

A molecular phylogeny and classification of the largely succulent and mainly African *Euphorbia* subg. *Athymalus* (Euphorbiaceae)

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Abstract *Euphorbia* subg. *Athymalus* consists of approximately 150 species and is one of the four main lineages that comprise the species-rich genus *Euphorbia*. Most species in the subgenus are stem succulents with greatly reduced leaves, but there are also leafy herbs, shrubs, trees and geophytes. The subgenus is restricted to arid regions of the Old World. Most species are found in sub-Saharan Africa, with one in Macaronesia and adjacent parts of western Africa, a few in the Arabian Peninsula (one of which extends into Iran) and one native to Madagascar. Twenty-three species are endemic to the northeastern Horn of Africa (SE Ethiopia, Socotra, Somalia), while 72 species are restricted to southern Africa (including Botswana, Lesotho, Namibia, South Africa and Swaziland). Sixty of those are endemic to South Africa alone, where they are particularly associated with the semi-arid west and south of the country in the Greater Cape Floristic Region and the Nama Karoo Region. We sampled 88 species and analyzed data from the nuclear ribosomal ITS and plastid *ndhF* regions. Analyses of the separate and combined datasets produced phylogenies that confirm the monophyly of *E.* subg. *Athymalus* and the placement of *E. antso* from Madagascar as sister to the rest of the subgenus. Our analyses also show that the subgenus consists of a grade of early-diverging lineages that are relatively poor in species and that the major radiation of succulent species in southern Africa forms a highly supported clade (*E.* sect. *Anthacanthae*). Species-level relationships within this southern African clade, however, remain largely unresolved. Our phylogenetic hypotheses allow us to propose a new classification for *E.* subg. *Athymalus* where seven sections are recognized, two of which are newly described. The large southern African *E.* sect. *Anthacanthae* is further divided into five subsections, and four series are recognized in *E.* subsect. *Florispiniae*.

Keywords biogeography; cpDNA; *Euphorbia* subg. *Athymalus*; Greater Cape Floristic Region; medusoids; nrITS; phylogeny; southern Africa; succulents

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

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■ INTRODUCTION

Recent molecular phylogenetic studies of *Euphorbia* L. (Steinmann & Porter, 2002; Bruyns & al., 2006, 2011; Zimmermann & al., 2010; Horn & al., 2012; Yang & al., 2012; Dorsey & al., 2013; Riina & al., 2013) have allowed us to propose a novel taxonomic framework for the genus that has redefined many past subgeneric and sectional classifications. Analyses of molecular data show that there are four well-defined clades within the genus, which are now treated as subgenera (Bruyns & al., 2006). For each of these subgenera, more extensive molecular phylogenetic studies have been undertaken, with the aim of recovering clades that could be recognized at the level of section (*E.* subg. *Chamaesyce* Raf., Yang & al., 2012; *E.* subg. *Euphorbia*, Dorsey & al., 2013; *E.* subg. *Esula* Pers., Riina & al., 2013; *E.* subg. *Athymalus* Neck. ex Rchb., this study). Together, these studies have analyzed molecular

data from nearly half of the 2000 species in *Euphorbia*. The sectional placement of the majority of the remaining species has been inferred from obvious morphological features or from similar geographical ranges. In some cases, however, placement has been difficult since distantly related *Euphorbia* species show extraordinary levels of convergence in many vegetative and reproductive characters.

Euphorbia subg. *Athymalus* is the last of the four subgenera to be examined for the revised delimitation of sections. It is the only subgenus that is absent from the New World, being restricted to arid regions in the Arabian Peninsula, Canary Islands, Madagascar and Africa, with a preponderance of species in southern Africa. Although it is the smallest of the four subgenera of *Euphorbia*, with fewer than 150 species, it displays a considerable diversity of growth forms (Fig. 1). This diversity, in large part, involves a trend toward increasing succulence manifested by a shift of the photosynthetic functions

from the leaves to the stems and branches through the development of morphologically distinctive stems, branches and short-shoots, as well as relatively prominent phyllopodia on which the leaves are borne (from here on referred to as tubercles). Besides these modifications and the resulting reduction in the size and persistence of leaves, there is also a small measure of sexual dimorphism in some of the taxa. *Euphorbia* subg. *Athymalus* is one of two subgenera in the genus, along with *E. subg. Euphorbia*, that is well known for the many succulent species that are cultivated worldwide by specialists and the general public.

The first study to recover *Euphorbia* subg. *Athymalus* in close to its current circumscription was Steinmann & Porter (2002), who informally named it “Clade A”, one of four major clades they identified within *Euphorbia*. They included a total of 28 species but had very different sets of taxa for their two separate datasets (ITS, *ndhF*), which led to an unclear picture of relationships within the group. Nevertheless, from their analyses it emerged that the Madagascan species *E. antso* was sister to all the other species, with *E. acalyphoides*, *E. crotonoides* and *E. longituberculosa* variably grouped near the base of the clade. They also showed that “Clade A” was a remarkable and unexpected mixture of species. Bruyns & al. (2006) included 32 species from “Clade A” and listed the species from southern Africa belonging to it. They also formalized the nomenclature of the clade and recognized it as *E. subg. Rhizanthium* (Boiss.) Wheeler. A more restricted sampling (15 species) was employed by Zimmermann & al. (2010), partly arising from an earlier paper on *E. subsect. Meleuphorbia* (Ritz & al., 2003), in which only southern African species were included. Although lacking representation of the subgenus from outside South Africa, this sampling demonstrated for the first time the striking lack of molecular differentiation among the highly succulent, southern African species of the subgenus. A wider sampling of 45 species (including several previously unsampled and little-known ones from northeastern Africa and the Arabian Peninsula and 33 species from South Africa) was included in Bruyns & al. (2011), and from there our current understanding of the structure within *E. subg. Athymalus* (an earlier name for *E. subg. Rhizanthium*) began to emerge.

