosen from tribe Hippomaneae because it is traditionally considered to be closely related to the Euphorbieae (Webster, 1994), and a broad molecular phylogenetic reconstruction of the

entire Euphorbiaceae also supports their affinity (Kenneth Wurdack, pers. comm.). An attempt was made to include as broad a sample as possible from Euphorbieae. Four species of Anthosteminae, 4 species of Neoguillauminiinae, and 215 species of Euphorbiinae were sequenced. These included all genera (except *Cubanthus*) recognized by Webster (1994). The sole representative of *Endadenium*, eight species of *Pedilanthus*, one species of *Synadenium*, eight species of *Chamaesyce*, and five species of *Monadenium* were included. One hundred ninety-two species of *Euphorbia* were represented, including all sections (except sects. *Bongium* Boiss. and *Caulanthium* Boiss.) treated by Boissier (1862) and most other important taxonomic groups recognized by subsequent workers (e.g., Webster, 1967; Gilbert, 1987; Carter, 1985, 1988a).

The ITS analysis included 216 species (4 outgroups, 3 Anthosteminae, 2 Neoguillauminiinae, and 207 Euphorbiinae). The sample for the *ndh*F analysis was smaller and included 114 species (4 outgroups, 4 Anthosteminae, 3 Neoguillauminiinae, and 103 Euphorbiinae). Following a preliminary analysis of the ITS sequence data, a subset of the sampled taxa representing the major clades and well-supported lineages was sequenced for the *ndh*F analysis. In addition, 15 species were included in the *ndh*F analysis that were not included in the ITS analysis because of problems obtaining "clean" ITS sequences for these taxa (see Appendix 1).

Total genomic DNA was isolated from either fresh, silica gel-dried, or herbarium material using a modified CTAB method (Doyle & Doyle, 1987). Two genic regions were employed in the phylogenetic reconstructions: the cpDNA coding region *ndh*F and the nrDNA internal transcribed spacer region (ITS). ITS amplification using the polymerase chain reaction (PCR) followed the procedures described by Baldwin (1992) and Baldwin et al. (1995). Amplification of the *ndh*F region generally followed the protocols described by Olmstead and Sweere (1994) and Kim and Jansen (1995). The 5' quarter of the *ndh*F region was excluded due to problems amplifying it. Also, a primer ca. 50 bp internal to the 3' end "2110Ri" (5'-TCA ATT ATT CGT TTA TCA A-3') was designed because many taxa would not amplify using primer "2110R." Four additional primers were specifically designed for this study: (1) (5'-TTA TTC AAT ATC TYT ATG GGG TAA-3'), (2) (5'-TAA CCC CAT ARA GAT ATT GAA TAA-3'), (3) (5'-TAG GAA TTC CYT TYA ATC AA-3'), and (4) (5'-TTG ATT RAA RGG AAT TCC TA-3').

The PCR products were electrophoresed using a

Table 1. Characteristics of the ITS and portion of the *ndh*F regions included in this study.

	ITS	ITS1	5.8s	ITS2	*ndh*F
Raw length (bp)	591–660	210–267	164–167	202–241	1467–1506
Aligned length	739	303	169	267	1587
Variable sites (proportion)	527 (0.71)	272 (0.90)	35 (0.21)	220 (0.82)	740 (0.47)
Parsimony-informative sites (proportion)	470 (0.64)	244 (0.81)	22 (0.13)	204 (0.76)	519 (0.33)
GC content, mean (range)	0.58 (0.50–0.70)	0.58 (0.46–0.71)	0.56 (0.51–0.58)	0.61 (0.48–0.76)	0.32 (0.30–0.33)

1.5% agrose gel in a 0.5x TBE (pH 8.3) buffer, stained with ethidium bromide, and then cleaned using the PEG precipitation protocol (Nickrent, 1996). Cycle-sequencing adhered to the manufacturer's specification using the PRISM™ Dye-Deoxy™ Terminator Kit (Perkin-Elmer, Inc.). Cycle-sequencing was followed by ethanol purification, and sequencing used an Applied Biosystems Model 373A Automated DNA Sequencing System.

Sequences were assembled from automated DNA sequence chromatograms using Sequencher 3.0 (Gene Codes Corporation, Inc.). ITS sequences were initially aligned with ClustalW v. 1.4 (Thompson et al., 1994), using a gap cost:gap extension cost ratio of 10:5, followed by visual modifications; *ndh*F sequences were aligned visually. Because of high divergence and the large number of taxa included in the study, alignment was problematic for certain highly variable regions of ITS sequences. However, the difficulties mostly occurred aligning the major lineages of Euphorbieae to each other, and alignment within major lineages was less problematic. Alignment of both ITS and *ndh*F introduced gaps into some sequences, and these sites were included in the analyses. Missing data were coded with a question mark in the matrix. Alignment matrices have been deposited at the library of Rancho Santa Ana Botanic Garden and submitted to TreeBASE (http://herbaria.harvard.edu/treebase.index.html).

The aligned ITS and *ndh*F sequence matrices were analyzed separately using PAUP* 4.0b4a for Macintosh™ (Swofford, 2000) on a Macintosh™ G3. Due to the large data sets, maximum parsimony using heuristic searches (Acctran, 10 random addition cycles, TBR branch swapping, steepest descent option not in effect) was employed. Maximum likelihood estimates of transition/transversion (TI/TV) biases were measured for both the ITS and *ndh*F data sets individually as implemented in PAUP* 4.0b4a under the HKY model of nucleotide substitution and using the equal-weighted parsimony trees. These estimates were used to produce a TI/TV step matrix, employed in further maximum parsimony analyses. This weighting scheme was employed in order to model more closely the maximum parsimony analyses to the given data set. Indels were coded as missing data. Multiple most parsimonious trees were combined in a strict consensus tree. Tree robustness was estimated using 10,000 "fast addition" heuristic bootstrap replicates.

RESULTS

Sequence variation for both ITS and *ndh*F is shown in Table 1. For ITS sequences, pairwise levels of divergence (uncorrected "p" values) for the entire Euphorbieae ranged from 34.4% (between *Anthostema* sp. nov. and *Euphorbia insulana*) to 1.1% (between *E. alta* and *E. spathulata*). For subtribe Anthosteminae, levels of divergence varied from 9.4% (between *Dichostemma glaucescens* and *Anthostema madagascariense*) to 2.2% (between *A. madagascariense* and *A.* sp. nov.); for the two included species of subtribe Neoguillauminiinae (*Neoguillauminia cleopatra* and *Calycopeplus casuarinoides*), the level of divergence was 7.6%; for subtribe Euphorbiinae levels of divergence varied from 30.9% (between *E. trichotoma* and *E. panchganiensis*) to 1.1% (between *E. alta* and *E. spathulata*). As expected, levels of divergence for *ndh*F sequences were much lower than levels observed in ITS sequences. For the entire Euphorbieae, these ranged from 11.7% (between *Anthostema* sp. nov. and *E. oaxacana*) to 0.1% (between *E. bilobata* and *E. exstipulata*). For subtribe Anthosteminae, levels of divergence varied from 2.6% (between *Anthostema* sp. nov. and *Dichostemma glaucescens*) to 0.4% (between *Anthostema* sp. nov. and *A. madagascariense*); for subtribe Neoguillauminiinae divergence levels varied from 2% (between *Calycopeplus collinus* and *C. paucifolius*) to 1.4% (between *Neoguillauminia cleopatra* and *Calycopeplus paucifolius*); for subtribe Euphorbiinae levels of divergence varied from 9.6% (between *E. aphylla* and

Table 2. Statistics from weighted maximum parsimony analyses of ITS and *ndh*F datasets and statistics for un-weighted characters of the same topology. For each analysis, number and length of most parsimonious trees, consistency index (CI), retention index (RI), and rescaled consistency index (RC) are reported.

Analysis	Number of trees	Tree length	CI	RI	RC
ITS (weighted)	2160	8838.2	0.1813	0.7219	0.1309
ITS (unweighted)	2160	6887	0.1802	0.7126	0.1284
*ndh*F (weighted)	19012	1818.2	0.5221	0.7926	0.4138
*ndh*F (unweighted)	19012	1985	0.5441	0.7992	0.4349

E. oaxacana) to 0.1% (between *E. bilobata* and *E. exstipulata*).

Transition/transversion biases were calculated to be 1.8 for the ITS data set and 0.85 for the *ndh*F data set. These biases were used in the weighted maximum parsimony analyses.

The ITS analysis resulted in the recovery of 2160 most parsimonious trees of 6887 steps (equal weighted). The *ndh*F analysis resulted in the recovery of 19,012 most parsimonious trees of 1985 steps (equal weighted). Statistics for both analyses are detailed in Table 2. The strict consensus of the 2160 trees obtained in the ITS analysis is depicted in Figures 1, 5, 7, 9, 10, 12, and 13. The strict consensus of the 19012 trees obtained in the *ndh*F analysis is depicted in Figures 2, 6, 8, 11, and 14. With the exception of Figures 3 and 4, phylograms are presented in Steinmann (2001).

For the ITS analysis, the bootstrap 50% majority rule tree (values depicted on strict consensus tree) is structurally identical to the strict consensus insofar as the majority rule tree is resolved. Many of the terminal clades are supported with high bootstrap (bs) percentage values. However, there is no support for the majority of the basal internal nodes. Notable exceptions are the ancestral nodes that define the tribe Euphorbieae and its subtribes. In the *ndh*F analysis, the bootstrap 50% majority rule tree (values depicted on strict consensus tree in Fig. 2) is structurally identical to the strict consensus with one significant difference. In the bootstrap analysis, clade A is not placed as the sister taxon of clade B but instead is located at the earliest diverging clade in a group that contains clades C and D, and this is supported by a bootstrap value of 77%. This incongruency suggests that the topology of the major clades within the subtribe Euphorbiinae should be viewed with caution. The majority of clades found in the *ndh*F strict consensus tree are supported in the bootstrap analysis, and in contrast to ITS (see Fig. 1), many of the internal, basal nodes also possess significant bootstrap support.

It is worth noting that a combined analysis was conducted for the 99 species in common between the ITS and *ndh*F data sets. The results are not presented here because results from the independent ITS and *ndh*F analyses agree strongly with each other, and the combined analysis does not provide novel insights. For the instances in which tree structure resulting from the ITS and *ndh*F analyses differed, the combined analysis generally provided the same structure as the *ndh*F analysis.

DISCUSSION

UTILITY OF THE *ndh*F AND ITS REGIONS IN EUPHORBIACEAE AND A COMPARISON OF THE RESULTING PHYLOGENIES

Despite being one of the largest angiosperm families and an important floristic component, especially in tropical regions, the Euphorbiaceae have not previously been the subject of a comprehensive molecular systematics investigation. If the results obtained here are any indication, both *ndh*F and the ITS data appear useful in inferring relationships within the family. In general, the two reconstructions of the Euphorbieae are similar, and thus corroborate evidence of their phylogenetic signal. The overall structure of both analyses is the same (Figs. 1, 2), and when differences do occur, these generally involve clades that lack bootstrap support in one or both of the analyses. There are very few instances in which well-supported clades are positioned differently in the separate analyses, e.g., the arrangement of *Euphorbia meenae* Blatt. & McCann, *E. abdelkuri* Balf.f., *E. drupifera* Thonn., and *E. poissonii* Pax (Figs. 10, 11).

MONOPHYLY OF THE EUPHORBIEAE AND ITS SUBTRIBES AND PARAPHYLY WITHIN SUBTRIBE EUPHORBIINAE

In both analyses, Euphorbieae form a monophyletic assemblage with respect to the four outgroups. However, there is not high bootstrap support for this grouping in either analysis. The unusual synapo-

Figure 1. Strict consensus of 2160 trees based on a weighted maximum parsimony analysis of the ITS region. Bootstrap values greater than 50% are shown above the branches. The tribes and subtribes of the classification of Webster (1994) are indicated. Individual strict consensuses for clades A–D are found in Figures 5, 7, 9, 10, 12, and 13.

morphic inflorescence structure of the tribe therefore supports this relationship, and it is highly probable that the tribe is indeed monophyletic. All three subtribes of Euphorbieae also form monophyletic groups (Figs. 1, 2), and these clades possess high bootstrap support, 100% for all three in the *ndh*F analysis. Further, in both analyses subtribe Anthosteminae is the earliest diverging subtribe in Euphorbieae and subtribes Neoguillauminiinae and Euphorbiinae are sister to each other. *Anthostema* and *Calycopeplus* are strongly supported to be monophyletic (bs 100% and 90% in *ndh*F, respectively), and presumably so too are the monotypic *Dichostemma* and *Neoguillauminia*. Therefore,

Webster's overall classification of the tribe Euphorbieae (1975) is consistent with the molecular results.

Within Euphorbiinae, both analyses demonstrate that *Chamaesyce, Pedilanthus, Monadenium, Synadenium,* and *Endadenium* are all nested within a paraphyletic *Euphorbia* (see clades C and D, Figs. 9–14). Also, both *Synadenium* and *Endadenium* are nested within a paraphyletic *Monadenium*.

RELATIONSHIPS AND MAJOR LINEAGES WITHIN THE EUPHORBIINAE

Both analyses support that there are four major lineages within the subtribe Euphorbiinae, here
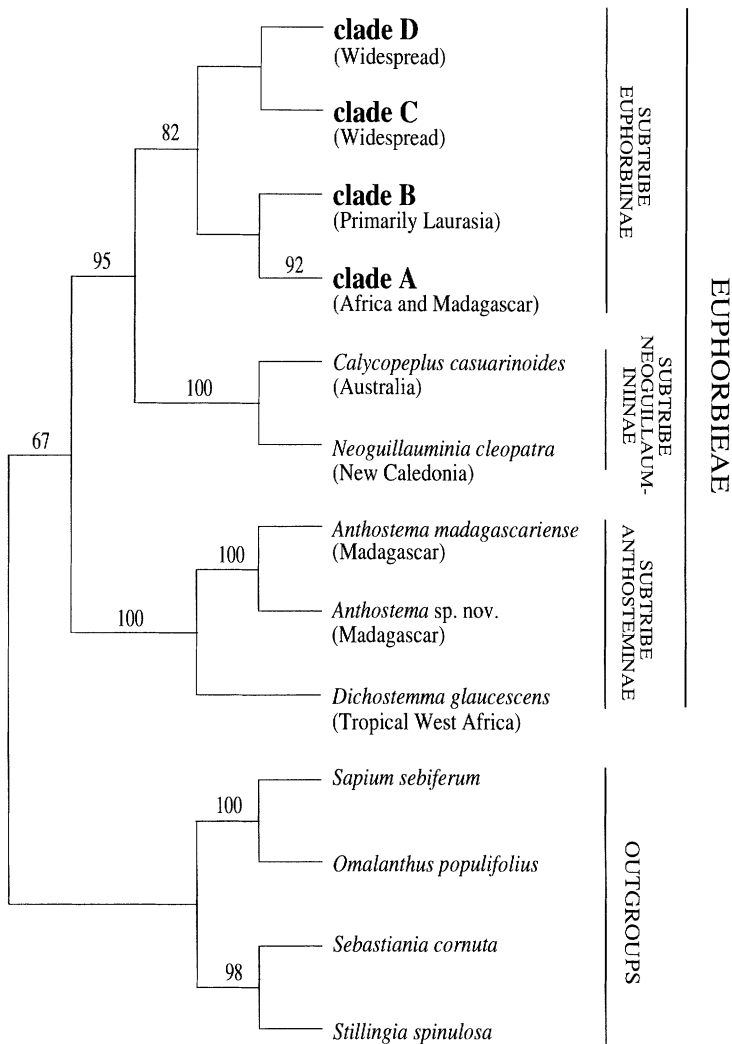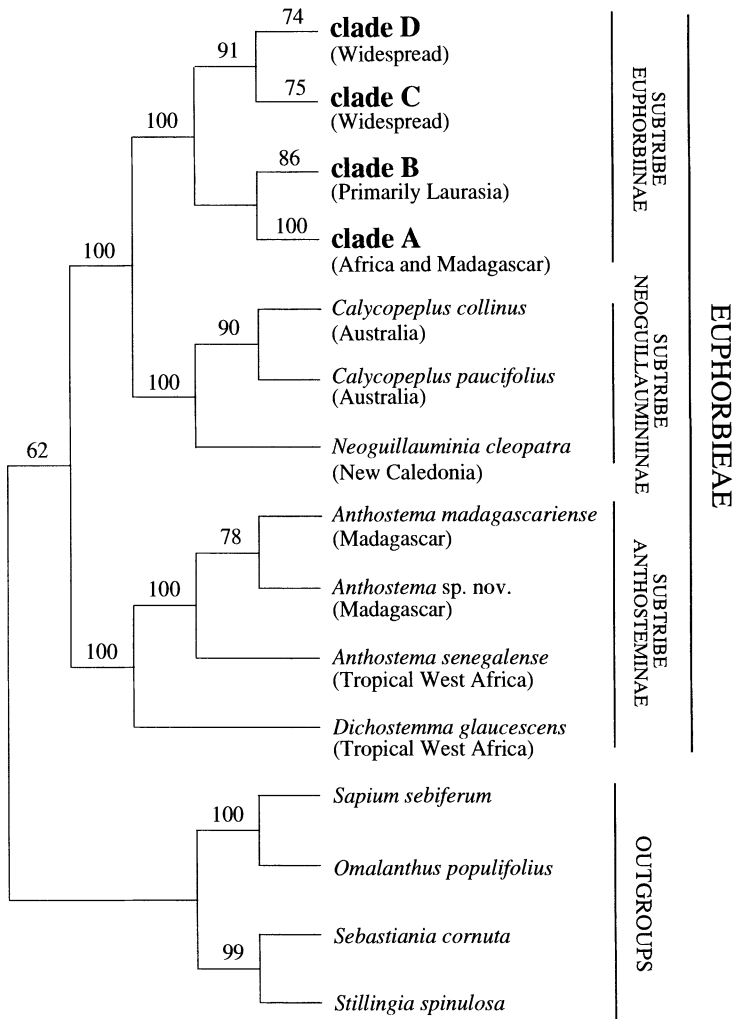
Figure 2. Strict consensus of 19,012 trees based on a weighted maximum parsimony analysis of the *ndh*F region. Bootstrap values greater than 50% are shown above the branches. The tribes and subtribes of the classification of Webster (1994) are indicated. Individual strict consensuses for clades A–D are found in Figures 6, 8, 11, and 14.

designated clades A–D. With the exception of clade B (primarily composed of the temperate herbaceous group of *Euphorbia* subg. *Esula*), none of these lineages closely correspond to any previously recognized taxon. Instead, they are conglomerates of various sections and subgenera. All of these major lineages possess significant bootstrap support in the *ndh*F analysis (bs 74–100%), while only clade A is supported in the ITS analysis (bs 92%). There still is some question, however, as to the exact relationship among these lineages. Although both the ITS and *ndh*F strict consensus trees show that clades A and B are sister to each other and together these are sister to clades C and D, there is no bootstrap support to this grouping in either analysis.

Due to the lack of a comprehensive classification, many sections of *Euphorbia* have not been accommodated within a currently recognized subgenus. Also, some sections that have been suggested to belong to a particular subgenus are demonstrated to not be closely related. Therefore, the following discussion about the major groups of Euphorbiinae is organized by taxa of various ranks.

Chamaesyce. Eight species from *Chamaesyce* were included. In both the ITS and *ndh*F analyses (Figs. 12, 14), these species form a well-supported, monophyletic group (bs 91% and 99%, respectively) in clade D. Species previously thought to intergrade with *Chamaesyce* (see Webster, 1967), such

Figure 3. Phylogram of one of the equally most parsimonious trees resulting from the ITS analysis, showing branch lengths within Euphorbieae. Only the species with the least and most changes are shown for each of the major clades of subtribe Euphorbiinae. Individual phylograms of clades A–D are given in Steinmann (2001). *E. = Euphorbia.*

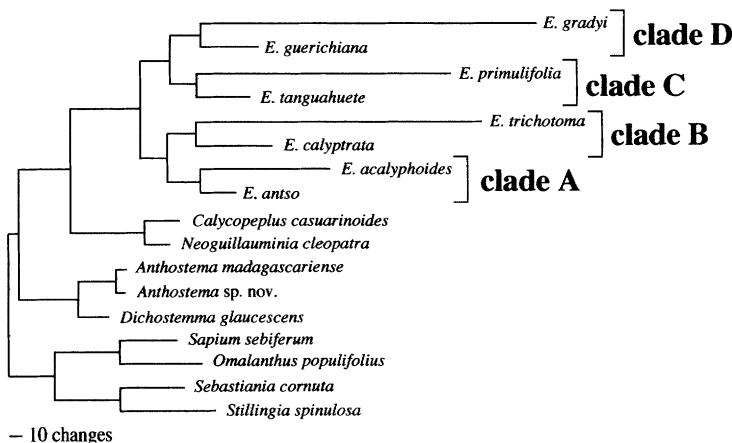as *Euphorbia innocua* L. C. Wheeler and *E. peperomioides* Boiss., appear to share their vegetative similarity due to convergence, as they do not group close to the *Chamaesyce* clade (Figs. 9, 12, 13). Similarly, *E. cheirolepis* Fisch. & C. A. Mey., suggested by Prokhanof (1949) to be possibly intermediate between *Chamaesyce* and other species of *Euphorbia*, is not supported to be closely related (Figs. 12, 14). At least based on the molecular results, these putative relatives are clearly outside *Chamaesyce*, and the characters presented in the introduction can distinguish all true species of *Chamaesyce*. As previously suggested by Dressler (1957) and Webster (1967), *Chamaesyce* is derived from within *E.* subg. *Agaloma* (Figs. 12, 14).

Sampling of *Chamaesyce* was not broad enough to determine the monophyly of the subsections proposed by Boissier (1862). However, it is noteworthy that *C. acuta* and *C. angusta*, both in *Chamaesyce* subsect. *Acutae* Boiss., lie sister to the remainder of the species sampled from *Chamaesyce* subsects. *Gymnadeniae* Boiss., *Cheloneae* Boiss., *Chamaesyce*, and *Hypericifoliae* Boiss. *Chamaesyce* subsect. *Acutae* is the only group within *Chamaesyce* not possessing the derived C_4 photosynthetic pathway otherwise characteristic of the genus (Webster et al., 1975; Mayfield, 1991).

Synadenium/Monadenium/Endadenium.   Although their composition differs between the ITS and *ndh*F analyses, a total of six species from these genera, here referred to as the *Synadenium* alliance, were included. They form a well-supported, monophyletic group (bs 100% in both analyses, see Figs. 10, 11). Both ITS and *ndh*F also suggest that *Monadenium* is paraphyletic with *Synadenium* and

Endadenium nested inside it. Morphologically, the genera are united in the possession of fused involucral glands. They belong to a well-supported clade C (bs 78% in ITS, 100% in *ndh*F) that also contains *Euphorbia* subg. *Euphorbia* and *Lacanthis*.

Pedilanthus.   As their unusual zygomorphic cyathia suggest, the eight species of *Pedilanthus* included here form a well-supported (bs 100% in both analyses), monophyletic group (Figs. 9, 11). Based primarily on its involucral appendages and predominantly Mexican distribution, Dressler (1957) and Webster (1967) suggested that *Pedilanthus* arose from *Euphorbia* subg. *Agaloma*, with *E. fulgens* Karw. ex Klotzsch as the closest potential living intermediate. However, this analysis does not support any relationship between these two groups. In fact, they do not even belong to the same major clade of Euphorbiinae, with *E. fulgens* (Fig. 13) and other members of subgenus *Agaloma* (Figs. 11–13) belonging to clade D. Beyond being a member of clade C, the exact position of *Pedilanthus* is not strongly supported. In the ITS analysis (Figs. 9, 10), it lies sister to the clade of Old World taxa that includes the *Synadenium* alliance and *E.* subg. *Euphorbia* and *Lacanthis*. However, there is no bootstrap support for the relationship. The *ndh*F analysis (Fig. 11) suggests a relationship with *E. elata* in a weakly supported clade (bs 72%) of various Neotropical species. At least based on biogeography, this association is more plausible. Involucral appendages have arisen on various occasions within Euphorbiinae, and their presence in *Pedilanthus* apparently represents an independent derivation of this feature.
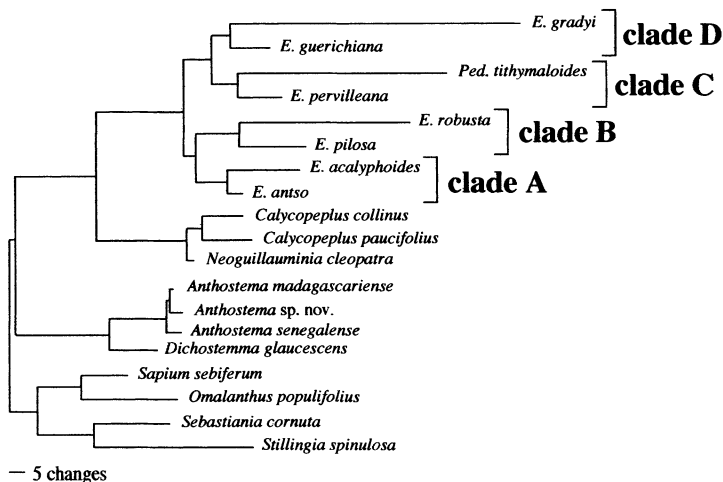
Figure 4. Phylogram of one of the equally most parsimonious trees resulting from the *ndh*F analysis, showing branch lengths within Euphorbieae. Only the species with the least and most changes are shown for each of the major clades of subtribe Euphorbiinae. Individual phylograms of clades A–D are given in Steinmann (2001). *E.* = *Euphorbia*, *Ped.* = *Pedilanthus*.

Cubanthus. *Cubanthus* was initially described as a section of *Pedilanthus,* but as noted by Millspaugh (1913) and confirmed by Dressler (1957), these two groups do not appear closely related. Although *Cubanthus* was not available for this study, *Euphorbia gymnonota* Urb. and *E. punicea* Sw. were included (clade C, Figs. 9, 11). Like members of *Cubanthus,* these two species possess involucral glands that are partially situated on the outside wall of the involucre in contrast to the rim of the involucre, as is generally the situation in *Euphorbia.* Based on this shared feature, an overall similarity in habit, and an allopatric distribution, *Cubanthus* is presumably closely related to these taxa and probably would associate with them in a molecular analysis.

Euphorbia *subg.* Trichadenia. Pax (1921) first proposed this taxon as a section of *Euphorbia,* but a decade later he synonymized it with *Euphorbia* sect. *Tithymalus* Roeper, without elaborating on which group within section *Tithymalus* he believed that it belonged. Carter (1985) resurrected *E.* sect. *Trichadenia* Pax as a subgenus and proposed two sections: sect. *Somalica* S. Carter (inflorescences umbellate and unbranched, with small deciduous bracts) and sect. *Trichadenia* (inflorescences branching, with large persistent bracts). Later she removed her section *Somalica* from *Euphorbia* subg. *Trichadenia* and placed it in subgenus *Lyciopsis* (Carter, 1988a). Although *E.* subg. *Trichadenia* (Pax) S. Carter is now generally accepted, its exact rank and placement are disputed. Based pre-

sumably on the fact that many species possess a pseudoumbellate inflorescence, Gilbert (1987, 1990), for example, preferred to treat it within *E.* subg. *Esula.*

Various species referred to *Euphorbia* subg. *Trichadenia* by Pax, Carter, and Gilbert were included in this study: *Euphorbia trichadenia* Pax, *E. goetzei* Pax, *E. platycephala* Pax, *E. grantii* Oliv., and *E. omariana* M. G. Gilbert. With the exception of *E. goetzei,* which falls out in clade D as related to *E. pirottae* N. Terrac. (Figs. 12, 14), the members of subgenus *Trichadenia* are supported to be closely related and belong to clade A (Figs. 5, 6). However, they do not form a monophyletic group. Instead, they belong to a group together with *Euphorbia* sects. *Dactylanthes* (Haw.) A. Berger, *Medusea* (Haw.) Baill., *Meleuphorbia* A. Berger, *Treisia* (Haw.) Baill., and *Anthacantha* (Lem.) A. Berger. These sections, which lack a current subgeneric placement, all contain tuberculate-stemmed South African succulents, many of which also possess glandular involucral processes. Their various characteristics are as follows: *E.* sect. *Anthacantha* (leaf-reduced stems, the inflorescences axillary with the cyathia borne at the tips of persistent, spiny peduncles; representative: *E. atrispina* N. E. Br.); *E.* sect. *Dactylanthes* (leaf-reduced, highly branched, short stems, the involucral glands with long, fingerlike divisions and curved lip at the base; representative: *E. globosa* (Haw.) Sims); *E.* sect. *Treisia* (leafy stems and three conspicuous bracts just below the cyathium; representative: *E. clava*
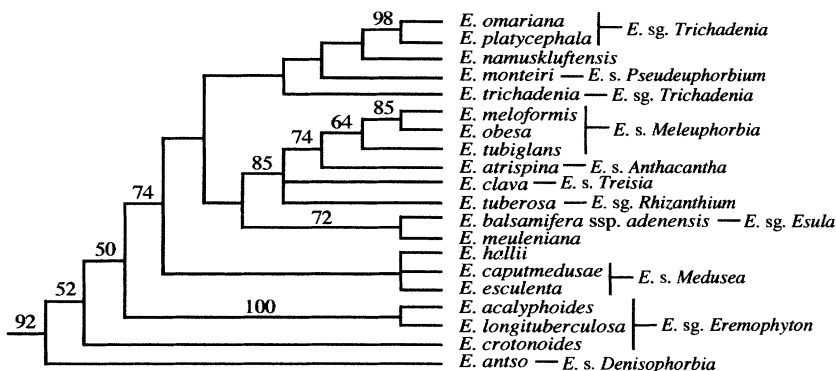
Figure 5.   Euphorbiinae clade A, strict consensus of 2160 trees based on a weighted maximum parsimony analysis of the ITS region. Bootstrap values greater than 50% are shown above the branches. E. = Euphorbia, s. = section, sg. = subgenus, ssp. = subspecies.

Jacq.); E. sect. Medusea (main stem normally partly sunken in the ground and with few to many secondary branches crowning and radiating from the apex; representatives: E. caputmedusae L. and E. esculenta Marloth); E. sect. Meleuphorbia (little-branched to unbranched aboveground stems that are frequently subglobose and with distinct angles; representatives: E. tubiglans Marloth ex R. A. Dyer, E. obesa Hook. f., and E. meloformis Aiton). The close relationship between the species of subgenus Trichadenia and these taxa is not surprising and was predicted by Gilbert (1987), who noted that there does not appear to be any important discontinuity between these groups. Also closely allied are E. tuberosa L., the type of E. subg. Rhizanthium; E. monteiri Hook. f., the type of E. sect. Pseudeuphorbium (Pax) A. Berger; and E. lignosa Marloth, the type of E. subg. Lyciopsis (Boiss.) L. C. Wheeler sect. Lignosae Pax & K. Hoffm.

Euphorbia subg. Rhizanthium.   This taxon was initially proposed by Boissier (1862) as a section of Euphorbia to accommodate various geophytes

from India and South Africa. Boissier (1862) treated another geophyte, Euphorbia sessiliflora Roxb. from Burma (not included here), in his E. sect. Caulanthium Boiss. Wheeler (1943) combined these two sections under the name Rhizanthium and elevated its rank to subgenus within Euphorbia. Gilbert (1987) provided a detailed overview of the group, concluding that subgenus Rhizanthium, as currently circumscribed, is a heterogeneous assemblage of many unrelated species. This study vindicates his contention, and members of this taxon belong to various unrelated groups in clades A and C (see Figs. 5, 6, 10, 11).

A number of species in Euphorbia subg. Rhizanthium were included here. Although Euphorbia sessiliflora, the sole member of Boissier's Euphorbia sect. Caulanthium, was not available for inclusion, the later-described and apparently closely related E. panchganiensis Blatt. & McCann and E. meenae S. Carter were represented. Both of these Indian geophytes are nested within the spine-shield succulents of E. subg. Euphorbia. Euphorbia tuberosa,
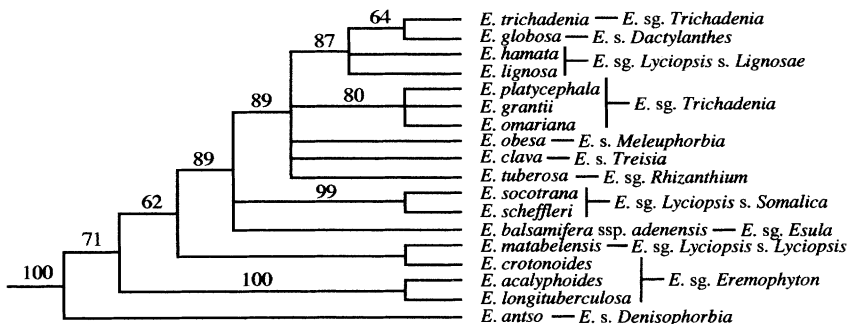

Figure 6.   Euphorbiinae clade A, strict consensus of 19,012 trees based on a weighted maximum parsimony analysis of the ndhF region. Bootstrap values greater than 50% are shown above the branches. E. = Euphorbia, s. = section, sg. = subgenus, ssp. = subspecies.

the type of subgenus *Rhizanthium*, is not closely related to the Indian species, but instead is related to a group of South African taxa currently recognized as *E.* subg. *Trichadenia* (clade A, Figs. 5, 6; see discussion above). Despite not truly being geophytes, *E. longituberculosa* Boiss. and *E. pirottae* were placed here by Pax and Hoffmann (1931). The first species is not closely related to any of the above members, but instead its position is near *E. acalyphoides* Hochst. ex Boiss. in *E.* subg. *Eremophyton* sect. *Pseudacalypha* Boiss. in clade A (Figs. 5, 6), where it was placed by Carter (1988a). The second species also shows no affinities with any of the above members and comes out related to *Euphorbia goetzei* within clade D (Figs. 12, 14). *Euphorbia primulifolia* Baker, a Madagascan species treated in subgenus *Rhizanthium* by Denis (1921) and in *E.* subg. *Lacanthis* by Gilbert (1987), belongs with other Madagascan species currently placed in subgenus *Lacanthis* (clade C, Fig. 10).

Euphorbia *subg.* Lyciopsis. When first described as a section (Boissier, 1862), this taxon contained only *Euphorbia cuneata* Vahl, a spinescent shrub from Africa with fasciculate leaves. The section was compared with *E.* sect. *Tirucalli* Boiss. in gland characters but distinguished by the fasciculate leaves and non-succulent stems. Pax and Hoffmann (1931) expanded section *Lyciopsis* Boiss. to include three subsections: subsect. *Lyciopsis* (as *Eulyciopsis*), subsect. *Espinosae* (Pax & K. Hoffm.) Pax & K. Hoffm., and subsect. *Lignosae* (Pax & K. Hoffm.) Pax & K. Hoffm. The latter two were based on sections proposed a decade earlier (Pax & Hoffmann in Pax, 1921). Wheeler (1943) followed Pax's circumscription and made changes only in rank when elevating this taxon to subgenus. Carter (1988a) expanded it to include an additional section, *E.* sect. *Somalica*, a group erected by her to accommodate about 10 east African species with woody semisucculent branches, small scarious deciduous bracts, crenulate or pectinate involucral glands, and large, often ornamented capsules (Carter, 1988b); *E.* sect. *Somalica* was previously placed in *E.* subg. *Trichadenia* (Carter, 1985).