As part of the *Euphorbia* Planetary Biodiversity Inventory project supported by the U.S. National Science Foundation (Esser & al., 2009; Riina & Berry, 2013a), we assembled a broad taxonomic and geographic sampling of the species in *E. subg. Athymalus*. The aims of this paper are to: (1) recover a robust molecular phylogeny that will allow us to examine the relationships between the species and the groups of species in *E. subg. Athymalus*; (2) develop a classification at the sectional level based upon this phylogeny; (3) infer the sectional membership of the many unsampled species using morphological features and geographical data; and (4) increase our understanding of the biogeographical and morphological evolution within the subgenus.

■ MATERIALS AND METHODS

Taxon and molecular sampling. — We sampled 88 species and a total of 209 accessions within *Euphorbia* subg. *Athymalus*,

covering a large proportion of the taxonomic and geographical breadth of the subgenus. For outgroups, we included 15 species from the remaining three subgenera of *Euphorbia* (five from each subgenus), as well as *Neoguillauminia cleopatra* (Baill.) Croizat and *Calycopeplus casuarinoides* L.S. Sm. Voucher information and GenBank accession numbers for all sequences used are listed in the Electr. Suppl.: Appendix S1. Destructive sampling was not possible for some greenhouse specimens, and those accessions were documented with digital photo vouchers that were deposited at MA and MICH.

DNA extraction, amplification and sequencing. — Genomic DNA was obtained from leaf or stem tissue dried in silica-gel, as well as from leaf fragments from herbarium specimens. For total DNA isolation and amplification of the nrITS region and chloroplast *ndhF* gene, we followed the protocols described in Yang & al. (2012) and Riina & al. (2013). The PCR products were purified using ExoSap-IT (USB Corporation, Cleveland, Ohio, U.S.A.) or the QIAquick PCR Purification Kit (Qiagen, Valencia, California, U.S.A.). The purified PCR products were sequenced using BigDye chemistry (Applied Biosystems Inc., Foster City, California, U.S.A.) on an AB 3730xl capillary sequencer at the University of Michigan DNA Sequencing Core.

Data assembly and phylogenetic analyses. — Chromatogram files were assembled and edited with Sequencher v.4.10.1 (Gene Codes, Ann Arbor, Michigan, U.S.A.). Initial sequence alignments were performed with MAFFT v.5 (Katoh & al., 2005) using the default parameters. Final alignments were refined using the Opalescent package in Mesquite v.2.75 (Wheeler & Kececioglu, 2007; Maddison & Maddison, 2011) and adjusted manually, using a similarity criterion as recommended by Simmons (2004). The number of parsimony-informative sites was estimated in PAUP* v.4.0b.10 (Swofford, 2003).

RAxML v.7.2.6 (Stamatakis, 2006) was used to conduct maximum likelihood (ML) phylogenetic analyses of the ITS, *ndhF* and combined ITS+*ndhF* datasets, with gaps treated as missing data and not coded. As recommended in the RAxML manual, the nucleotide substitution model was set to GTR+ γ . We performed 500 ML bootstrap (BS) replicates, followed by a thorough ML search for the best tree. The resulting ITS and *ndhF* trees were inspected for congruence and to identify problematic sequences. There were several areas of minor incongruence between the ITS and *ndhF* phylogenies, in particular with respect to the arrangement of several of the basal lineages and to placement of some species within *E. sect. Anthacanthae*. The incongruences were poorly supported so the sequences were retained in the combined dataset. For the combined ML analyses, we partitioned the dataset into the ITS and *ndhF* regions.

MrBayes v.3.1.2 (Huelsenbeck & Ronquist, 2001; Ronquist & Huelsenbeck, 2003) was used to conduct a Bayesian (BI) analysis of the combined ITS+*ndhF* dataset, partitioning the dataset between the ITS and *ndhF* regions. The ITS region was not further partitioned. The nucleotide substitution model GTR+I+ γ was applied to both partitions, as selected by AIC in jModelTest v.0.1.1 (Posada, 2008). Two independent runs of four chains each (three heated, one cold) were run for 10 million generations, starting from random trees, using the default



Fig. 1. Examples of morphological diversity in *Euphorbia* subg. *Athymalus*. **A**, tree habit of *E. antso* (*E.* sect. *Antso*); **B**, dimorphic unisexual cyathia of *E. antso*, with a sessile central pistillate cyathium surrounded by four pedunculate staminate cyathia; **C**, fruiting individual of *E. hadramautica* (*E.* sect. *Pseudacalypha*); **D**, flowering branch of *E. crotonoides* (*E.* sect. *Crotonoides*); **E**, leafy branch and fruit of *E. scheffleri* (*E.* sect. *Somalica*); **F**, pencil-stemmed habit of *E. larica* (*E.* sect. *Balsamis*); **G**, cactoid habit of *E. polygona* (*E.* sect. *Anthacanthae* subsect. *Florispinae* ser. *Meleuphorbia*); **H**, medusoid habit of *E. caput-medusae* (*E.* sect. *Anthacanthae* subsect. *Medusea*); **I**, cyathium of *E. smithii*, with entire outer margins of glands (*E.* sect. *Lyciopsis*); **J**, cyathium of *E. caput-medusae*, with outer margins of glands extended into finger-like appendages (*E.* sect. *Anthacanthae* subsect. *Medusea*); **K**, cyathium of *E. grantii*, with outer margins of glands extended into many slender, ►

temperature of 0.2 and sampling trees every 100 generations. The Log likelihoods from the independent runs were inspected with Tracer v.1.5 (Rambaut & Drummond, 2007) to verify that stationarity had been reached. The first 25,000 trees (25%) were discarded as burn-in, using the remaining 75,001 trees to compute the majority rule consensus tree.

Sectional and subsectional delimitation. — The primary taxonomic groupings we recognize within *Euphorbia* subg. *Athymalus* are sections. We used the criterion of monophyly to define sections. Despite weak molecular differentiation within the large *E. sect. Anthacanthae*, there are clear morphologically distinctive groups of species, and we therefore further divided that section into five subsections. Likewise, within the horticulturally important *E. subsect. Florispinae*, we circumscribed four morphologically cohesive series.

RESULTS

Our sampling of *Euphorbia* subg. *Athymalus* covered approximately 60% of the species in the subgenus (Table 1; Electr. Suppl.: Appendix S1). From the ingroup, we sampled 71 species (164 accessions) for the nuclear ribosomal ITS region and 84 species (176 accessions) for the chloroplast *ndhF* region, for a total of 88 species (209 accessions) of *E. subg. Athymalus* sampled. We generated 56 new ITS and 108 new *ndhF* sequences. For many species this study represents their first inclusion in a phylogenetic analysis. We sampled 66 of the 87 species (~76%) in *E. sect. Anthacanthae*. More significant gaps in the sampling remain among species from outside of southern Africa, for example from *E. sect. Pseudacalypha* (3 out of 11 species sampled), *E. sect. Lyciopsis* (5 out of 19 species sampled), *E. sect. Crotonoides* (4 out of 8 species sampled), *E. sect. Somalica* (4 out of 13 species sampled) and *E. sect. Balsamis* (5 out of 9 species sampled). As a result of this more comprehensive sampling, many of the clades of *E. subg. Athymalus* identified by Bruyns & al. (2011) and Horn & al. (2012) were significantly expanded here.

Individual and combined datasets. — A summary of the statistics for the molecular markers sequenced is provided in Table 1. The ITS dataset contained a higher proportion of variable sites than *ndhF* (74.7% vs. 30.8%). Results of the separate ITS and *ndhF* ML analyses (with all sampled accessions

Table 1. Summary statistics from ITS, *ndhF* and combined ITS+*ndhF* datasets for *Euphorbia* subg. *Athymalus* and outgroup species analyzed in this study. Likelihood scores for the maximum likelihood trees from RAxML are provided (see Electr. Suppl.: Figs. S1–S3 for the ML trees).

	ITS	<i>ndhF</i>	combined ITS+ <i>ndhF</i>
Total no. of accessions	164	176	128
No. of ingroup species	71	84	88
No. of outgroup species	17	17	17
Unaligned length [bp]	456–648	902–1499	456–2127
Aligned length [(bp)]	725	1523	2222
Variable characters (%)	540 (74.7)	469 (30.8)	970 (43.6)
Missing data (%)	15.4	4.1	20.3
Parsimony-informative sites			
<i>E. subg. Athymalus</i>	345	131	367
<i>E. subg. Athymalus</i> +outgroup	432	291	656
ML score (lnL)	–13303.7	–7415.9	–18755.1

included) are shown in the online supplement (Electr. Suppl.: Figs. S1–S2). The monophyly of *E. subg. Athymalus* is strongly supported by ML analysis of both the ITS and *ndhF* datasets (BS ≥ 98%; Electr. Suppl.: Figs. S1–S2). Most sections circumscribed from the analyses of the combined ITS+*ndhF* dataset (see below) are also strongly to moderately supported as monophyletic in both the ITS (BS = 100% for 5 of the 7 sections; Electr. Suppl.: Fig. S1) and the *ndhF* (BS ≥ 87% for all 7 of the sections; Electr. Suppl.: Fig. S2) gene trees.

BI and ML results for the combined dataset are congruent for most moderately or highly supported nodes (posterior probability [PP] ≥ 0.80 and BS ≥ 50%). Overall, the reconstruction of the phylogeny obtained is well-resolved and well-supported among the earlier-diverging branches but is somewhat poorly resolved within the most species-rich clade, *E. sect. Anthacanthae* (Figs. 2–3; Electr. Suppl.: Fig. S3). *Euphorbia* subg. *Athymalus* is strongly supported as monophyletic in both the ML and BI analyses of the combined dataset (PP = 1.00; BS = 100%).

- finger-like appendages with bifurcating tips (*E. sect. Anthacanthae* subsect. *Platycephalae*); **L**, cyathium of *E. patula*, with characteristic finger-like appendages on the outer margins of the glands and the inner margins folded back over base of gland (*E. sect. Anthacanthae* subsect. *Dactylanthos*); **M**, branch of *E. stellispina*, showing tubercles partly fused into angles with short-shoots that develop into pseudostellate spines and short-lived leaf-rudiments (*E. sect. Anthacanthae* subsect. *Florispinae* ser. *Meleuphorbia*); **N**, stem of male individual of *E. meloformis*, showing tubercles almost completely fused into angles and branched synflorescences that persist after fruiting (*E. sect. Anthacanthae* subsect. *Florispinae* ser. *Meleuphorbia*); **O**, branch of female plant of *E. mammilaris* (*E. sect. Anthacanthae* subsect. *Florispinae* ser. *Meleuphorbia*) showing a mixture of spiny sterile and fertile short-shoots. Note tubercles joined into angles and ephemeral leaf-rudiments; **P**, *Euphorbia schoenlandii*, with spirally tuberculate stem, cyathia on short peduncles and longer sterile short-shoots that develop into sharp spines (*E. sect. Anthacanthae* subsect. *Medusea*); **Q**, spherical seeds of *E. antso*, the largest seeds within the subgenus (*E. sect. Antso*); **R**, smooth, angled seeds of *E. dregeana* (*E. sect. Anthacanthae* subsect. *Pseudeuphorbium*); **S**, seeds of *E. benthamii* (*E. sect. Crotonoides*), showing the characteristic seed shape of *E. sect. Pseudacalypha* and sect. *Crotonoides*, with seeds wider at the base and with one or more furrows encircling the entire seed; **T**, seeds of *E. hadramautica* (*E. sect. Pseudacalypha*). — Photographs are by the authors except for N, which was provided by Volker Buddensiek of the International Euphorbia Society.