Members of all four currently recognized sections of *Euphorbia* subg. *Lyciopsis* were included in this analysis. The results suggest that the subgenus is polyphyletic, and its component sections represent four distinct groups. In both molecular analyses, *E. espinosa* Pax and *E. guerichiana* Pax form a well-supported lineage (bs 97% in ITS, 100% in *ndh*F) in the early diverging portion of clade D (Figs. 12, 14). They are far removed from the remainder of the sections of subgenus *Lyciopsis*, all of which be-

long to clade A (Fig. 6). Due to problems obtaining ITS sequences, the other species of this subgenus were included only in the *ndh*F analysis. Both *E. lignosa* and *E. hamata* (Haw.) Sweet, members of subgenus *Lyciopsis* sect. *Lignosae*, are placed in a well-supported clade (bs 87%) together with *E. trichadenia* and *E. globosa*. Their relationship here is not unexpected; Pax and Hoffmann (in Pax, 1921), when first describing this section, noted that the appendages of *E. lignosa* were similar to those of species in *E.* sect. *Dactylanthes*, of which *E. globosa* is a member.

The only species of *Euphorbia* subg. *Lyciopsis* sect. *Lyciopsis* that was included in this study is *E. matabelensis*. It comes out as an early diverging member of clade A, sister to *E. crotonoides* Boiss. However, this relationship should be viewed with reservation because there is little morphological similarity between these two species and no bootstrap support for this grouping.

The final section, *Euphorbia* subg. *Lyciopsis* sect. *Somalica*, was represented in this study by two species, *E. scheffleri* Pax and *E. socotrana* Balf. f. These two form a well-supported group (bs 99% in *ndh*F, Fig. 6) in a subclade containing *E. balsamifera* Aiton and various other *Euphorbia*. *Euphorbia balsamifera* is vegetatively similar to species of subgenus *Lyciopsis* sect. *Somalica*, so the suggestion that they have arisen from common ancestry is reasonable.

Euphorbia *subg.* Esula. This subgenus largely corresponds to Boissier's *Euphorbia* sect. *Tithymalus*. Wheeler (1943), when implementing his system of subgenera, resurrected the application of *E.* subg. *Esula* for this assemblage. Its current use corresponds to the circumscriptions of these authors with some subsequent modifications. For example, *E. ipecacuanhae* L., the type of Boissier's section *Tithymalus* subsect. *Ipecacuanhae* Boiss., has been transferred to *E.* subg. *Agaloma*, and *Tithymalus* subsect. *Inundatae* has been proposed to accommodate the remainder of the species treated in this subsection (Webster, 1967). In addition, *E.* sect. *Tithymalus* subsect. *Crotonopsideae* Boiss. was removed by Radcliffe-Smith (1974) and placed in subgenus *Cystidospermum* (Prokh.) Prokh. (see discussion under *Euphorbia* subg. *Eremophyton*). As employed in the discussion below, many of Boissier's subsections are elevated to the rank of section when *E.* sect. *Tithymalus* is treated as *E.* subg. *Esula*.

With as many as 500 species, this is the largest subgenus currently recognized within *Euphorbia*. It probably is also the most taxonomically difficult.

The greatest diversity is in northern temperate regions. Plants are mostly perennial herbs, but a variety of growth forms exist from diminutive annuals to shrubs or rarely small trees. The majority of *E.* subg. *Esula* possess alternate lower leaves and a well-developed pseudoumbellate inflorescence in which the stem terminates in a whorl of leaves and a fascicle of three to many branches with opposite leaves and dichotomous branching; cyathia are situated in the axils of these upper leaves. The involucral glands lack appendages and are often truncate or bicornute. Exstipulate leaves also characterize this group, but some members currently placed here possess stipules, e.g., the species of subgenus *Esula* sect. *Adenorima* (Raf.) G. L. Webster and section *Tithymalus* subsect. *Inundatae*.

About 45 species of *Euphorbia* subg. *Esula*, from the majority of Boissier's subsections, were included in this study. Although most of Boissier's subsections were sampled, not enough members from each were included to make any definitive inferences concerning their monophyly. Still, a number of conclusions can be reached.

Euphorbia ipecacuanhae, the basis of Boissier's section *Tithymalus* subsect. *Ipecacuanhae*, was indeed supported as being unrelated to other members of this subsection (currently treated as *E.* subg. *Esula* sect. *Tithymalus* subsect. *Inundatae*) as well as unrelated to other members of subgenus *Esula*; thus, its removal by Webster (1967) is justified. *Euphorbia ipecacuanhae* belongs with members of subgenus *Agaloma* in clade D (see Fig. 13). Also justified is Radcliffe-Smith's placement of section *Tithymalus* subsect. *Crotonopsideae* within *Euphorbia* subg. *Cystidospermum* (see discussion under *E.* subg. *Eremophyton*).

Euphorbia subg. *Esula* sect. *Tithymalus* subsect. *Inundatae* was represented by three South American species: *E. papillosa* A. St.-Hil., *E. stenophylla* (Klotzsch & Garcke) Boiss., and *E. thinophila* Phil. These do not demonstrate any close relationship to other members of subgenus *Esula*. Instead, the molecular evidence supports that they are related to *E. peperomioides* Boiss. of section *Nummulariopsis* Boiss. and *E. germainii* Phil. of section *Portulacastrum* Boiss. Together these form a monophyletic group in clade C (see Fig. 9).

Euphorbia subg. *Esula* sect. *Balsamis* Webb. & Berthel., a taxon corresponding to Boissier's section *Tithymalus* subsect. *Pachycladae*, is clearly polyphyletic (Figs. 5–9, 11). This is not surprising, considering that the only features uniting its members are their shrubby habit together with branches that are leafy only toward the tips but leafless with prominent leaf scars proximally. *Euphorbia balsamifera* subsp. *adenensis* (see Figs. 5, 6) does not appear closely related to any other species of subgenus *Esula* sect. *Balsamis* sampled here. Instead, it belongs to clade A and based on the ITS results (Fig. 5), it has its affinity with *E. meuleniana* O. Schwartz from Yemen, a vegetatively similar species. *Euphorbia plumerioides* Teijsm. ex Hassk., also referred to this group by Boissier, shows no close relationship to *E. balsamifera* but instead belongs to clade C (Fig. 9). *Euphorbia plumerioides* is a member of a group of about eight species occurring in Australia, Malesia, and Melanesia (Foster, 1994). In this analysis, the Hawaiian species, *E. haeleeleana* D. R. Herbst, is suggested to belong to this group. Also related is *E. boöphthona* C. A. Gardner, an herbaceous plant from Australia previously treated in subgenus *Eremophyton*. Both *E. balsamifera* and members of the *E. plumerioides* group differ from typical members of subgenus *Esula* by lacking the characteristic pseudoumbellate inflorescence described above. A third group of species sampled from subgenus *Esula* sect. *Balsamis*, *E. dendroides* L., *E. longifolia* Lam., *E. regis-jubae* Webb. & Berthel., and *E. atropurpurea* Brouss. ex Willd., are demonstrated by the molecular evidence to be related to typical members of the north temperate group of subgenus *Esula* discussed below (see Figs. 7, 8), although collectively these do not form a monophyletic group.

Another group that does not appear related to the remainder of *Euphorbia* subg. *Esula* is its section *Adenorima*. This taxon corresponds to Boissier's section *Tithymalus* subsect. *Laurifoliae*; another synonym is the genus *Euphorbiodendron* Millsp. As the last name suggests, the ca. 20 species composing *E.* subg. *Esula* sect. *Adenorima* are usually trees. They occur primarily in tropical forests from Mexico to northern South America and the Caribbean and possess the pseudoumbellate inflorescence structure typical of subgenus *Esula*. It is for this reason that they traditionally have been placed here. A number of species presently referable to subgenus *Esula* sect. *Adenorima* were included in this study: *E. punicea* Sw., *E. cestrifolia* HBK, *E. laurifolia* Juss., *E. elata* Brandegee, *E. tanquahuete* Sessé & Mociño, *E. calyculata* HBK, and *E. gymnonota* Urb. (Figs. 9, 11). These taxa do not appear closely related to the core *Esula* group discussed below, and the two groups are in separate major clades of Euphorbiinae, clades C and B, respectively. In addition, the species of subgenus *Esula* sect. *Adenorima* do not form a monophyletic group, but instead appear to represent an ancestral New World grade from which various other groups of *Eu-*
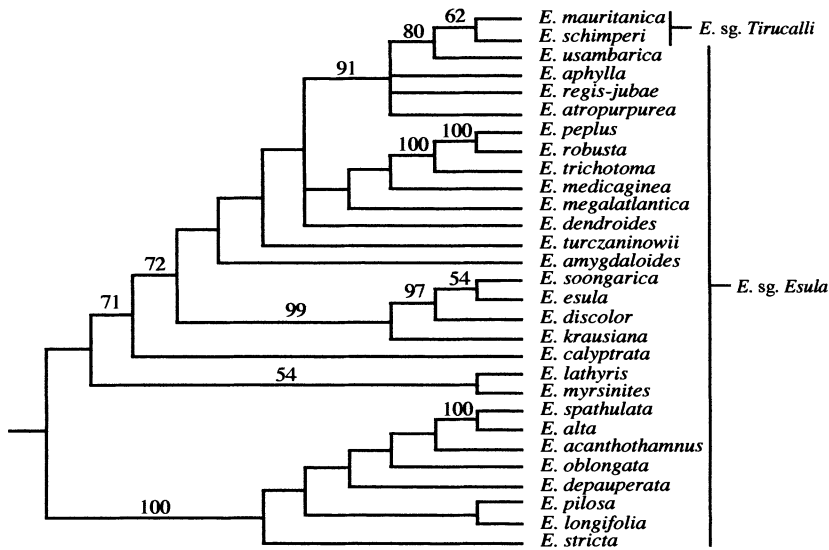
Figure 7.   Euphorbiinae clade B, strict consensus of 2160 trees based on a weighted maximum parsimony analysis of the ITS region. Bootstrap values greater than 50% are shown above the branches. *E.* = *Euphorbia*, sg. = subgenus.

phorbia have evolved. Dressler (1957) suggested that this taxon includes the most primitive members of the genus. Although that assumption is not strongly supported here, the species do represent some of the earliest diverging taxa in clade C and possess many traits that appear primitive for the genus.

In both the ITS and *ndh*F analyses, the remaining species of *Euphorbia* subg. *Esula* sampled come out together (see Figs. 7, 8). This group corresponds to the following subsections of Boissier's section *Tithymalus*: subsect. *Decussatae* Boiss., subsect. *Oppositifoliae* Boiss., subsect. *Carunculares* Boiss., subsect. *Galarrhaei* Boiss., subsect. *Esulae* Boiss., and subsect. *Myrsiniteae* Boiss. They form a well-supported, monophyletic assemblage (bs 86% in *ndh*F) only after the inclusion of the third group of species discussed above in subgenus *Esula* sect. *Balsamis* and the inclusion of *E. schimperi* Presl and *E. mauritanica* L. The latter two species have been placed in *E.* subg. *Tirucalli*, but it should be emphasized that their association with *E. tirucalli*

L. and relatives is based primarily on gross morphology; the possession of pseudoumbellate inflorescences and the lack of stipules supports their placement in subgenus *Esula*, as the molecular data here strongly suggest.

Collectively the taxa mentioned in the previous paragraph compose clade B and correspond broadly to the temperate, Northern Hemisphere group of *Euphorbia* subg. *Esula*. The presence of *Euphorbia* in temperate regions is almost entirely the result of the radiation of this lineage, and very few other species of *Euphorbia* are found in such areas. Although the great majority of this group are restricted to temperate, Northern Hemisphere environments or high-elevation montane tropical regions, this is not a strict characterization. *Euphorbia mauritanica* and relatives are found in arid tropical and subtropical regions; *E. dendroides*, *E. longifolia*, *E. regis-jubae*, and *E. atropurpurea* occur in subtropical vegetation on the Canary Islands; and *E. trichotoma* inhabits beaches in the New World tropics.

Figure 8.   Euphorbiinae clade B, strict consensus of 19,012 trees based on a weighted maximum parsimony analysis of the *ndh*F region. Bootstrap values greater than 50% are shown above the branches. *E.* = *Euphorbia*, sg. = subgenus.

Figure 9.   Euphorbiinae clade C (in part), strict consensus of 2160 trees based on a weighted maximum parsimony analysis of the ITS region. Bootstrap values greater than 50% are shown above the branches. *E.* = *Euphorbia*, *Ped.* = *Pedilanthus*, s. = section, sg. = subgenus, ssp. = subspecies.

Figure 10.   Euphorbiinae clade C (in part), strict consensus of 2160 trees based on a weighted maximum parsimony analysis of the ITS region. Bootstrap values greater than 50% are shown above the branches. *E.* = *Euphorbia*, *End.* = *Endadenium*, *Mon.* = *Monadenium*, *Syn.* = *Synadenium*, s. = section, sg. = subgenus.
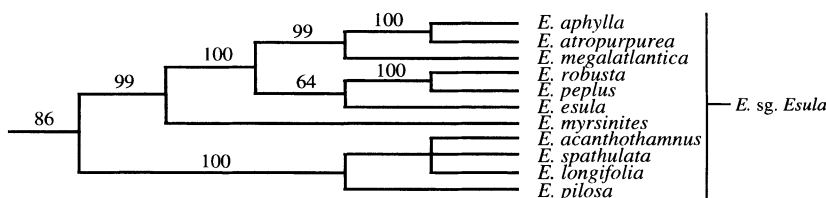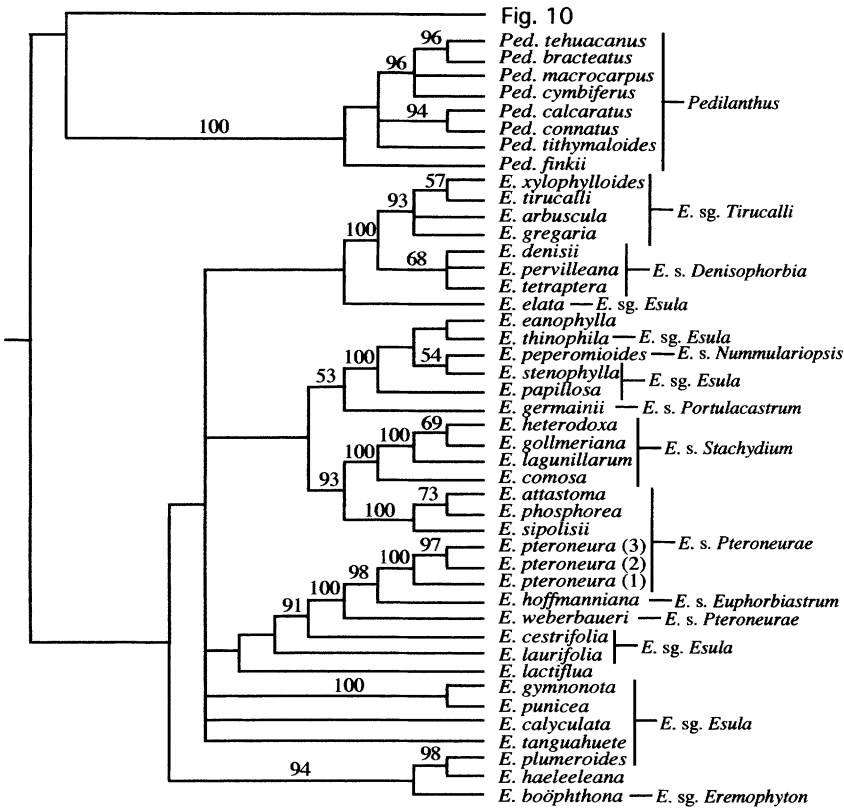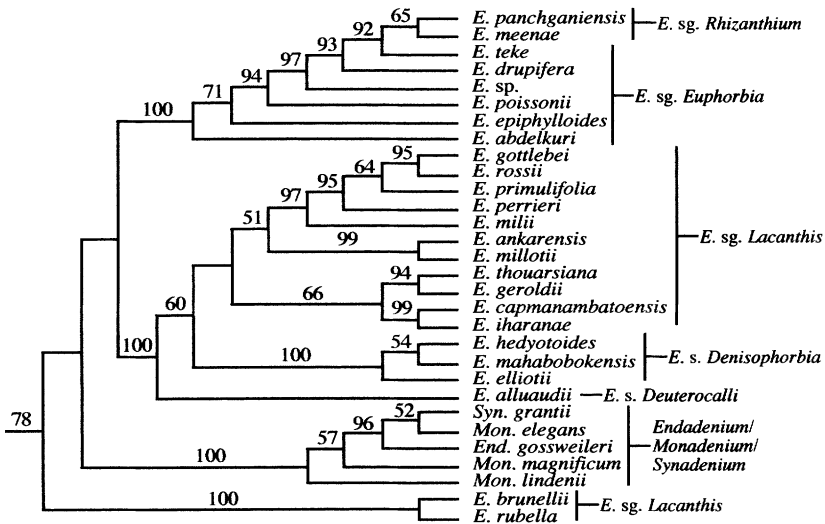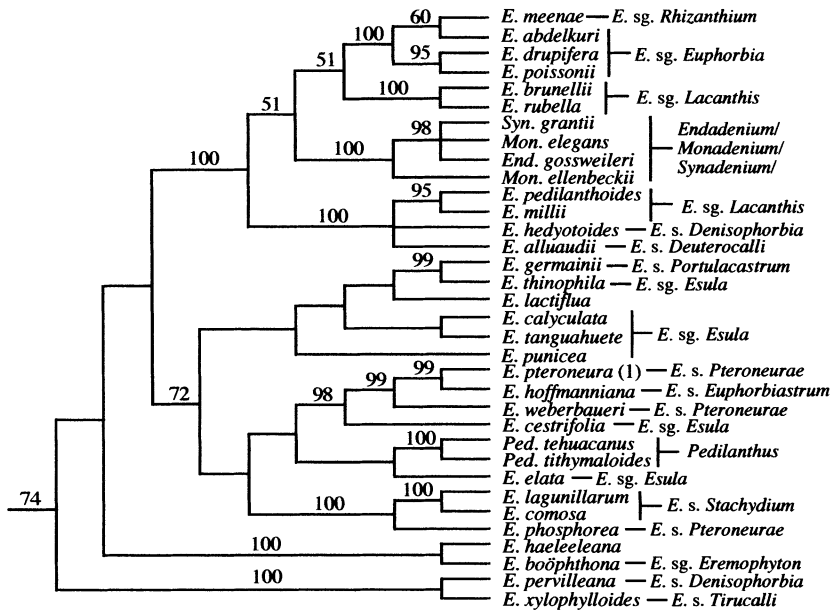
Figure 11. Euphorbiinae clade C, strict consensus of 19,012 trees based on a weighted maximum parsimony analysis of the *ndh*F region. Bootstrap values greater than 50% are shown above the branches. *E.* = *Euphorbia*, *End.* = *Endadenium*, *Mon.* = *Monadenium*, *Ped.* = *Pedilanthus*, *Syn.* = *Synadenium*, s. = section, sg. = subgenus.

At least from the limited sample examined in this study, the primary division within the restricted circumscription of *Euphorbia* subg. *Esula*, discussed in the previous two paragraphs, is between those species that possess tuberculate ovaries and those species whose ovaries are smooth. It remains to be seen whether this distinction will withstand an increase in sampling. If so, this would have important taxonomic implications because many of Boissier's subsections contain both tuberculate- and smooth-ovaried species.

It is worth emphasizing that the occurrence of a pseudoumbellate inflorescence in all of the major lineages of *Euphorbia* suggests this is a symplesiomorphic feature that was present before the differentiation of subtribe Euphorbiinae. The structure bears some resemblance to the inflorescence of *Neoguillauminia* and may be homologous. Therefore, the possession of this type of inflorescence should not be viewed as the defining characteristic of *E.* subg. *Esula*. Instead, it is the combination of a pseudoumbellate inflorescence together with exstipulate leaves that better characterizes the core subgenus *Esula* group, as represented by clade B.

Euphorbia sect. Nummulariopsis. *Euphorbia peperomioides* and the very similar *E. paranensis* Dusén (the latter not included) are the only two species belonging to *E.* sect. *Nummulariopsis*. Both are prostrate Brazilian perennial herbs with oppo-

site, asymmetrical leaves and elongate, glandular stipules. These features together with axillary, 4-glanded involucres are reminiscent of *Chamaesyce*, to which Wheeler (1943) believed that this section belonged. Webster (1967) noted that *E. peperomioides* bordered *Chamaesyce*. In this analysis, *E. peperomioides* shows no affinity with *Chamaesyce*. It is instead related to *E. stenophylla*, a South American member of subgenus *Esula* sect. *Tithymalus* subsect. *Inundatae* (Fig. 9). Although in habit *E. peperomioides* and *E. paranensis* differ greatly from other members of this subsection, a close relationship is suggested by the common possession of subulate, sepal-like lobes below the pistillate flowers, a feature otherwise very rare in subtribe Euphorbiinae.

Euphorbia sect. Portulacastrum. Two species, *Euphorbia germainii* and *E. pentlandii* Boiss. (the latter not included), are contained in this section. Both are South American annuals with cleft involucral appendages. Based on the presence of these involucral appendages, section *Portulacastrum* has been placed in *E.* subg. *Agaloma*, e.g., Wheeler (1943). However, according to the molecular data, at least *E. germainii* does not fall out as related to the core *Agaloma* group. Instead, it nests within South American members of subgenus *Esula* sect. *Tithymalus* subsect. *Inundatae* in clade C (Fig. 9). This placement is anomalous, and *E. germainii* and

E. pentlandii are morphologically incongruous there because they possess well-developed involucral appendages and lack the characteristic sepal-like lobes below the pistillate flowers of the subsection *Inundatae*.

Euphorbia sect. Denisophorbia. This is a small group of approximately 20 species of leafy trees and shrubs, mostly confined to Madagascar. It was first proposed as a subsection of *Euphorbia* sect. *Euphorbia* by Leandri (1957). Croizat (1972) elevated the group to the rank of section. As mentioned by Leandri (1957), section *Denisophorbia* is difficult to define. The leaves are entire and alternate to spirally arranged. The cyathia are relatively large, lack appendages, and are solitary or in terminal pseudoumbellate inflorescences. Seven species belonging to this group were included here: *Euphorbia antso* Denis, *E. denisii* Oudejans, *E. elliotii* Leandri, *E. hedyotoides* N. E. Br., *E. mahabobokensis* Rauh, *E. pervilleana* Baill., and *E. tetraptera* Baker.

These species do not form a monophyletic clade but instead come out as representing three separate groups. *Euphorbia antso* is the earliest diverging species in clade A (Figs. 5, 6) and shows no affinity with the other species of *E.* sect. *Denisophorbia* sampled here, all of which belong to clade C (Figs. 9–11). *Euphorbia denisii*, *E. pervilleana*, and *E. tetraptera* form a monophyletic group that is sister to *E. tirucalli* and relatives, currently treated in subgenus *Tirucalli*. Not closely related to this group are *E. elliotii*, *E. hedyotoides*, and *E. mahabobokensis*. These form a monophyletic clade sister to *E.* subg. *Lacanthis* proper.

Euphorbia sect. *Denisophorbia* was proposed to be the most primitive group in *Euphorbia* (Webster et al., 1982). In part, this may be correct because *Euphorbia antso* is the earliest diverging species of clade A and possesses many of the primitive features for the subtribe (see discussion below under origin and biogeography of Euphorbieae). Also, with regard to ITS and *ndh*F molecular evolution this species possesses the least amount of genetic divergence in relation to the outgroup taxa (see Figs. 3, 4).

Euphorbia subg. Tirucalli. The section *Tirucalli* Boiss. was proposed in *Euphorbia* to accommodate arid-adapted shrubs with long, slender, semi-succulent branches (Boissier, 1862). The leaves are reduced and the stem is green and photosynthetic. The section was elevated to subgenus by Carter (1985), and she later noted that it contains two well-defined groups (Carter, 1992a). The first group corresponds to *E. tirucalli* and relatives and is characterized by small scarious bracts, tightly congested inflorescences, and glandular stipules. The second group corresponds to species such as *E. mauritanica* and is characterized by leafy bracts, pseudoumbellate inflorescences, and a lack of stipules.

Various members of *Euphorbia* subg. *Tirucalli* were included in this analysis, and the two groups recognized by Carter do not appear closely related. Instead, their similarities in growth form appear to have resulted from convergent evolution. *Euphorbia tirucalli* and relatives (represented here by *E. arbuscula* Balf. f., *E. gregaria* Marloth, and *E. xylophylloides* Brongn. ex Lem.) come out in clade C as sister to a group of leafy shrubs from Madagascar that are currently treated in section *Denisophorbia* (Figs. 10, 11). The remainder of the species of subgenus *Tirucalli* (represented here by *E. mauritanica* and *E. schimperi*) are found nested within the north-temperate group of subgenus *Esula* in clade B (Fig. 7). The leafy bracts, pseudumbellate inflorescences, and lack of stipules of these latter plants substantiate this placement.

Euphorbia lactiflua Phil. ex Boiss., a shrub from the deserts of Chile and the only New World species referred to this group (Boissier, 1862), is not related to any other species of the subgenus (Figs. 9, 11). In fact, its initial placement by Boissier is in itself very peculiar because this species is a leafy, scarcely succulent shrub. *Euphorbia lactiflua* is taxonomically isolated and shows no close relationship with any other species of *Euphorbia*. In this analysis, its affinities are not determined with precision, but belongs to clade C, in a group of various Neotropical *Euphorbia*.

Euphorbia sect. Euphorbiastrum. This taxon was first erected as a genus by Klotzsch and Garcke (1860) to accommodate their new species, *Euphorbiastrum hoffmanniana* Klotzsch & Garcke. Boissier (1862) then reduced *Euphorbiastrum* Klotzsch & Garcke to a section of *Euphorbia*. Its most distinctive feature is that the involucres are solitary in the leaf axils and subtended by a condensed spiral of small, imbricate bracts. In this analysis, *Euphorbia hoffmanniana* (Klotzsch & Garcke) Boiss. occurs in clade C where it is related to *E. weberbaueri* Mansf. and *E. pteroneura* A. Berger in a well-supported group (bs 91% in ITS, 98% in *ndh*F) together with *E. cestrifolia* (Figs. 9, 11). According to the ITS evidence (Fig. 9), *E. laurifolia* is the basal member of this assemblage, but there is no bootstrap support for its placement.

Members of this group are morphologically quite different. *Euphorbia cestrifolia* and *E. hoffmanniana* are leafy shrubs; *E. weberbaueri* is a leaf-re-

duced, stem-succulent shrub; and *E. pteroneura* is a leafy, drought-deciduous herbaceous succulent. Despite their gross differences in habit, some features suggest relationships among these plants. For one, both *E. cestrifolia* and *E. weberbaueri* possess complex, well-developed glandular stipules. As well, in all taxa the cyathia are closely subtended and sometimes enclosed in a pair of bracts, the styles are entire or emarginate, and the seeds are similar in size and shape and possess a minute caruncle. The involucres of *E. weberbaueri* and *E. pteroneura* possess four glands while those of *E. cestrifolia* and *E. hoffmanniana* possess five glands.

Euphorbia pteroneura was the basis for *E.* sect. *Pteroneurae* A. Berger (1906). Other taxa have been placed in this section, e.g., *E. sipolisii* and *E. phosphorea*, but a close relationship between these and *E. pteroneura* is not supported here (Figs. 9, 11). Given the close affinity of *E. hoffmanniana* and *E. pteroneura*, section *Pteroneurae* is best reduced to synonymy under *E.* sect. *Euphorbiastrum*.

Euphorbia sect. Stachydium. This section is characterized by a congested, primarily monochasial inflorescence on which the pairs of bracts are closely imbricate and fold over to obscure the involucres within. There are about five species in South America and one species, *Euphorbia phylloclada* Boiss., in Namibia. Boissier (1862), who first described *E.* sect. *Stachydium* Boiss., recognized two subsections: subsect. *Americanae* Boiss. (for the American species) and subsect. *Capensis* Boiss. (for *E. phylloclada*). Five species were included here: *E. comosa* Vell., *E. gollmeriana* Klotzsch ex Boiss., *E. heterodoxa* Müll. Arg., *E. lagunillarum* Croizat, and *E. phylloclada*. In this analysis, the two subsections are placed in different major clades of Euphorbiinae (clades C and D, respectively), and a close relationship between them is not supported. The similarity between the two subsections is due mostly to the unusual architecture of the inflorescence. Pax (1921) treated *Euphorbia phylloclada* as a member of *E.* sect. *Pseudacalypha*, based presumably on the axillary cyathia, but there is no affinity between this species and other members of *Pseudacalypha* either.

Based on the possession of involucral appendages, *Euphorbia* sect. *Stachydium* has been suggested to belong to subgenus *Agaloma* (Wheeler, 1943). However, only *E. phylloclada* occurs within this group (see discussion under subg. *Agaloma*). The South American species are members of clade C (Figs. 9, 11) and form a well-supported group (bs 93% in ITS, 100% in *ndh*F) that is sister to the *E. phosphorea* complex, a small assemblage of leafless,

stem-succulents from eastern Brazil. Beyond its association with the *E. phosphorea* complex, the relationship of section *Stachydium* to other members of the genus is obscure, although the *ndh*F results suggest that it belongs to a weakly supported clade of various Neotropical taxa, including *Pedilanthus* and subgenus *Esula* sect. *Adenorima*.

Euphorbia subg. Euphorbia. Following the most recent modifications in *Euphorbia* classification (Gilbert, 1987; Carter, 1988a), the subgenus *Euphorbia* is restricted to about 250 Old World stem succulents in which the base of each leaf is surrounded by a callous pad, termed a spine-shield, bearing a pair of spiny outgrowths and stipules modified into spines. It corresponds to Haworth's (1812) and Klotzsch and Garcke's (1859, 1860) restricted genus *Euphorbia*. Boissier treated these species together with *E. milii* Des Moul. (= *E. splendens* Boj. ex Hook.) under his *E.* sect. *Diacanthium* Boiss. Although Bentham's (1880) and Pax and Hoffmann's (1931) classifications recognized section *Diacanthium* in the same sense as Boissier, it was reduced to a subsection of section *Euphorbium* Boiss., a taxon these authors used to accommodate essentially all of the succulent *Euphorbia* species. Wheeler (1943) followed Bentham's and Pax and Hoffmann's circumscription but under the misapplied name *E.* subg. *Tithymalus*; the name *Tithymalus* has otherwise usually been applied to the north temperate members of *E.* subg. *Esula*. Webster (1967) essentially followed Wheeler's classification but correctly applied the name *E.* subg. *Euphorbia* to this assemblage.

In both the *ndh*F and ITS analyses, *Euphorbia* subg. *Euphorbia* belongs to a well-supported clade (bs 78% in ITS, 100% in *ndh*F) together with subgenus *Lacanthis* and the *Synadenium* alliance (Figs. 10, 11). Within this clade, all of subgenus *Euphorbia* sampled form a monophyletic group, but only after the inclusion of a few additional taxa. *Elaeophorbia*, an African group of four species with drupaceous fruits, has been recognized as a genus by some (e.g., Carter, 1988a) and a section by others (e.g., Webster, 1967). It was represented in this study by *E. drupifera* Thonn. and well supported (bs 100% in both analyses) to be nested within subgenus *Euphorbia* (Figs. 10, 11). In addition, *E. panchganiensis* and *E. meenae* are also strongly supported (bs 100% in ITS) to be nested within subgenus *Euphorbia* (Figs. 10, 11). Both of these species are dwarf geophytes from India that are very different in appearance from the typical members of the subgenus. At least in the mature phase, they lack the characteristic spine-shield structure.

Euphorbia panchganiensis is apparently closely allied to *E. fusiformis* Hamilton ex D. Don, which was placed by Boissier in *E.* sect. *Rhizanthium* (= *E.* subg. *Rhizanthium* sensu Wheeler, 1943). Based on almost identical capsules and seeds, Gilbert (1987) first suggested that *E. fusiformis* might have evolved from Asian members of subgenus *Euphorbia*. The molecular evidence supports his suspicions. The reduction to geophytic herbs has been documented in at least one African lineage of subgenus *Euphorbia* (Carter, 1994), and it appears that the Indian geophytes represent a parallel derivation of this growth form from spiny shrubs. The Indian geophytic species should be examined at early ontogenetic stages to determine if indeed spine-shields are present in the seedlings.

Carter (1994) recognized two sections and many subsections in her classification of *Euphorbia* subg. *Euphorbia*, but not enough taxa were included in this study to test the validity of these groups.

Euphorbia *subg.* Lacanthis. *Lacanthis* Raf. (Rafinesque, 1837) originally contained only *Lacanthis splendens* Raf. (= *Euphorbia milii*). The name slipped into obscurity until Gilbert (1987) resurrected it at the rank of subgenus, applying it to a group of species from Madagascar previously treated together with the spine-shield taxa of *E.* subg. *Euphorbia*, sensu stricto, discussed above. Gilbert also included within subgenus *Lacanthis* (Raf.) Gilbert the species of *E.* sect. *Goniostema* Baill. ex Boiss. and the Madagascan members of *E.* subg. *Rhizanthium*. As discussed in detail (Gilbert, 1987), there are numerous differences that suggest these species should be treated separately from the narrowly defined subgenus *Euphorbia*. For example, in subgenus *Lacanthis* the inflorescences are much branched (vs. little branched), the bracts are well developed (vs. greatly reduced), and the seeds are oblong-cylindrical (vs. ovoid to subglobose). Additionally, in subgenus *Euphorbia* the spines are borne on a differentiated spine-shield and the stipules are represented by prickles just above the leaf, but in subgenus *Lacanthis* the spines are actually the stipules and a spine-shield is absent. Besides the Madagascan species, Gilbert also included in subgenus *Lacanthis* a few geophytes from tropical east Africa that are morphologically very similar to some of those from Madagascar.

A broad array of species from *Euphorbia* subg. *Lacanthis* were sampled. Those from Madagascar included *E. milii*, *E. pedilanthoides* Denis, *E. gottlebei* Rauh, *E. rossii* Rauh & Buchloh, *E. primulifolia*, *E. thouarsiana* Baill., *E. perrieri* Drake, *E. ankarensis* Boiteau, *E. millotii* Ursch & Leandri, *E.*

geroldii Rauh, *E. capmanambatoensis* Rauh, and *E. iharanae* Rauh. From tropical East Africa, *E. rubella* Pax and *E. brunellii* Choiv. ex Chiarugi were represented. All taxa belong to clade C in a subclade containing subgenus *Euphorbia* and the *Synadenium* alliance (Figs. 10, 11). The tropical east African and the Madagascan taxa belong to different lineages within this subclade. The Madagascan members of subgenus *Lacanthis* are supported as a monophyletic assemblage belonging to a clade also containing species not previously associated with the group. *Euphorbia alluaudii* Drake, a Madagascan endemic very similar in habit to *E. tirucalli* but treated by Croizat (1972) in his *E.* sect. *Deuterocalli* Croizat, represents the earliest diverging species within the group. Another group not previously associated with subgenus *Lacanthis* is the *E. hedyotoides* complex of *E.* sect. *Denisophorbia*. In this analysis, the complex forms the sister clade to subgenus *Lacanthis* proper.

It is suggested that the origin of *Euphorbia* subg. *Lacanthis*, sensu Gilbert, is separate from that of subgenus *Euphorbia* and spinescence and succulence in these two groups have resulted from independent derivations.

Euphorbia *sect.* Arthrothamnus. Klotzsch and Garcke (1860) first proposed this group as a genus to accommodate *Euphorbia tirucalli* and seven species from the Cape Region of South Africa. Boissier (1862) later treated it as *Euphorbia* sect. *Arthrothamnus*. He removed *E. tirucalli* but expanded the group to include two species from the West Indies. The latter two were treated within his *E.* sect. *Arthrothamnus* subsect. *Americanae* Boiss., while the remainder of the Old World taxa were placed in section *Arthrothamnus* subsect. *Capenses* Boiss.