Phylogenetic structure. — The phylogenetic structure of *Euphorbia* subg. *Athymalus*, as recovered from analyses of the combined ITS+*ndhF* datasets (Figs. 2–4; Electr. Suppl.: Fig. S3), agrees with the general structure of *E. subg. Athymalus* recovered in Bruyns & al. (2011) and Horn & al. (2012). Our combined analysis recovered *E. sect. Antso* as the earliest diverging lineage, strongly supported as sister to the remainder of the subgenus (PP = 1.00; BS = 100%). The next branch to diverge is a strongly supported *E. sect. Pseudacalypha* (PP = 1.00; BS = 100%), whose sister relationship to the remainder of the subgenus is again strongly supported (PP = 1.00; BS = 97%). Relationships within *E. sect. Pseudacalypha* are all strongly supported (PP = 1.00; BS ≥ 99%). The remaining sections in the subgenus form two clades. The first is a weakly supported clade (PP = 0.67; BS = 63%) made up of *E. sect. Somalica*, sect. *Crotonoides* and sect. *Lyciopsis*; each of these is strongly supported as monophyletic, with the relationships of their component species well resolved and well supported. The second weakly to moderately supported clade consists of

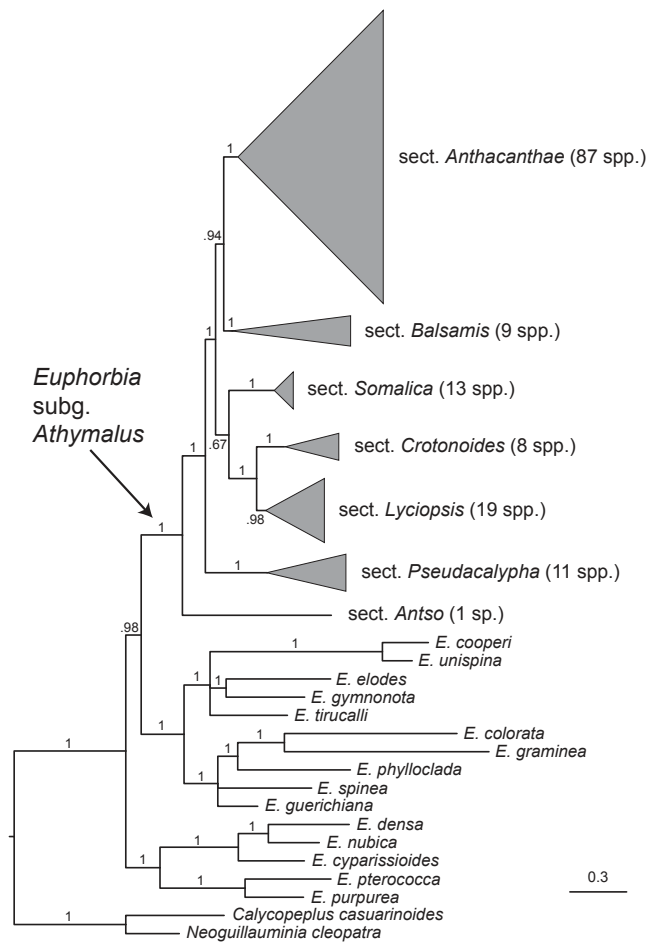


Fig. 2. Schematic representation of the Bayesian phylogram from analysis of the combined ITS+*ndhF* dataset of *Euphorbia* subg. *Athymalus* and outgroups. Sections recognized in our classification are represented by filled triangles whose vertical axes are scaled to reflect the number of species in each section. Bayesian posterior probabilities (≥ 0.50) are indicated above the branches.

a strongly supported *E. sect. Balsamis* (PP = 1.00; BS = 93%) sister to a strongly supported *E. sect. Anthacanthae* (PP = 1.00; BS = 96%). *Euphorbia* sect. *Anthacanthae* contains most of the species in the subgenus that we sampled for this study (66 out of the 88 total sampled). We were able to circumscribe five strongly to moderately supported subsections within this section (Figs. 3, 5). However, species-level relationships within the subsections were generally unresolved or poorly supported when resolved. The ML and Bayesian analyses of the combined ITS+*ndhF* dataset produced slightly different and weakly supported placements of *E. dregeana*. On the basis of shared morphological features, we place it in *E. subsect. Pseudeuphorbium* (as suggested by the ML phylogeny in Fig. S3, Electr. Suppl.) rather than in *E. subsect. Medusea* (as suggested by the Bayesian phylogeny in Fig. 3). The short branches in this entire clade show that there is very little variation in the gene-regions examined among the species (Electr. Suppl.: Figs. S1–S3).

Maximum likelihood analysis of the ITS dataset yielded a phylogenetic hypothesis (Electr. Suppl.: Fig. S1) that was largely congruent with the topology of the *ndhF* tree (Electr. Suppl.: Fig. S2). The few areas of minor incongruence between the ITS and *ndhF* phylogenies largely centered on the arrangement of several of the basal lineages. For example, *E. sect. Somalica*, sect. *Lyciopsis*+sect. *Crotonoides* and sect. *Balsamis* form a poorly supported clade in the ITS phylogeny (Electr. Suppl.: Fig. S1), whereas they form a moderately to strongly supported grade in the *ndhF* phylogeny (Electr. Suppl.: Fig. S2). There were also differences in the placement of some species within *E. sect. Anthacanthae* in the analyses of the two datasets, but resolution in this part of the tree was generally low and relationships poorly supported.

DISCUSSION

Our results are consistent with previous broad studies of *Euphorbia* (Steinmann & Porter, 2002; Bruyns & al., 2006, 2011; Zimmermann & al., 2010; Horn & al., 2012) in recovering a monophyletic *E. subg. Athymalus* that is sister to a clade comprised of *E. subg. Euphorbia* and *E. subg. Chamaesyce*. These studies all found that *E. subg. Athymalus* was restricted to the Old World, with its greatest diversity in southern Africa. Bruyns & al. (2006) recognized this clade at the subgeneric level (as *E. subg. Rhizanthium*) but did not subdivide it further.

Earlier phylogenetic studies of *Euphorbia* showed that *E. subg. Athymalus* (as currently circumscribed) was a novel combination of species and groups of species that had not been present in previous taxonomic treatments (Steinmann & Porter, 2002; Bruyns & al., 2006). The pattern that was revealed at the subgeneric level is now found to be repeated at the sectional level. In previous taxonomic treatments of African species of *Euphorbia*, the species were placed in subgenera and sections (Carter, 1988) or subgenera only (Holmes, 1993), but almost all of these included some members that we now know to belong to different subgenera. For example, *E. subg. Eremophyton* (Boiss.) Wheeler, *E. subg. Lyciopsis* (Boiss.) Wheeler and *E. subg. Trichadenia* (Pax) S. Carter (Carter, 1988) each included species

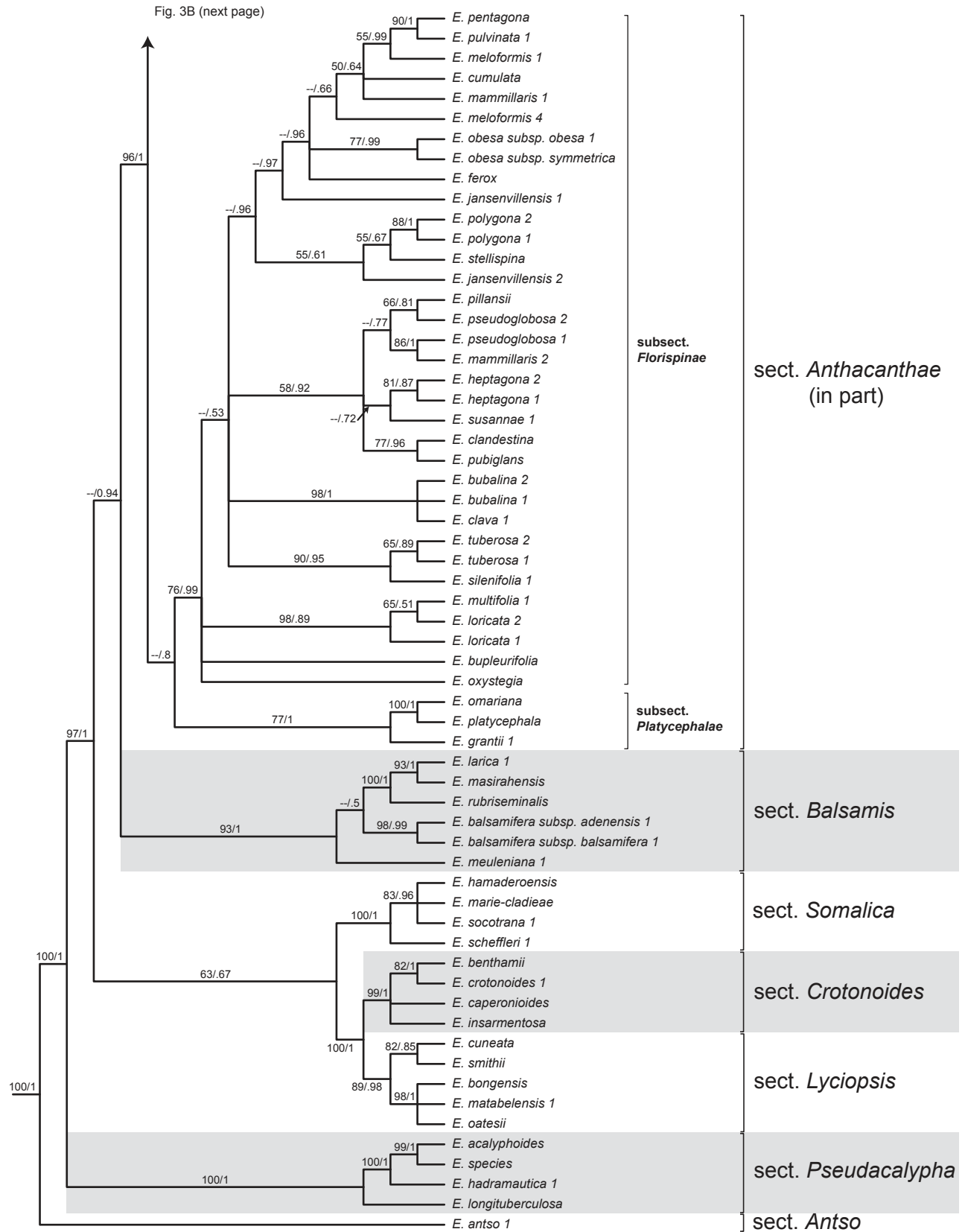


Fig. 3. The 50% majority-rule consensus cladogram from Bayesian analysis of the combined ITS+*ndhF* dataset of *Euphorbia* subg. *Athymalus* (outgroups have been pruned from the figure; see Fig. 2). Maximum likelihood bootstrap values ($\geq 50\%$) and Bayesian posterior probabilities (≥ 0.50) are indicated above the branches, separated by a slash mark. Sections are indicated to the right.

that we now assign to both *E.* subg. *Athymalus* and *E.* subg. *Chamaesyce*. The same is true for *E.* subg. *Esula* (Holmes, 1993) that contained species of *E.* subg. *Athymalus* (*E. balsamifera*) and *E.* subg. *Esula* (*E. schimperiana* Scheele). Thus none of the subgenera or sections used in these recent treatments could be taken over wholly into our new sectional arrangement for *E.* subg. *Athymalus*. Within the southern African species, where over the last 60 years there has been little taxonomic activity, we find that several earlier names of groupings correspond to taxa that we have recovered as clades. These are incorporated into the subsectional classification that we propose below.

Basal lineages. — Our sampling and analyses show that *Euphorbia* subg. *Athymalus* consists of a grade of early-diverging lineages that are widely distributed geographically and relatively poor in species. *Euphorbia antso* (Fig. 1A, B, Q), the sole species in the subgenus from Madagascar, is sister to the rest of the subgenus. Steinmann & Porter (2002) considered that *E. antso* retained several “ancestral” features for the genus, such as the shrub- or tree-like habit, spiral phyllotaxy, pseudo-umbellate synflorescences and five involucre glands (in the pistillate cyathia). A reconstruction of ancestral states conducted by Horn & al. (2012) supported this hypothesis.