As discussed further under *Euphorbia* subg. *Agaloma*, the two subsections of *Arthrothamnus* do not appear closely related, and this section should be restricted to about 20 species in South Africa and Namibia. These are dioecious, dichotomously branching shrubs with photosynthetic, articulate branches and small, opposite leaves. Two species of the group were included here, *E. juttae* Dinter and *E. rhombifolia* Boiss., and the close relationship of both of these is well supported (bs 100% in both analyses, see Figs. 12, 14). They belong to clade D and represent an early diverging lineage of this clade. Further relationships of these species to other *Euphorbia* are unclear.

Euphorbia *subg.* Eremophyton. This group was first erected by Boissier (1862) as a section of *Euphorbia* to include *Euphorbia eremophila* A. Cunn., *E. agowensis* Hochst. ex Boiss., and *E. gueinzii*

Fig. 13

E. pentadactyla
E. hormorhiza
E. heterophylla
E. zonosperma
E. pulcherrima ⎫ E. sg. *Poinsettia*
E. bifurcata
E. exstipulata
E. bilobata ⎫ E. sg. *Agaloma* s. *Zygophyllidium*
E. chersonesa
E. pumicola
E. radians
E. strigosa ⎫ E. sg. *Poinsettia*
E. eriantha
E. lacera
E. jaliscensis ⎫ E. sg. *Agaloma* s. *Zygophyllidium*
Cham. degeneri
Cham. hypericifolia
Cham. prostrata
Cham. articulata
Cham. carunculata
Cham. polycnemoides
Cham. angusta
Cham. acuta ⎫ Chamaesyce
E. crossadenia
E. sessilifolia (2)
E. sessilifolia (1)
E. sarcodes
E. gymnoclada
E. appariciana
E. sp. nov. 1 ⎫ E. sg. *Agaloma* s. *Crossadenia/Ephedropeplus*
E. petiolata
E. chierolepis ⎫ E. sg. *Cystidospermum*
E. eremophila
E. tannensis ⎫ E. sg. *Eremophyton*
E. glanduligera
E. phylloclada — E. s. *Stachydium*
E. rhombifolia
E. juttae ⎫ E. s. *Arthrothamnus*
E. guerichiana ⎫ E. sg. *Lyciopsis* s. *Espinosae*
E. espinosa
E. agowensis
E. scatorhiza ⎫ E. sg. *Eremophyton*
E. platyclada
E. goetzei — E. sg. *Trichadenia*
E. pirottae — E. sg. *Eremophyton*

Figure 12. Euphorbiinae clade D (in part), strict consensus of 2160 trees based on a weighted maximum parsimony analysis of the ITS region. Bootstrap values greater than 50% are shown above the branches. *E.* = *Euphorbia*, *Cham.* = *Chamaesyce*, s. = section, sg. = subgenus.

E. oaxacana
E. guatemalensis
E. calcicola
E. whitei
E. gradyi
E. ocymoidea
E. rzedowskii
E. subpeltata
E. eglandulosa
E. adiantoides
E. sonorae
E. rossiana
E. rossiana var. nov.
E. ceroderma
E. antisyphilitica
E. delicatula
E. fulgens
E. colletioides
E. segoviensis
E. leucocephala ⎫ E. sg. *Agaloma* s. *Alectoroctonum/Cyttarospermum/Petaloma/Tithymalopsis/Trichosterigma*
E. californica
E. gentryi
E. misera
E. macvaughii
E. sinaloensis
E. succedanea
E. innocua
E. aaron-rossii
E. ipecacuanhae
E. bicolor
E. cassythoides — E. s. *Arthrothamnus*
E. equisetiformis
E. misella
E. macropus
E. lagunensis
E. aff. ariensis
E. graminea
E. insulana
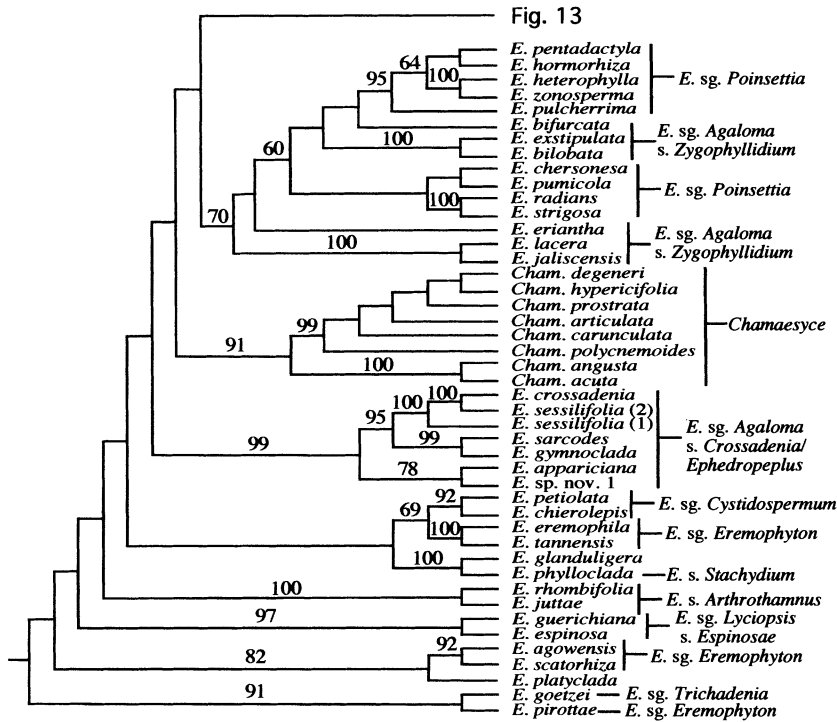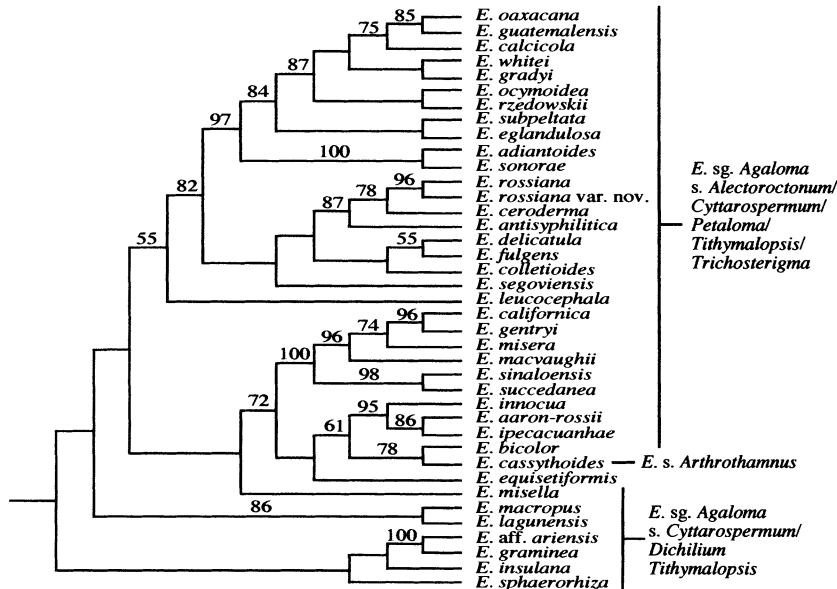E. sphaerorhiza ⎫ E. sg. *Agaloma* s. *Cyttarospermum/Dichilium Tithymalopsis*

Figure 13. Euphorbiinae clade D (in part), strict consensus of 2160 trees based on a weighted maximum parsimony analysis of the ITS region. Bootstrap values greater than 50% are shown above the branches. *E.* = *Euphorbia*, s. = section, sg. = subgenus.
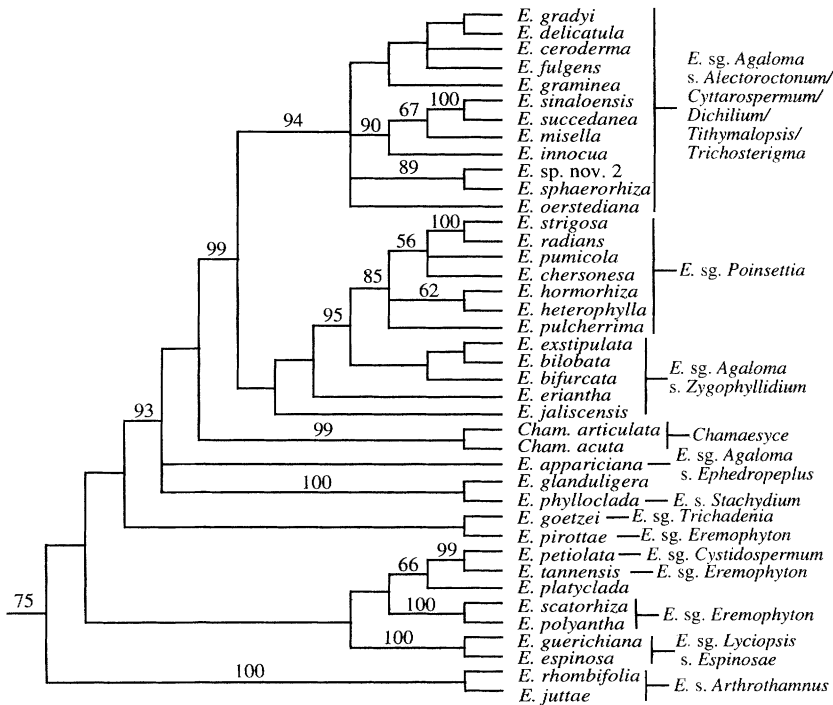
Figure 14. Euphorbiinae clade D, strict consensus of 19,012 trees based on a weighted maximum parsimony analysis of the *ndh*F region. Bootstrap values greater than 50% are shown above the branches. *E. = Euphorbia, Cham. = Chamaesyce.*

Boiss. It was originally circumscribed to contain herbs or subshrubs with alternate lower and opposite upper stem leaves; glandular or subulate stipules; axillary or terminal, solitary involucres with four to five glands lacking appendages; and carunculate to ecarunculate seeds. Carter (1985) emphasized also petiolate leaves and exserted capsules as characteristics of subgenus *Eremophyton*. As these traits suggest, there is no single synapomorphy that unites this group, and all of the features used to delineate the subgenus can be found in various combinations in other taxa of *Euphorbia*. In 1880, Bentham synonymized Boissier's *E.* sects. *Bongium* Boiss., *Cheirolepidium* Boiss., and *Pseudacalypha* under his expanded section *Eremophyton*, and this system was followed by Wheeler (1943) when he elevated the section to subgenus. *Euphorbia* sect. *Cheirolepidium* was removed by Prokhanov (1933) and formed the basis of his genus *Cystidopermum* Prokh. *Cystidospermum* was later reduced to a subgenus of *Euphorbia* (Prokhanov, 1949), and Radcliffe-Smith (1974) agreed that subgenus *Cystidospermum* was sufficiently distinct from the remainder of *E.* subg. *Eremophyton* to warrant its separate recognition. He additionally referred to it

Boissier's *E.* sect. *Tithymalus* subsect. *Crotonopsideae.*

Two species of *Euphorbia* subg. *Cystidospermum* (sensu Radcliffe-Smith, 1974) were included in this study: *E. cheirolepis* and *E. petiolata* Banks & Sol. Various species of subgenus *Eremophyton* proper were also included: *E. boöphthona, E. pirottae, E. agowensis, E. scatorhiza* S. Carter, *E. cheirolepis, E. eremophila, E. tannensis* Spreng., *E. polyantha* Pax, *E. crotonoides, E. longituberculosa,* and *E. acalyphoides.* In the analyses these taxa do not group together and are widely scattered throughout the subtribe Euphorbiinae (Figs. 5, 6, 9, 11, 12, 14). Therefore, subgenus *Eremophyton,* as currently recognized, is highly polyphyletic.

The three species of *Euphorbia* subg. *Eremophyton* sect. *Pseudacalypha* included in this study (*E. acalyphoides, E. crotonoides,* and *E. longituberculosa*) all grouped as closely related members of clade A. However, they did not form a strictly monophyletic group but instead a grade of taxa (Figs. 5, 6). Interestingly, *E. matabelensis* (a member of subg. *Lyciopsis* sect. *Lyciopsis*) also occurred together with the species of subgenus *Eremophyton* sect. *Pseudacalypha* as sister to *Euphorbia croto-*

noides in the *ndh*F analysis, although there is no bootstrap support for this relationship and the two are morphologically very different.

One of the more unusual results of this study is the placement of *Euphorbia boöphthona,* an Australian member of subgenus *Eremophyton,* in a strongly supported clade (bs 94% in ITS) together with *E. plumerioides* and *E. haeleeleana,* two arborescent Pacific Island taxa presently treated in subgenus *Esula* sect. *Balsamis.* In most respects, *E. boöphthona* closely resembles other Australian members of subgenus *Eremophyton,* e.g., *E. tannensis* and *E. eremophila,* and these Australian taxa have been thought to represent a natural group (Hassall, 1977). It is worth noting that according to Hassall (1977), *E. boöphthona* differs from these two species as well as the other Australian members of the subgenus in being an octoploid (n = 28), but no tetraploid has yet been found in this subgenus.

Radcliffe-Smith's (1974) decision to unite Boissier's *Euphorbia* sect. *Tithymalus* subsect. *Crotonopsideae* (represented here by *E. petiolata*) with subgenus *Cystidospermum* (represented here by *E. cheirolepis*) was supported, and the two species are sister to each other (bs 92% in ITS, see Fig. 12) in this analysis. They belong to a clade also containing two members of *E.* subg. *Eremophyton* proper, *E. tannensis* and *E. eremophila.* Thus, subgenus *Cystidospermum* probably is best treated as a synonym of subgenus *Eremophyton.* The Madagascan endemic *E. platyclada* Rauh, whose relationship with other *Euphorbia* was previously unknown (Rauh, 1998), also groups with these taxa in the *ndh*F analysis, but this relationship is not well supported (Fig. 14). In the ITS analysis (Fig. 12), *E. platyclada* comes out with *E. scatorhiza* and *E. polyantha.* As suggested by Carter (1992b), these latter two species are sister taxa in so far as this sample is concerned.

Many species of *Euphorbia* subg. *Eremophyton* possess a great similarity to those of subgenus *Agaloma,* especially taxa of its section *Zygophyllidium* Boiss. For example, contrary to reports in the literature, the southwest Asian *E. petiolata* and *E. cheirolepis* actually possess involucral appendages. Undoubtedly, if these species occurred in the New World, they would be treated within subgenus *Agaloma* without question. Therefore, the molecular evidence that *E.* subg. *Agaloma* has either evolved from a portion of subgenus *Eremophyton* or that the two are sister taxa and share common ancestry is plausible.

Euphorbia *subg.* Agaloma. This taxon is based

on another one of Rafinesque's genera, *Agaloma* Raf. It was first erected (Rafinesque, 1838) to accommodate *Euphorbia corollata* L. and two related species. Interestingly, Rafinesque also published six other genera that correspond to the current circumscription of this subgenus (*Aklema* Raf., *Lepadena* Raf., *Peccana* Raf., *Petaloma* Raf., *Vallaris* Raf., and *Zalitea* Raf.). *Euphorbia* subg. *Agaloma* was first treated at this rank by House (1924). At that time it only accommodated *E. corollata* L., and other members of modern subgenus *Agaloma* were placed in subgenus *Lepadena* (Raf.) House. Wheeler (1943) was the first to adopt subgenus *Agaloma* in its current circumscription, a concept corresponding to *E.* sect. *Adenopetalum* Boiss., sensu Bentham (1880) and Pax and Hoffmann (1931). The group is broadly defined to contain New World members of Euphorbiinae with petaloid involucral appendages but excludes species of *Chamaesyce* and *Pedilanthus.* Beside the presence of involucral appendages, little else unites all members of the group. Trees, shrubs, perennial herbs, geophytes, annuals, and stem-succulents are represented. The subgenus comprises about 150 species and is considered taxonomically difficult (Johnston, 1975; Buck & Huft, 1977). In addition, it has frequently been suspected of being paraphyletic, with both *Chamaesyce* and *E.* subg. *Poinsettia* nested within it.

Euphorbia subg. *Agaloma* was the best-sampled group in this study. Fifty-six species from all of its recognized sections were included. With the exception of two of these sections, *Euphorbia* sects. *Stachydium* and *Portulacastrum* (discussed previously), all species of subgenus *Agaloma* belong to clade D and form a single subclade (Figs. 12–14). Indeed, previous suspicions were supported, and both *Chamaesyce* and *E.* subg. *Poinsettia* are shown to have evolved from within subgenus *Agaloma.* Therefore, a monophyletic subgenus *Agaloma* must also include both *Chamaesyce* and *E.* subg. *Poinsettia.* This entire subclade is hereafter referred to as the *Agaloma* alliance.

The *ndh*F analysis strongly supports (bs 93%) that *Euphorbia phylloclada* and *E. glanduligera* Pax, two annual African species from the Namibian desert, also belong to the *Agaloma* alliance (Fig. 14). Both species possess well-developed involucral appendages and morphologically are easily accommodated within subgenus *Agaloma,* where they certainly would have been placed if it were not for their African distribution. Boissier treated *Euphorbia phylloclada* as the sole representative of *E.* sect. *Stachydium* subsect. *Capensis.* However, the molecular data do not support a close relationship be-

tween this species and other members of the section (see discussion under *E.* sect. *Stachydium*). Pax (1894b) placed *E. glanduligera* in *Chamaesyce*, and the similarity is indeed strong. In the ITS analysis, these two species are placed in a clade sister to some members of subgenus *Eremophyton* (Fig. 12). However, this relationship lacks any bootstrap support, and the *ndh*F analysis probably provides a more accurate reflection of relationships.