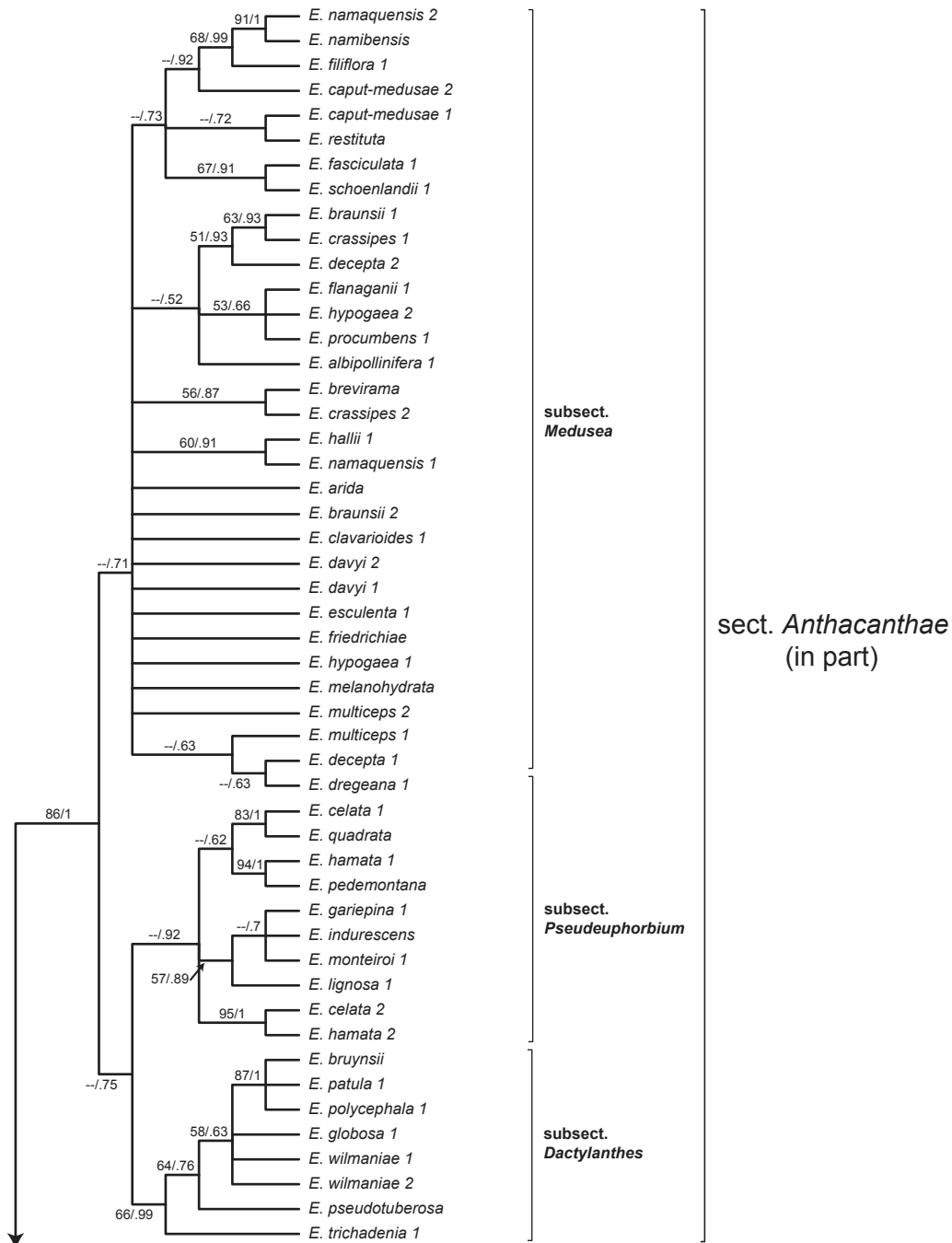


Fig. 3A (previous page)

Biogeographically, it is interesting that the only species from Madagascar is sister to the rest of the subgenus. According to Bruyns & al. (2011), *E. antso* diverged from the other members of *E.* subg. *Athymalus* around 28 Ma. This implies that there must have been a dispersal event in the early evolution of the subgenus between Madagascar and mainland Africa, since

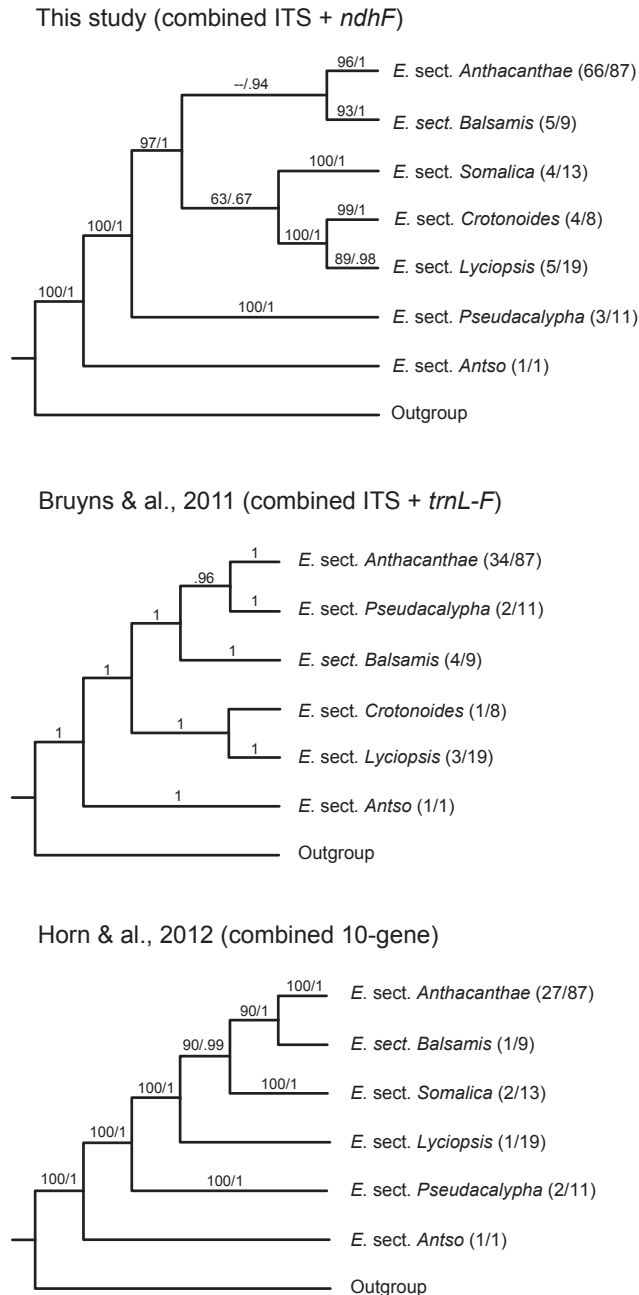


Fig. 4. Comparison of cladogram backbone topologies for *Euphorbia* subg. *Athymalus* from this study, Bruyns & al. (2011) and Horn & al. (2012). Maximum likelihood bootstrap values ($\geq 50\%$) and Bayesian posterior probabilities (≥ 0.50) are indicated above the branches, separated by a slash mark (only Bayesian values are shown for Bruyns & al., 2011). Section names refer to those recognized in this study and the numbers of sampled vs. total species in each section are indicated to the right.

Madagascar has been separated from mainland Africa by the Mozambique Channel for ~120 Ma (Ali & Huber, 2010). Where the subgenus originated is unclear at this point. This pattern contrasts markedly with those in the other three subgenera of *Euphorbia*, which all have many species present on Madagascar that are more deeply embedded within their respective subgenera (Yang & al., 2012; Dorsey & al., 2013; Riina & al., 2013).

The other basal lineages in *Euphorbia* subg. *Athymalus* include many species that occur north of the equator. They represent a wide array of growth forms, including shrubs, trees, and annual to perennial herbs, many of them leafy-deciduous and some slightly succulent. After *E. antso*, the next diverging lineage is *E. sect. Pseudacalypha* (Fig. 1C, T), a group of 11 species from northeastern Africa and the southern Arabian Peninsula that includes both leafy herbs as well as tuberculate-stemmed succulents. This section is followed by a weakly supported clade (PP = 0.67; BS = 63%) that is made up of three well-defined sections. The shrubby to arborescent *E. sect. Somalica* (11 species; Fig. 1E) is restricted to east and northeastern Africa and has three species endemic to the island of Socotra. A novel grouping of species recognized here is *E. sect. Crotonoides*, which was formerly included in *E. sect. Pseudacalypha* (Boissier, 1862; Holmes, 1993). These two sections are similar in their herbaceous habit and ribbed seeds, but *E. sect. Crotonoides* differs in its consistently serrate leaves (Fig. 1D). It is sister to *E. sect. Lyciopsis*, a diverse group of 19 woody species with often shiny, peeling bark that is widely distributed across sub-Saharan Africa to the Arabian Peninsula and south to Angola, Botswana and Namibia. *Euphorbia* sect. *Balsamis* is the last of the basal lineages within the subgenus and is weakly supported as sister to the large, southern African clade (PP = 0.94; BS $\leq 50\%$). It consists of nine species of shrubs and pencil-stemmed shrubs (Fig. 1F) distributed primarily from the Arabian Peninsula to the Horn of Africa region; *E. balsamifera* has the widest distribution of any taxon in the subgenus and extends to Macaronesia and adjacent parts of western Africa.

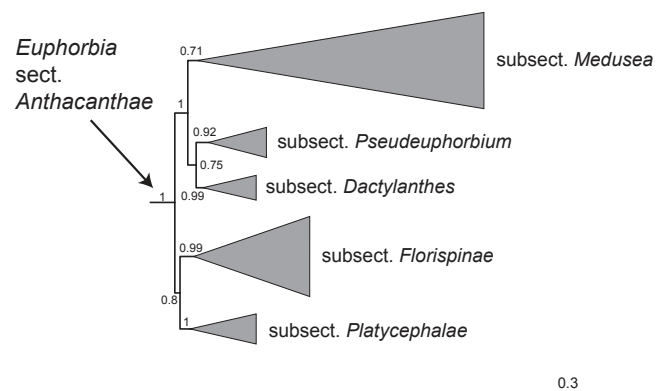


Fig. 5. Schematic representation of the Bayesian phylogram of *Euphorbia* sect. *Anthacanthae* from the analysis of the combined ITS+*ndhF* dataset. Subsections recognized in our classification are represented by filled triangles whose vertical axes are scaled to reflect the number of species in each subsection. Bayesian posterior probabilities (≥ 0.50) are indicated above the branches.

Our arrangement of the basal lineages (Fig. 4) in *E.* subg. *Athymalus* (with 22 species sampled) is similar to but not the same as the topologies found by Bruyns & al. (2011) and Horn & al. (2012). Bruyns & al. (2011) sequenced the nrITS region and *trnL-F* chloroplast spacer for 11 species from the basal lineages, representing all sections except *E.* sect. *Somalica*. Their study recovered *E. antso* as sister to the remainder of the subgenus, but their next diverging lineage was a clade consisting of what we now recognize as *E.* sect. *Crotonoides*+*E.* sect. *Lyciopsis*. In their phylogeny, *E.* sect. *Balsamis* was strongly supported as sister to a clade of *E.* sect. *Pseudacalypha*+the mainly southern African *E.* sect. *Anthacanthae*. Horn & al. (2012) included only seven species from the basal lineages of the subgenus, representing all sections recognized here except *E.* sect. *Crotonoides*. Similar to our results, they recovered *E. antso* and our circumscription of *E.* sect. *Pseudacalypha* as the earliest diverging lineages, but they then recovered a moderately to strongly supported grade with the remaining sections as successive sisters. We assume that the substantial differences in sampling and the different gene regions used led to differing topologies, and it remains unclear which topology best reflects the evolutionary history of the basal lineages.