Within the New World, the earliest diverging group in the *Agaloma* alliance consists of *Euphorbia* subg. *Agaloma* sects. *Ephedropeplus* Müll. Arg. and *Crossadenia* Boiss. The former section is represented here by *E. appariciana* Rizzini, *E.* sp. nov. 1, and *E. gymnoclada* Boiss., while the latter section is represented here by *E. crossadenia, E. sessilifolia,* and *E. sarcodes*. In the ITS analysis, these two sections form a single well-supported clade (bs 99%) sister to the remainder of the *Agaloma* alliance (Figs. 12, 13). The sample in the *ndh*F study was not sufficient to investigate their monophyly, but here too the single species included, *E. appariciana,* is sister to the remainder of the *Agaloma* alliance. Both sections are restricted to eastern Brazil and represent a morphologically diverse assemblage of about a dozen arid-adapted perennial herbs, small shrubs, or stem succulents. The involucral appendages are deeply cleft to subentire, and in one species they are lacking. Traditionally subgenus *Agaloma* sects. *Crossadenia* and *Ephedropeplus* have been separated by the possession of opposite or whorled, highly reduced scalelike leaves in section *Ephedropeplus* and the possession of alternate, well-developed leaves in section *Crossadenia*. However, this distinction does not appear to hold, and with respect to each other, the sections are not monophyletic. Therefore, *E.* subg. *Agaloma* sect. *Ephedropeplus* is best reduced to synonymy under section *Crossadenia*.

In both the ITS and *ndh*F analyses, *Chamaesyce* is the next diverging lineage in the *Agaloma* alliance, and it is sister to the remainder of the species, excluding the earlier diverging Namibian taxa and members of *Euphorbia* subg. *Agaloma* sect. *Crossadenia* (Figs. 12–14). However, statistical support for this topology is lacking. What is supported is that *Chamaesyce* is an ancient lineage that diverged earlier in the evolution of the *Agaloma* alliance. Beyond this, however, the exact relationship of its members to other Euphorbiinae is not evident.

After the divergence of *Chamaesyce*, there are two major groups within the *Agaloma* alliance. These are sister to each other and present in both the ITS and *ndh*F analyses, with considerable sup-

port (bs 99%) in the latter (Figs. 12–14). The first clade contains species currently placed in *Euphorbia* subg. *Agaloma* sect. *Zygophyllidium* together with members of subgenus *Poinsettia*; the second clade contains the remainder of sections treated in subgenus *Agaloma*.

Euphorbia subg. *Agaloma* sect. *Zygophyllidium* corresponds to a North American and Mexican assemblage of about a dozen species. The group is poorly defined, but united by their annual or rarely short-lived perennial habit. In addition, many species possess serrate leaves. The section was represented in this study by *E. bifurcata* Engelm., *E. bilobata* Engelm., *E. eriantha* Benth., *E. exstipulata* Engelm., *E. jaliscensis* B. L. Rob. & Greenm., and *E. lacera* Boiss. It is not monophyletic because subgenus *Poinsettia* is nested within it (see discussion under *E.* subg. *Poinsettia*).

Sister to the *Zygophyllidium/Poinsettia* group is the core of *Euphorbia* subg. *Agaloma*, an assemblage comprised of section *Alectoroctonum* (Schltdl.) Baill. (representatives: *E. colletioides* Benth., *E. leucocephala* Lotsy, and *E.* sp. nov. 2), section *Cyttarospermum* Boiss. (representatives: *E. adiantoides* Lam., *E.* aff. *ariensis* HBK, *E. calcicola* Fern., *E. delicatula* Boiss., *E. eglandulosa* V. W. Steinm., *E. gradyi* V. W. Steinm. & A. Ram.-Roa, *E. graminea* Jacq., *E. guatemalensis* Standl. & Steyerm., *E. lagunensis* Huft, *E. misella* S. Watson, *E. oaxacana* B. L. Rob. & Greenm., *E. ocymoidea* L., *E. rzedowskii* McVaugh, *E. segoviensis* (Klotzsch & Garcke) Boiss., *E. sinaloensis* Brandegee, *E. sonorae* Rose, *E. subpeltata* S. Watson, *E. succedanea* L. C. Wheeler, and *E. whitei* L. C. Wheeler), section *Dichilium* Boiss. (representatives: *E. insulana* Vell. and *E. oerstediana* (Klotzsch & Garcke) Boiss.), section *Petaloma* (Raf.) Boiss. (representative: *E. bicolor* Engelm. & A. Gray), section *Tithymalopsis* (Klotzsch & Garcke) Boiss. (representatives: *E. aaron-rossii* A. H. Holmgren & N. H. Holmgren, *E. innocua* L. C. Wheeler, *E. ipecacuanhae* L., *E. macropus* (Klotzsch & Garcke) Boiss., and *E. sphaerorhiza* Benth.), and section *Trichosterigma* (Klotzsch & Garcke) Boiss. (representatives: *E. antisyphilitica* Zucc., *E. californica* Benth., *E. ceroderma* I. M. Johnst., *E. fulgens* Karw. ex Klotzsch, *E. gentryi* V. W. Steinm. & T. F. Daniel, *E. macvaughii* Carvajal & Lomelí, *E. misera* Benth., *E. rossiana* Pax, and *E. rossiana* var. nov.). In comparison to members of subgenus *Agaloma* sect. *Zygophyllidium*, species of this group are highly variable in habit, and the leaves are strictly entire. This group accounts for nearly 90% of the species that have been treated in subgenus *Agaloma*, and it ranges from Argentina and Chile to

the northern United States and the Caribbean. Collectively, these sections form a monophyletic group in both analyses. However, the clade only has bootstrap support (94%) in the *ndh*F analysis (Fig. 14). Here too belong *E. cassythoides* Boiss., a Caribbean taxon previously placed in *Euphorbia* sect. *Arthrothamnus* (Boissier, 1862) and *E. equisetiformis* A. Stewart, an endemic to the Galapagos Islands whose relationship to other *Euphorbia* was uncertain (Burch, 1971).

Although the sample of species is not broad enough to make a definitive conclusion, this study supports Park's (1998) narrow circumscription of *Euphorbia* subg. *Agaloma* sect. *Tithymalopsis*. According to the molecular data, the section, as defined by Huft (1979) and Boissier (1862), is polyphyletic and composed of at least three separate lineages. However, neither Huft nor Boissier can be criticized. In fact, the placement of similar-appearing, geophytic taxa such as *E. macropus* and *E. sphaerorhiza* in separate clades with nongeophytic taxa is odd and represents one instance where molecular results are counterintuitive. Of the remaining five sections of subgenus *Agaloma*, only sections *Petaloma* and *Dichilium* are likely to be monophyletic, but not enough taxa from these were included to test this hypothesis. What is clearly shown is that subgenus *Agaloma* sects. *Alectoroctonum*, *Cyttarospermum*, and *Trichosterigma* are polyphyletic.

Euphorbia *subg*. Poinsettia. According to the most recent treatment of *Euphorbia* subg. *Poinsettia* (Mayfield, 1997), this taxon is a strictly New World assemblage of 24 species. Dressler (1962) recognized 11 species. The group is characterized by cup-shaped involucral glands that are generally reduced to one (rarely more) per involucre. Pigmentation of the subcyathial leaves, as exemplified by *E. pulcherrima*, occurs in many but not all of the species. Growth form varies from annuals, perennial herbs, geophytes, to shrubs. Nine species of subgenus *Poinsettia* were included in this study: *E. chersonesa* Huft, *E. heterophylla* L., *E. hormorhiza* Radcl.-Sm., *E. pentadactyla* Griseb., *E. pulcherrima*, *E. pumicola* Huft, *E. radians* Benth., *E. strigosa* Hook. & Arn., and *E. zonosperma* Müll. Arg.

In both analyses, these species are nested within a clade that corresponds to *Euphorbia* subg. *Agaloma* sect. *Zygophyllidium* (Figs. 12, 14). This is not surprising because some species of this section (e.g., *E. bifurcata*) possess involucres with a single gland and nearly identical seeds to those of members of subgenus *Poinsettia*. In addition, other taxa (e.g., *E. jaliscensis*) possess panduriform leaves that

are otherwise known only from a few species of subgenus *Poinsettia*. The subgenus is noteworthy because of the extreme amount of genetic divergence among its members. It forms a monophyletic group only in the *ndh*F analysis (Fig. 14). In the ITS analysis, subgenus *Poinsettia* comes out in two groups nested within subgenus *Agaloma* sect. *Zygophyllidium* (Fig. 12). A close affinity between subgenus *Poinsettia* and species of subgenus *Agaloma* sect. *Dichilium* has been suggested (Dressler, 1962; Webster, 1967), but the two groups do not appear closely related (Figs. 12–14). Dressler's (1962) removal of *E. eriantha* from subgenus *Poinsettia* is justified by molecular evidence. *Euphorbia chersonesa* (= *E. heterophylla* L. var. *eriocarpa* Millsp.) was placed in subgenus *Poinsettia* by Millspaugh (1889) but placed in subgenus *Agaloma* by Huft (1984). The molecular data strongly support that it is sister to *E. pumicola* in subgenus *Poinsettia*. Morphologically, *E. chersonesa* is noteworthy because it is intermediate between subgenus *Agaloma* sect. *Zygophyllidium* and other members of subgenus *Poinsettia* in involucral gland characteristics; the glands are not deeply cupped, but they do apparently lack appendages.

The herbaceous habit of the species of *Euphorbia* subg. *Agaloma* sect. *Zygophyllidium* and many of the early diverging members of subgenus *Poinsettia* suggests that woodiness in species such as *E. pulcherrima* is secondarily derived. In addition, the lack of involucral appendages appears to represent a reversal to unappendaged involucres.

ORIGIN AND BIOGEOGRAPHY OF EUPHORBIEAE

The tribe Euphorbieae demonstrates a complex biogeographical pattern. The earliest diverging clade, subtribe Anthosteminae, is strictly African and Madagascan (Figs. 1, 2). The next diverging clade, subtribe Neoguillauminiinae, occurs in Australia and New Caledonia (Figs. 1, 2). Of the four major clades of Euphorbiinae, one, clade A (Figs. 5, 6), is strictly African and Madagascan, and one, clade B (Figs. 7, 8), is primarily distributed in temperate regions of the Northern Hemisphere. The two remaining clades, C (Figs. 9–11) and D (Figs. 12–14), are widespread, but the earliest diverging lineages within these two clades occur in Africa and Madagascar. If present-day distributions are indicative of historical ranges, then the molecular evidence is consistent with a hypothesized African origin of the tribe before the breakup of Gondwanaland.

Although clade B is almost entirely Laurasian in distribution, there are a few members in Africa. The

clade is absent from Australia and essentially absent from South America, where only two species occur, *Euphorbia spathulata* and *E. philippiana* Boiss. The first of these has an amphitropical distribution and also occurs in North America. The second is a Chilean endemic similar to North American species. Considering that approximately 85% of the temperate South American species of angiosperms have an origin in the Northern Hemisphere (Raven, 1963), the presence of these species in South America is likely the result of dispersal events from North America. Within clade B there are two major subclades, and both possess species in North America and Eurasia. It is possible that the current distribution of clade B represents either an ancient dispersal event to Laurasia or evidence that the diversification of Euphorbiinae predates the split up of Pangaea.

Clade C has a wide distribution that is best described as pantropical. According to the *ndh*F results herein, the earliest diverging lineages of this clade occur in Africa, Madagascar, and Australasia. The Hawaiian endemic species *Euphorbia haeleeleana* belongs here and appears to have arrived at the islands by long-distance dispersal from related taxa, e.g., *Euphorbia plumerioides*, in the Pacific Islands. In the *ndh*F analysis, all of the Neotropical members of clade C form a single lineage that is sister to a lineage containing the subgenera *Euphorbia* and *Lacanthis* together with the *Synadenium* alliance, again suggesting that these two groups arose before the breakup of Gondwanaland. Similarly, the sister clade relationship of subgenus *Lacanthis* and subgenus *Euphorbia* together with the *Synadenium* alliance suggest that the common ancestor of both these groups was present before Madagascar began to separate from Africa.

Clade D has a distribution similar to clade C. Both ITS and *ndh*F analyses indicate that the earliest diverging lineages are in Africa, Madagascar, and southwest Asia. Also like in clade C, all of the New World species belong to a single lineage. Interestingly, according to the *ndh*F evidence, of the two earliest-diverging groups in the lineage containing the New World taxa of clade D, one occurs in Namibia and the other occurs in arid eastern Brazil. Thus, there is a clear, well-supported link between New and Old World species in this group.

The near parallel distribution in the sister clades C and D provides further evidence that the distribution of New and Old World taxa is the result of vicariance caused by the breakup of Gondwanaland. Therefore, the molecular evidence corroborates that despite being a very specialized group, the Euphorbiinae are also a very ancient group.

Based on biogeographic patterns, Croizat (1940) postulated that *Euphorbia* was already differentiated into modern subgenera by the mid Cretaceous (ca. 100 million years ago), and this appears quite possible.

The fruits in Euphorbieae are generally dry, explosively dehiscent, and initially dispersed only a few meters from their source. For this reason, there are few instances of long-distance dispersal within the tribe. One notable exception involves species of *Chamaesyce*, a primarily New World taxon whose range parallels that of the entire Euphorbieae. Webster (1967) proposed that this group probably originated in the New World and molecular evidence supports his hypothesis. Because many *Chamaesyce* possess mucilaginous seeds, much of their great success in distribution is likely because seeds are able to adhere to animals and thus achieve long-distance dispersal (see discussion in Jordan & Hayden, 1992). This feature is otherwise rare in *Euphorbia* and helps explain why *Chamaesyce* is one of the few relatively derived taxa within Euphorbiinae that exhibits a transoceanic distribution.

Webster et al. (1982) stated that the most-likely primitive Euphorbiinae were in *Euphorbia* sect. *Denisophorbia*. Dressler (1957) believed that they were in sections *Balsamis* and *Adenorima*. Although the molecular evidence does not support their hypotheses, it does not provide solid insight as to what actually is the most primitive *Euphorbia* either, and it appears difficult to identify a single most-ancestral group. Dressler's and Webster's choices are sound because all three sections represent early diverging lineages within the genus.

The molecular evidence does provide some insight as to the features that ancestral *Euphorbia* likely possessed. First, they were probably a tropical tree or shrub, because early diverging lineages within the various clades of *Euphorbia* are mostly woody tropical plants. Phyllotaxy was presumably spiral, and it is likely that a pseudoumbellate inflorescence structure was well developed; these characteristics are found in all the major clades of *Euphorbia*, and their widespread presence is parsimoniously explained by their presence in the common ancestor of all four major clades. Stipules were probably absent or minute and glanduliform. There were likely five glands on the involucre. Although gland reduction is common, in many species with reduced glands, e.g., *E. graminea* Jacq., the first involucre formed in an inflorescence often possesses five glands and only subsequent involucres possess fewer glands. Presumably involucral appendages were absent, because they are present only in derived groups of Euphorbiinae. It is note-

worthy that the Madagascan endemic *Euphorbia antso* is the least derived species with regard to molecular evolution (see Figs. 3, 4) and possesses most of the features discussed above as ancestral. Although the ancestral condition is probably woody, in terms of species number, the two most successful lineages within the subtribe, *Chamaesyce* and the temperate *E.* subg. *Esula* clade, are primarily comprised of herbaceous species.

The large amount of diversification within Euphorbiinae compared to the other subtribes of Euphorbieae and the sister tribe Hippomaneae suggests that one or more key innovations may have promoted rapid evolution and diversification within this lineage. If such innovations actually exist, they likely involve the cyathium. Although cyathiate inflorescences also occur in Anthosteminae and Neoguillauminiinae, both these subtribes contain very few species and have narrow distributions. The particular feature that occurs in Euphorbiinae but is absent in the other subtribes is that, with few exceptions, the nectar-producing involucral glands are situated on the rim of the involucre and not partially enclosed within this structure. Therefore, this feature may have greatly enhanced successful insect attraction and pollination, thus giving members of Euphorbiinae a selective advantage, which in turn has driven the patterns of speciation and diversification presently observed in extant members of the subtribe.

COMPARISON WITH MORPHOLOGICAL DATA

There are two previous phylogenetic studies of the Euphorbieae based on morphological characters (Park, 1996; Park & Elisens, 2000). The first of these treated only the New World taxa of subtribe Euphorbiinae, while the second treated the entire tribe. The molecular results differ drastically from the results obtained in either analysis. Even the two separate morphological analyses yielded different topologies, and in neither study was there significant statistical support for the majority of the clades. Part of the problem with these morphological analyses may be that too few characters were included to resolve the taxa. For example, in the first study of the New World species only 37 characters were used to resolve relationships among 49 terminal taxa, in this case species groups. In addition, many characters employed in both analyses are highly variable even among closely related species, and their use to discern relationships within such a large and diverse tribe as Euphorbieae is unlikely to provide accurate results.

FUTURE OF EUPHORBIINAE CLASSIFICATION

The current classification of Euphorbieae subtribes Anthosteminae and Neoguillauminiinae is well supported herein and recognizes only monophyletic groups. No taxonomic adjustments are necessary for these subtribes, but as mentioned above, problems remain for the classification of subtribe Euphorbiinae.

The current taxonomic trend is going in the direction of splitting *Euphorbia*. This has already been observed with Webster's (1967) removal of *Chamaesyce*. More recently, Carter (1994: 378) stated that subgenus *Euphorbia* "could be separated as a genus in its own right." Likewise, Gilbert (1987: 235) also leaned toward an eventual dismemberment of *Euphorbia*, but well aware of the "profound nomenclatural consequences" associated with such a change, he justified only changes in rank within *Euphorbia*.

We disagree that *Euphorbia* should be divided. Our opinion is that the best long-term solution to the problem of Euphorbiinae classification is to expand *Euphorbia* to encompass all members of the subtribe. Some might contend that this is an undesirable step backward 250 years to Linnaeus's broad concept of *Euphorbia*. However, we believe that this solution is more favorable than leaving the genus in its current paraphyletic circumscription or restricting *Euphorbia* to only the subgenus *Euphorbia*.

The first taxonomic problem with limiting *Euphorbia* to subgenus *Euphorbia* is that ca. 90% of the species currently in the genus would need to be accommodated in other genera. Thus, *Euphorbia*, a well-known and easily identifiable taxon known throughout the world, would no longer exist in most parts of the globe. Instead, there would be a multitude of genera completely unknown to most, and the boundaries and circumscription of these would be vague and certainly debated for quite some time. On the contrary, a broad *Euphorbia* would require changing the names of ca. 100 (vs. ca. 1700!) species and would only affect groups with relatively limited distributions. These changes would only mildly broaden the current concept of *Euphorbia* to encompass taxa that possess an unusual involucral morphology, a feature we believe has received undue taxonomic weight.

Another reason that splitting *Euphorbia* is unsatisfactory concerns the unusual nature of evolution within this group. The situation here is that basic cyathial morphology in the genus is highly conserved, but vegetative morphology is highly plastic. This has led to much parallel evolution in

growth form with little change in floral form. There-
fore, if the relationships suggested by the molecular
evidence do indeed accurately depict the phylog-
eny of the group, then there are a number of well-
defined monophyletic lineages nested within a par-
aphyletic background of relatively undifferentiated
groups or groups that have undergone a high degree
of parallel vegetative evolution.

To propose various genera whose members are
superficially nearly identical fails to serve one of
the primary purposes of a system of classification,
i.e., to provide a predictable system that allows for
the separation of taxa and for the ability to make
assumptions about relationship based on morpho-
logical features. If *Euphorbia* classification is to ac-
tually reflect relationship, then there will be excep-
tions and inconsistencies in defining new genera.
We fear that any system that attempts to dismember
Euphorbia will continue to have only limited suc-
cess and acceptance.

Croizat (1965: 574) emphasized the problem as-
sociated with subgeneric groups within *Euphorbia*
and stated "the infraspecific combinations of char-
acters are so intricate as to make it really difficult
to identify a truly natural subgeneric taxon." The
same problem occurs with an elevation in rank to
genus, but the broad implications are greatly more
severe. Recognizing highly similar subgeneric taxa
is much less of a problem because such rank is
usually of primary interest to specialists in the
group. Webster (1967: 398) stated, "If the various
microgenera of Euphorbieae cannot be easily dis-
tinguished, there seems little reason to adopt them
simply because they represent evolutionary units;
it is quite easy to discuss the evolution of these
taxa if they are referred to as infrageneric compo-
nents of *Euphorbia*." We could not agree more.

As mentioned in the introduction, the majority
of genera currently segregated from *Euphorbia* are
distinguished by cyathial traits. In some regards,
cyathial morphology has received undue weight,
and this may be because there has been great di-
versification in vegetative morphology throughout
Euphorbiinae, but the overall structure of the cy-
athium has remained relatively conserved. Thus,
changes in cyathial morphology are viewed as tax-
onomically significant occurrences, and little sys-
tematic emphasis has been placed on other fea-
tures, including relationships. Leach (1973: 32),
when describing *Endadenium*, justified his new ge-
nus on the basis of its distinctive arrangement of
glands within the involucre, further saying that *En-
dadenium* "combines so many of the characteristics
of the other African members of the tribe that its
assignment to any one of the genera involved would

so effectively blur, if not nullify, the diagnostic cri-
teria as to make it virtually impossible to retain
these as separate genera on any but purely arbitrary
grounds." However, the current recognition of gen-
era separated solely on the basis of cyathial char-
acters while ignoring, as in the case of *Endaden-
ium,* all of the characters that do indeed blend the
segregate genera into *Euphorbia,* is in itself some-
what arbitrary.

One of the arguments frequently used to justify
the division of *Euphorbia* is that the genus is so
large and heterogeneous that it is unwieldy. The
incredible speciation and diversification that have
occurred within *Euphorbia* are largely biological
facts. Dismembering the genus would make it
smaller and less heterogeneous but collectively as
unwieldy an assemblage as ever. Another argument
advocated by splitters is that the generic concept
used for these assemblages is too broad in com-
parison with other groups; for the sake of taxonomic
consistency, *Euphorbia* must be divided. In re-
sponse to this, it is worth pointing out that no two
lineages of plants are completely comparable to
each other. Each has an independent evolutionary
history. Therefore, the argument that *Euphorbia*
should be divided simply because its evolutionary
past has involved amazing speciation, dispersal,
and diversification is unfounded. In our opinion,
recognizing the genus in its broad sense has some
benefit because it conveys the incredible evolution-
ary history of this group.

Can a workable system of classification be de-
veloped for the Euphorbiinae that is based on the
concept of monophyly? We believe that the answer
is yes, but the units of such a classification should
be infrageneric. Certainly many modifications will
be necessary and time required before a stable sys-
tem of classification is developed. However, it is
better that such a process be undertaken at the
infrageneric level, where the far-reaching nomen-
clatural implications associated with generic
changes can be avoided.

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Appendix 1. Voucher information for the included species of Euphorbieae and outgroups sequenced in this study. For cultivated and introduced taxa, the native origin of the plant is given in parentheses.

Taxon	Origin and voucher	ITS GenBank accession	ndhF GenBank accession
OUTGROUPS			
Omalanthus populifolius Graham	Cultivated (nat. Australia), *Steinmann 1423* (RSA)	AF537585	AF538262
Sapium sebiferum (L.) Roxb.	Cultivated (nat. China), *Steinmann 1424* (RSA)	AF537586	AF538261
Sebastiania cornuta McVaugh	Mexico, Sonora, *Steinmann 589* (RSA)	AF537587	AF538263
Stillingia spinulosa Torr.	Mexico, Sonora, *Felger 92-381* (RSA)	AF537588	AF538264
EUPHORBIEAE SUBTRIBE ANTHOSTEMINAE			
Anthostema madagascariense Baill.	Madagascar, *Pascal 586* (MO)	AF537582	AF538257
Anthostema senegalense A. Juss.	Senegal, *Bamps 7759* (MO)	—	AF538259
Anthostema sp. nov.	Madagascar, *Miller et al. 8840* (MO)	AF537583	AF538258
Dichostemma glaucescens L. Pierre	Gabon, *McPherson 15531* (DAV)	AF537584	AF538260
EUPHORBIEAE SUBTRIBE NEOGUILLAUMINIINAE			
Calycopeplus casuarinoides L.S. Sm.	Cultivated (nat. Australia), *Steinmann 1407* (RSA)	AF537580	—
Calycopeplus collinus P.I. Foster	Australia, *van der Werff 11848* (DAV)	—	AF538254
Calycopeplus paucifolius (Klotzsch) Baill.	Australia, *Craven 7139* (RSA)	—	AF538255
Neoguillauminia cleopatra (Baill.) Croizat	New Caledonia, *McPherson 17882* (MO)	AF537581	AF538256
EUPHORBIEAE SUBTRIBE EUPHORBIINAE			
Chamaesyce acuta (Engelm.) Millsp.	U.S.A., Texas, *Mayfield 1989* (RSA)	AF537450	AF538176
Chamaesyce angusta (Engelm.) Small	Mexico, Coahuila, *Mayfield 1328* (RSA)	AF537449	—
Chamaesyce articulata (Burm.) Britton	U.S.A., Virgin Isalnds, *Steinmann 94-10* (RSA)	AF537446	AF538175
Chamaesyce carunculata (Waterf.) Shinners	Mexico, Chihuahua, *Bowers et al. 2939* (ARIZ)	AF537447	—
Chamaesyce degeneri (Sherff) Croizat & Degener	U.S.A., Hawaii, *Motley 338* (NY)	AF537444	—
Chamaesyce hypericifolia (L.) Millsp.	U.S.A., Hawaii, *Motley 1804* (NY)	AF537443	—
Chamaesyce prostrata (Aiton) Small	U.S.A., Hawaii, *Motley 1802* (NY)	AF537445	—
Chamaesyce polycnemoides (Boiss.) J. Soják	Botswana, *Snow & Chatakuta 6905* (MO)	AF537448	—
Endadenium gossweileri (N.E. Br.) L.C. Leach	Cultivated (nat. Angola), *Steinmann 1457* (RSA)	AF537471	AF538198
Euphorbia aaron-rossii A.H. Holmgren & N.H. Holmgren	U.S.A., Arizona, *Ross s.n.* (RSA)	AF537396	—
Euphorbia abdelkuri Balf.f.	Cultivated (nat. Abd-el-Kuri), *Steinmann 1437* (RSA)	AF537458	AF538194
Euphorbia acalyphoides Hochst. ex Boiss.	Kenya, *Luke et al. TPR177* (MO)	AF537576	AF538251
Euphorbia acanthothamnus Heldr. & Sart. ex Boiss.	Cultivated (nat. Greece/Turkey), *Steinmann 1425* (RSA)	AF537554	AF538232
Euphorbia adiantoides Lam.	Ecuador, *Harling & Anderson 22548* (GB)	AF537395	—
Euphorbia agowensis Hochst. ex Boiss.	Ethiopia, *Gilbert & Thulin 132* (MO)	AF537419	—
Euphorbia alluaudii Drake	Cultivated (nat. Madagascar), *Steinmann 1481* (RSA)	AF537468	AF538197
Euphorbia alta Norton	U.S.A., Arizona, *Sanders 5905* (RSA)	AF537553	—
Euphorbia amygdaloides L.	Cultivated (nat. Europe), *Steinmann 1428* (RSA)	AF537544	—

Appendix 1.   Continued.

Taxon	Origin and voucher	ITS GenBank accession	ndhF GenBank accession
Euphorbia ankarensis Boiteau	Cultivated (nat. Madagascar), *Steinmann 1482* (RSA)	AF537462	—
Euphorbia antisyphilitica Zucc.	Cultivated (nat. U.S.A., Texas), *Steinmann 1451* (RSA)	AF537398	—
Euphorbia antso Denis	Cultivated (nat. Madagascar), *Steinmann 1473-B* (RSA)	AF537579	AF538253
Euphorbia aphylla Brouss. ex Willd.	Cultivated (nat. Canary Islands), *Steinmann 1466* (RSA)	AF537540	AF538225
Euphorbia appariciana Rizzini	Cultivated (nat. Brazil), *Steinmann 1442* (RSA)	AF537455	AF538177
Euphorbia arbuscula Balf.f.	Cultivated (nat. Socotra), *Steinmann 1435* (RSA)	AF537496	—
Euphorbia aff. *ariensis* HBK	Mexico, Nayarit, *Steinmann 1148* (RSA)	AF537409	—
Euphorbia atrispina N.E. Br.	Cultivated (nat. Republic of S. Africa), *Steinmann 1478* (RSA)	AF537568	—
Euphorbia atropurpurea Brouss. ex Willd.	Cultivated (nat. Canary Islands), *Steinmann 1489* (RSA)	AF537542	AF538230
Euphorbia attastoma Rizzini	Cultivated (nat. Brazil), *Steinmann 1487* (RSA)	AF537511	—
Euphorbia balsamifera Aiton ssp. *adenensis* (Deflers) Bally	Cultivated (northeast tropical Africa), *Steinmann 1480* (RSA)	AF537571	AF538250
Euphorbia bicolor Engelm. & A. Gray	U.S.A., Texas, *Van Devender 96-290* (RSA)	AF537386	—
Euphorbia bifurcata Engelm.	Mexico, Nuevo León, *Nesom 7703* (RSA)	AF537434	AF538173
Euphorbia bilobata Engelm.	U.S.A., Arizona, *Steinmann 938* (RSA)	AF537435	AF538172
Euphorbia boöphthona C.A. Gardner	Australia, *Coveny 3054* (RSA)	AF537515	AF538207
Euphorbia brunellii Chiov.	Cultivated (nat. east tropical Africa), *Steinmann 1495* (RSA)	AF537486	AF538203
Euphorbia calcicola Fern.	Mexico, Morelos, *Steinmann 801* (RSA)	AF537385	—
Euphorbia californica Benth.	Cultivated (nat. Mexico), *Steinmann 1492* (RSA)	AF537377	—
Euphorbia calyculata HBK	Mexico, Puebla, *Tenorio L. 7261c* (NY)	AF537524	AF538221
Euphorbia calyptrata Coss. & Kralik	Morocco, *Podlech 45138* (RSA)	AF537549	—
Euphorbia capmanambatoensis Rauh	Cultivated (nat. Madagascar), *Steinmann 1468* (RSA)	AF537476	—
Euphorbia caputmedusae L.	Cultivated (nat. Republic of S. Africa), *Steinmann 1463* (RSA)	AF537574	—
Euphorbia cassythoides Boiss.	Cayman Islands, *Proctor 47858* (NY)	AF537387	—
Euphorbia ceroderma I.M. Johnst.	Mexico, Sonora, *Steinmann 1393* (RSA)	AF537389	AF538153
Euphorbia cestrifolia HBK	Ecuador, *Harling 27200* (GB)	AF537521	AF538213
Euphorbia cheirolepis Fisch. & C.A. Mey.	Central Asia, *Vasák s.n.* (NY)	AF537424	—
Euphorbia chersonesa Huft	Mexico, Baja California Sur, *Steinmann 1252* (RSA)	AF537436	AF538174
Euphorbia clava Jacq.	Cultivated (nat. Republic of S. Africa), *Steinmann 1472-B* (RSA)	AF537569	AF538245
Euphorbia colletiodes Benth.	Mexico, Sonora, *Steinmann 93-387* (ARIZ)	AF537405	—
Euphorbia comosa Vell.	Brazil, *Webster 25425* (DAV)	AF537503	AF538222
Euphorbia crossadenia Pax & K. Hoffm.	Brazil, *Graças et al. 886* (SP)	AF537451	—
Euphorbia crotonoides Boiss.	Tanzania, *M.R. 23765* (NY)	AF537578	AF538238
Euphorbia delicatula Boiss.	Mexico, Guerrero, *Steinmann 1199* (RSA)	AF537393	AF538152

Appendix 1.   Continued.

Taxon	Origin and voucher	ITS GenBank accession	*ndh*F GenBank accession
Euphorbia dendroides L.	Greece, *Strid 25582* (RSA)	AF537539	—
Euphorbia denisii Oudejans	Cultivated (nat. Madagascar), *Steinmann 1434* (RSA)	AF537497	—
Euphorbia depauperata Hochst. ex A. Rich.	Malawi, *Kaunda & Tawakali 906* (NY)	AF537556	—
Euphorbia discolor Ledeb.	Former U.S.S.R., *McNeal 710* (RSA)	AF537547	—
Euphorbia drupifera Thonn.	Cultivated (nat. Africa), *Steinmann 1488* (RSA)	AF537480	AF538191
Euphorbia eanophylla Croizat	Bolivia, *Beck 11399* (DAV)	AF537498	—
Euphorbia eglandulosa V.W. Steinm.	Mexico, Chiapas, *Breedlove 70137* (CAS)	AF537394	—
Euphorbia elata Brandegee	Brazil, *Daly 6694* (NY)	AF537495	AF538217
Euphorbia elliotii Leandri	Madagascar, *Dorr et al. 3985* (MO)	AF537478	—
Euphorbia epiphylloides Kurz	Cultivated (nat. Andaman Islands), *Steinmann 1459* (RSA)	AF537484	—
Euphorbia equisetiformis A. Stewart	Ecuador, Galapagos Islands, *Eliason & Eliason 1573* (K)	AF537388	—
Euphorbia eremophila A. Cunn.	Australia, *Vasek 680914-51* (RSA)	AF537423	—
Euphorbia eriantha Benth.	U.S.A., Arizona, *Steinmann 925* (RSA)	AF537440	AF538167
Euphorbia esculenta Marloth	Cultivated (nat. Republic of S. Africa), *Steinmann 1474* (RSA)	AF537575	—
Euphorbia espinosa Pax	Cultivated (nat. Africa), *Steinmann 1494* (RSA)	AF537416	AF538190
Euphorbia esula L.	U.S.A., New Jersey (nat. Eurasia), *Steinmann 1427* (RSA)	AF537546	AF538229
Euphorbia exstipulata Engelm.	U.S.A., Arizona, *Steinmann 934* (RSA)	AF537433	AF538171
Euphorbia fulgens Karw. ex Klotzsch	Mexico, Oaxaca, *Campos 813* (RSA)	AF537404	AF538154
Euphorbia gentryi V.W. Steinm. & T.F. Daniel	Mexico, Sonora, *Steinmann 94-357* (ARIZ)	AF537406	—
Euphorbia germainii Phil.	Chile, *Teillier 4267* (SGO)	AF537499	AF538205
Euphorbia geroldii Rauh	Cultivated (nat. Madagascar), *Steinmann 1467* (RSA)	AF537475	—
Euphorbia glanduligera Pax	Namibia, *Koutnik 2015* (DAV)	AF537426	AF538178
Euphorbia globosa (Haw.) Sims	Cultivated (nat. Republic of S. Africa), *Steinmann 1454-A* (RSA)	—	AF538239
Euphorbia goetzei Pax	Tanzania, *Taylor et al. 8490* (MO)	AF537413	AF538185
Euphorbia gollmeriana Klotzsch ex Boiss.	Venezuela, *Ramírez 2696* (DAV)	AF537501	AF538220
Euphorbia gottlebei Rauh	Cultivated (nat. Madagascar), *Steinmann 1471* (RSA)	AF537459	—
Euphorbia gradyi V.W. Steinm. & A. Ram.-Roa	Mexico, Oaxaca, *Steinmann 784* (RSA)	AF537407	AF538151
Euphorbia graminea Jacq.	Mexico, Sonora, *Steinmann 94-107* (RSA)	AF537410	AF538155
Euphorbia grantii Oliv.	Tanzania, *Bidgood et al. 1186* (MO)	—	AF538242
Euphorbia gregaria Marloth	Cultivated (nat. Republic of S. Africa), *Steinmann 1445-B* (RSA)	AF537527	—
Euphorbia guatemalensis Standl. & Steyerm.	Mexico, Chiapas, *Steinmann 1170* (RSA)	AF537408	—
Euphorbia guerichiana Pax	Republic of South Africa, *Balkwill et al. 6022* (MO)	AF537415	AF538182
Euphorbia gymnoclada Boiss.	Brazil, *Webster 25853* (DAV)	AF537456	—
Euphorbia gymnonota Urb.	Bahama Islands, *Correll & Wasshausen 46769* (NY)	AF537507	—

Appendix 1.   Continued.

Taxon	Origin and voucher	ITS GenBank accession	*ndh*F GenBank accession
Euphorbia haeleeleana D.R. Herbst	U.S.A., Hawaii, *Fernstemacher s.n.* (NY)	AF537514	AF538206
Euphorbia hallii R.A. Dyer	Cultivated (nat. Republic of S. Africa), *Steinmann 1475* (RSA)	AF537573	—
Euphorbia hamata (Haw.) Sweet	Cultivated (nat. Republic of S. Africa), *Steinmann 1454-B* (RSA)	—	AF538237
Euphorbia hedyotoides N.E. Br.	Cultivated (nat. Madagascar), *Steinmann 1472-A* (RSA)	AF537460	AF538196
Euphorbia heterodoxa Müll. Arg.	Brazil, *Webster 25810* (DAV)	AF537500	—
Euphorbia heterophylla L.	Mexico, Sonora, *Van Devender 98-1157* (ARIZ)	AF537429	AF538170
Euphorbia hoffmanniana (Klotzsch & Garcke) Boiss.	Costa Rica, *Haber 10501* (F)	AF537508	AF538211
Euphorbia hormorhiza Radcl.-Sm.	Mexico, Tamaulipas, *Mayfield & Patterson 1843* (TEX)	AF537431	AF538165
Euphorbia iharanae Rauh	Cultivated (nat. Madagascar), *Steinmann 1458* (RSA)	AF537477	—
Euphorbia innocua L.C. Wheeler	U.S.A., Texas, *Mayfield 2168* (RSA)	AF537380	AF538161
Euphorbia insulana Vell.	Brazil, *Hora 03* (NY)	AF537411	—
Euphorbia ipecacuanhae L.	U.S.A., South Carolina, *Spongberg & Boufford 1718* (MO)	AF537397	—
Euphorbia jaliscensis B.L. Rob. & Greenm.	Mexico, Jalisco, *Steinmann 754* (RSA)	AF537442	AF538166
Euphorbia juttae Dinter	Cultivated (nat. Namibia), *Steinmann 1493* (RSA)	AF537418	AF538188
Euphorbia kraussiana Bernh.	Republic of S. Africa, *Stalmans 372* (MO)	AF537548	—
Euphorbia lacera Boiss.	Mexico. E. de Mexico, *Castilla & Tejero 958* (ENCB)	AF537441	—
Euphorbia lactiflua Phil.	Chile, *Dillon & Teillier 5105* (F)	AF537528	AF538219
Euphorbia lagunensis Huft	Mexico, Baja California Sur, *Steinmann 1272* (RSA)	AF537379	—
Euphorbia lagunillarum Croiz.	Cultivated (Venezuela), *Steinmann 1621* (RSA)	AF537502	—
Euphorbia lathyris L.	U.S.A., California (nat. Eurasia), *Steinmann 1426* (RSA)	AF537550	—
Euphorbia laurifolia Juss.	Ecuador, *Mena C61* (NY)	AF537509	—
Euphorbia leucocephala Lotsy	Cultivated (nat. Guatemala), *Steinmann 94-17* (RSA)	AF537381	—
Euphorbia lignosa Marloth	Cultivated (nat. Namibia), *Steinmann 1455* (RSA)	—	AF538240
Euphorbia longifolia Lam.	Canary Islands, *Lægaard 9905* (DAV)	AF537558	AF538235
Euphorbia longituberculosa Boiss.	Cultivated (nat. east tropical Africa), *Steinmann 1479* (RSA)	AF537577	AF538252
Euphorbia macropus (Klotzsch & Garcke) Boiss.	Mexico, Nuevo León, *Mayfield 1294* (TEX)	AF537378	—
Euphorbia macvaughii Carvajal & Lomelí	Cultivated (nat. Mexico, Michoacán), *Steinmann 1486* (RSA)	AF537382	—
Euphorbia mahabobokensis Rauh	Cultivated (nat. Madagascar), *Steinmann 1456* (RSA)	AF537522	—
Euphorbia matabelensis Pax	Botswana, *Smith 4229* (MO)	—	AF538247
Euphorbia mauritanica L.	Cultivated (nat. southern Africa), *Steinmann 1432* (RSA)	AF537531	—
Euphorbia medicaginea Boiss.	Morocco, *Podlech 41883* (RSA)	AF537535	—
Euphorbia meenae S. Carter	India, *Singh s.n.* (RSA)	AF537483	AF538202

Appendix 1. Continued.

Taxon	Origin and voucher	ITS GenBank accession	*ndh*F GenBank accession
Euphorbia megalatlantica Ball	Morocco, *Podlech 41177* (RSA)	AF537536	AF538226
Euphorbia meloformis Aiton	Cultivated (nat. Republic of S. Africa), *Steinmann 1490* (RSA)	AF537565	—
Euphorbia meuleniana O. Schwartz	Cultivated (nat. Yemen), *Steinmann 1448* (RSA)	AF537572	—
Euphorbia milii Des Moul.	Cultivated (nat. Madagascar), *Steinmann 1476* (RSA)	AF537461	AF538195
Euphorbia millotii Ursch & Leandri	Cultivated (nat. Madagascar), *Steinmann 1477* (RSA)	AF537463	—
Euphorbia misella S. Watson	Mexico, Chihuahua, *Steinmann 1032* (RSA)	AF537384	AF538160
Euphorbia misera Benth.	Mexico, Baja California, *Steinmann 1285* (RSA)	AF537383	—
Euphorbia monteiri Hook.f.	Botswana, *Long & Rae 290* (K)	AF537563	—
Euphorbia myrsinites L.	U.S.A., Colorado (nat. Eurasia), *Steinmann 1430* (RSA)	AF537551	AF538231
Euphorbia namuskluftensis L.C. Leach	Cultivated (nat. Namibia), *Steinmann 1491* (RSA)	AF537562	—
Euphorbia oaxacana B.L. Rob. & Greenm.	Mexico, Colima, *Steinmann 1094* (RSA)	AF537373	—
Euphorbia obesa Hook.f.	Cultivated (nat. Republic of S. Africa), *Steinmann 1465* (RSA)	AF537566	AF538244
Euphorbia oblongata Griseb.	U.S.A., California (nat. Europe), *Halse 4334* (RSA)	AF537555	—
Euphorbia ocymoidea L.	Mexico, Jalisco, *Steinmann 1139* (RSA)	AF537392	—
Euphorbia oerstediana (Klotzsch & Garcke) Boiss.	U.S.A., Puerto Rico, *Axelrod & Sastre 6278* (NY)	—	AF538159
Euphorbia omariana M.G. Gilbert	Ethiopia, *Friss et al. 3674* (K)	AF537560	AF538243
Euphorbia panchganiensis Blatt. & McCann	India, *Singh s.n.* (RSA)	AF537375	—
Euphorbia papillosa A. St.-Hil.	Argentina, *Renvoize 3068* (RSA)	AF537510	—
Euphorbia pedilanthoides Denis	Cultivated (nat. Madagascar), *Steinmann 1438* (RSA)	—	AF538192
Euphorbia pentadactyla Griseb.	Argentina, *Cantino 700* (ARIZ)	AF537428	—
Euphorbia peperomioides Boiss.	Brazil, *Nakjima et al. 1596* (DAV)	AF537523	—
Euphorbia peplus L.	U.S.A., California (nat. Eurasia), *Steinmann 1433* (RSA)	AF537532	AF538228
Euphorbia perrieri Drake	Cultivated (nat. Madagascar), *Steinmann 1483* (RSA)	AF537463	—
Euphorbia pervilleana Baill.	Cultivated (nat. Madagascar), *Steinmann 1444* (RSA)	AF537518	AF538209
Euphorbia petiolata Banks & Sol.	Middle East, *Liston 7-85-388/3* (RSA)	AF537422	AF538180
Euphorbia phosphorea Mart.	Cultivated (nat. Brazil), *Steinmann 1446* (RSA)	AF537512	AF538223
Euphorbia phylloclada Boiss.	Republic of S. Africa, *Oliver et al. 6611* (K)	AF537427	AF538179
Euphorbia pilosa L.	Former U.S.S.R., *Elias et al. 7182* (RSA)	AF537557	AF538234
Euphorbia pirottae N. Terrac.	Cultivated (nat. Tanzania), *Steinmann 1440* (RSA)	AF537417	AF538186
Euphorbia platycephala Pax	Tanzania, *Bidgood et al. 2249* (K)	AF537561	AF538241
Euphorbia platyclada Rauh	Cultivated (nat. Madagascar), *Steinmann 1447* (RSA)	AF537421	AF538187
Euphorbia plumerioides Teijsm. ex Hassk.	Australia, *Fryxell & Craven 4022* (RSA)	AF537513	—

Appendix 1.   Continued.

Taxon	Origin and voucher	ITS GenBank accession	*ndh*F GenBank accession
Euphorbia poissonii Pax	Cultivated (west tropical Africa), *Steinmann 1498* (RSA)	AF537482	AF538193
Euphorbia polyantha Pax	Kenya, *Faden & Faden 74/477* (K)	—	AF538189
Euphorbia primulifolia Baker	Cultivated (nat. Madagascar), *Steinmann 1484* (RSA)	AF537466	—
Euphorbia pteroneura A. Berger (1)	Mexico, Chiapas, *Mayfield 980* (TEX)	AF537506	AF538210
Euphorbia pteroneura A. Berger (2)	Cultivated (nat. Mexico/Cent. America), *Steinmann 1622* (RSA)	AF537505	—
Euphorbia pteroneura A. Berger (3)	Cultivated (nat. Mexico/Cent. America), *Steinmann 1623* (RSA)	AF537504	—
Euphorbia pulcherrima Willd. ex Klotzsch	Mexico, Nayarit, *Steinmann 1070* (RSA)	AF537432	AF538168
Euphorbia pumicola Huft	Mexico, Baja California Sur, *Steinmann 1241* (ARIZ)	AF537437	AF538164
Euphorbia punicea Sw.	Cultivated (nat. Jamaica), *Raz 193* (NY)	AF537516	AF538208
Euphorbia radians Benth.	Mexico, Sonora, *Steinmann 944* (RSA)	AF537438	AF538169
Euphorbia regis-jubae Webb & Berthel.	Cultivated (nat. Canary Islands), *Steinmann 1431* (RSA)	AF537541	—
Euphorbia rhombifolia Boiss.	Cultivated (nat. Republic of S. Africa), *Steinmann 1439* (RSA)	AF537414	AF538183
Euphorbia robusta (Engelm.) Small	U.S.A., Colorado, *Steinmann 1429* (RSA)	AF537533	AF538227
Euphorbia rossiana Pax	Mexico, Puebla, *Steinmann 1195* (RSA)	AF537374	—
Euphorbia rossiana var. nov.	Mexico, Guerrero, *Steinmann 1199* (RSA)	AF537390	—
Euphorbia rossii Rauh & Buchloh	Cultivated (nat. Madagascar), *Steinmann 1449* (RSA)	AF537465	—
Euphorbia rubella Pax	Cultivated (nat. east tropical Africa), *Steinmann 1464* (RSA)	AF537487	AF538204
Euphorbia rzedowskii McVaugh	Mexico, Michoacán, *Steinmann 1110* (RSA)	AF537399	—
Euphorbia sarcodes Boiss.	Brazil, *Cordeiro et al. 2233* (SP)	AF537454	—
Euphorbia scatorhiza S. Carter	Cultivated (nat. Somalia), *Steinmann 1441* (RSA)	AF537420	AF538181
Euphorbia scheffleri Pax	Cultivated (nat. Kenya), *Steinmann 1452* (RSA)	—	AF538249
Euphorbia schimperi Presl	Cultivated (nat. Arabian Peninsula/NE tropical Africa), *Steinmann 1499* (RSA)	AF537537	—
Euphorbia sessilifolia Klotzsch ex Boiss. (1)	Brazil, *Arbo 5418* (DAV)	AF537453	—
Euphorbia sessilifolia Klotzsch ex. Boiss. (2)	Brazil, *Cordeiro et al. 2218* (SP)	AF537452	—
Euphorbia segoviensis (Klotzsch & Garcke) Boiss.	Mexico, Chiapas, *Steinmann 1174* (RSA)	AF537400	—
Euphorbia sinaloensis Brandegee	Mexico, Sonora, *Steinmann 94-130* (ARIZ)	AF537401	AF538156
Euphorbia sipolisii N.E. Br.	Cultivated (nat. Brazil), *Steinmann 1443* (RSA)	AF537517	—
Euphorbia socotrana Balf.f.	Cultivated (nat. Socotra), *Steinmann 1436* (RSA)	—	AF538248
Euphorbia sonorae Rose	Mexico, Sonora, *Steinmann 964* (RSA)	AF537402	—
Euphorbia soongarica Boiss.	Former U.S.S.R., *Elias 9850* (RSA)	AF537545	—
Euphorbia spathulata Lam.	U.S.A., California, *Banks 1601* (RSA)	AF537552	AF538233
Euphorbia sphaerorhiza Benth.	Mexico, Sonora, *Steinmann 1020* (RSA)	AF537412	AF538158

Appendix 1.   Continued.

Taxon	Origin and voucher	ITS GenBank accession	*ndh*F GenBank accession
Euphorbia stenophylla (Klotzsch & Garcke) Boiss.	Brazil, *Aparecida da Silva & dos Santos 3267* (DAV)	AF537529	—
Euphorbia stricta L.	Austria, *Wallnofer 8531* (NY)	AF537559	—
Euphorbia strigosa Hook. & Arn.	Mexico, Nayarit, *Steinmann 1079* (RSA)	AF537439	AF538163
Euphorbia subpeltata S. Watson	Mexico, Morelos, *Steinmann 794* (RSA)	AF537376	—
Euphorbia succedanea L.C. Wheeler	Mexico, Aguascalientes, *Steinmann 745* (RSA)	AF537403	AF538162
Euphorbia tannensis Spreng.	Australia, *Fryxell et al. 4475* (RSA)	AF537425	AF538184
Euphorbia tanquahuete Sessé & Mociño	Cultivated (Mexico), *Steinmann 1620* (RSA)	AF537525	AF538224
Euphorbia teke Schweinf. ex Pax	Cultivated (nat. east tropical Africa), *Steinmann 1470* (RSA)	AF537485	—
Euphorbia tetraptera Baker	Madagascar, *Rabevohita 2093* (DAV)	AF537526	—
Euphorbia thinophila Phil.	Chile, *Dillon & Teillier 5127* (F)	AF537530	AF538218
Euphorbia thouarsiana Baill.	Madagascar, *Leeuwenburg & Ranaivojaona 14585* (K)	AF537474	—
Euphorbia tirucalli L.	Cultivated (nat. Africa/Madagascar), *Steinmann 1445-A* (RSA)	AF537479	—
Euphorbia trichadenia Pax	Cultivated (nat. Zimbabwe/Angola), *Steinmann 1461* (RSA)	AF537564	AF538236
Euphorbia trichotoma HBK	Belize, *Hill 20357* (MO)	AF537534	—
Euphorbia tuberosa L.	Cultivated (nat. Republic of S. Africa), *Steinmann 1472-C* (RSA)	AF537570	AF538246
Euphorbia tubiglans Marloth ex R.A. Dyer	Cultivated (nat. Republic of S. Africa), *Steinmann 1462* (RSA)	AF537567	—
Euphorbia turczaninowii Kar. & Kir.	China, *Liston 827-4* (RSA)	AF537543	—
Euphorbia usambarica Pax	Tanzania, *Balslev 291* (NY)	AF537538	—
Euphorbia weberbaueri Mansf.	Cultivated (nat. Peru), *Steinmann 1347* (RSA)	AF537519	AF538212
Euphorbia whitei L.C. Wheeler	Mexico, Oaxaca, *Torres 10833* (DAV)	AF537391	—
Euphorbia zonosperma Müll.Arg.	Brazil, *Plowman et al. 8579* (F)	AF537430	—
Euphorbia xylophylloides Brongn. ex Lem.	Cultivated (nat. Madagascar), *Steinmann 1450* (RSA)	AF537467	AF538214
Euphorbia sp.	Cultivated (nat. probably Africa), *Steinmann 1469* (RSA)	AF537481	—
Euphorbia sp. nov. 1	Brazil, *Coredeiro et al. 2203* (SP)	AF537457	—
Euphorbia sp. nov. 2	Mexico, Tamaulipas, *Mayfield 1851* (TEX)	—	AF538157
Monadenium elegans S. Carter	Cultivated (nat. Tanzania), *Steinmann 1473-A* (RSA)	AF537470	AF538199
Monadenium ellenbeckii N.E. Br.	Cultivated (nat. east tropical Africa), *Steinmann 1453* (RSA)	—	AF538200
Monadenium lindenii S. Carter	Cultivated (nat. Somalia), *Steinmann 1485* (RSA)	AF537473	—
Monadenium magnificum E.A. Bruce	Cultivated (nat. Tanzania), *Steinmann 1496* (RSA)	AF537472	—
Pedilanthus bracteatus Jacq.	Cultivated (nat. Mexico), *Steinmann 1460* (RSA)	AF537489	—
Pedilanthus calcaratus Schltdl.	Mexico, Veracruz, *Cházaro B. & de Cházaro 7294* (NY)	AF537492	—
Pedilanthus connatus Dressler & Sacamano	Mexico, Jalisco, *Sacamano s.n.* (MO)	AF537493	—
Pedilanthus cymbiferus Schltdl.	Mexico, Puebla, *Steinmann 1624* (RSA)	AF537491	—

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Taxon	Origin and voucher	ITS GenBank accession	*ndh*F GenBank accession
Pedilanthus finkii Boiss.	Mexico, Oaxaca, *Meave del Castillo 1551* (MO)	AF537520	—
Pedilanthus macrocarpus Benth.	Mexico, Baja California, *Steinmann 1235* (RSA)	AF537490	—
Pedilanthus tehuacanus Brandegee	Mexico, Puebla, *Steinmann 1400* (RSA)	AF537488	AF538215
Pedilanthus tithymaloides (L.) Poit.	Guatemala, *Castillo 2713* (NY)	AF537494	AF538216
Synadenium grantii Hook.f.	Cultivated (east tropical Africa), *Steinmann 1497* (RSA)	AF537469	AF538201