***Euphorbia* sect. *Anthacanthae*, the mainly southern African clade.** — Eighty-seven of the species (~60%) of *Euphorbia* subg. *Athymalus* fall into a single strongly supported clade (*E.* sect. *Anthacanthae*; Fig. 1G, H, J–P). Our analyses allowed us to recognize five strongly to moderately supported subsections within this clade, and these are grouped into two subclades (Figs. 3, 5). Four of the five subsections are restricted to southern Africa, but *E.* subsect. *Platycephalae* is more widely distributed, from the central portion of southern Africa (*E. platycephala* in Botswana) to East Africa and Ethiopia. It is a strongly supported (PP = 1.00; BS = 77%) and well-resolved group of semi-succulent to geophytic species and is sister to *E.* subsect. *Florispinae*, forming one of the two subclades in the section.

Relationships among the species within the other subsections are largely unresolved. Variation in the two gene-regions examined is low across this entire group and most species lie on very short branches (Electr. Suppl.: Figs. S1–S3), despite the fact that many of them are morphologically very well-defined. This phenomenon is known in several other semi-succulent to succulent groups that have diversified strongly in southern Africa (e.g., *Zygophyllum* [Zygophyllaceae]: Bellstedt & al., 2008; Ruschieae [Aizoaceae]: Klak & al., 2004; the “southern clade” of the stapeliads [Apocynaceae–Ceropegieae]: Meve & Liede, 2002; *Aloe* [Asphodelaceae–Aloioideae]: Daru & al., 2013). This lack of resolution suggests recent radiations due to large-scale climatic changes (see below) where the morphological diversity is not matched by diversity in the gene-regions studied.

The most succulent members of *E.* subg. *Athymalus* belong to *E.* sect. *Anthacanthae*. Their greatest diversity is associated with the semi-arid to arid regions of the central, southern and western parts of South Africa, in the Nama Karoo Region (Jürgens, 1991) and especially within and around the margins of the Greater Cape Floristic Region (GCFR). The GCFR is

made up of the Cape Floristic Region and the considerably more arid Succulent Karoo Region (Jürgens, 1991, 1997; Born & al., 2007). The GCFR is characterized by winter rainfall and dry summers and is well known as an area of high diversity in succulents, especially in the families Aizoaceae, Apocynaceae, Asteraceae, Crassulaceae and Euphorbiaceae (Snijmann, in press). The Succulent Karoo Region is one of the few global hotspots of succulent diversity in the world, with the only other such region in Africa lying in the Horn of Africa (Bally, 1959; Davis & al., 1994). Much of this diversity in the Succulent Karoo Region has arisen within the last 5–10 million years in response to increasingly pronounced and reduced winter rainfall and summer droughts on the western side of South Africa (Coetzee, 1980; Hendey, 1981; Partridge & Maud, 2000). Pivotal to these climatic changes were an increase around 10 million years ago in the strength of the cold Benguela Current running up the west coast of South Africa and Namibia (Siesser, 1980) and a substantial increase in altitude by 700–900 m of the eastern escarpment of South Africa 3–5 million years ago (Partridge & Maud, 2000). It was found that most of this diversity in *E.* subg. *Athymalus* also arose during this period (Bruyns & al., 2011). In the other three subgenera, the only significant radiation of succulents in the same area took place in *E.* subg. *Chamaesyce* sect. *Articulofruticosae*, and this also happened during the last 10 million years (Bruyns & al., 2011). Both of these ages correspond to a worldwide trend of recent radiations in succulent groups that is most pronounced in both Africa and the Americas (Arakaki & al., 2011).

Morphological diversity and evolution in *Euphorbia* sect. *Anthacanthae*. — In this clade the species range from geophytes (*E. tuberosa*) to small, rigid shrubs (*E. lignosa*) to very large, succulent shrubs (*E. polygona*; Fig. 1G), enormous cushion-like shrubs (*E. pulvinata*) or dwarf, globose succulents (*E. obesa*). Unlike in *E.* subg. *Euphorbia*, the succulent tree habit is not represented in *E.* sect. *Anthacanthae*. Apart from the geophytes, where the perennial stems and branches are wholly subterranean, all have green bark on the stem and branches. The generally slender leaves are prominent in a few species (such as *E. bubalina* and *E. monteiroi*) but are mostly ephemeral and highly reduced, often to minute rudiments. In these cases photosynthesis is carried out by the stem and branches.

Succulence. — A so-called “pencil-stemmed” growth form (shrubs or dwarf succulents where the stem and branches are slender, cylindrical and green, with small and ephemeral leaves) appears to be a typical stage in *Euphorbia* in the evolution of more highly succulent forms. It has been established that all four subgenera contain pencil-stemmed succulents (Steinmann & Porter, 2001; Bruyns & al., 2006; Horn & al., 2012), and in *E.* subg. *Chamaesyce* sect. *Articulofruticosae* Bruyns and *E.* subg. *Esula* the succulent members are all pencil-stemmed. While *E.* sect. *Anthacanthae* also contains pencil-stemmed species (for example, *E. dregeana*, *E. gariepina* and *E. lignosa*), the morphological diversity in this clade arose primarily from further modifications, mostly towards increased succulence and presumably in response to increasing aridity. Three separate directions appear to have been followed:

(i) the “medusoid” form (typified most clearly by the widespread and quite variable *E. caput-medusae*; Fig. 1H). Here the stem is highly swollen to provide the main body of the plant and the principal storage organ, with less succulent and relatively ephemeral branches arising in the axils of tubercles from near its apex and radiating from it.

(ii) the geophytic form. In *E.* subg. *Athymalus*, this occurs in three distinct clades, in *E. trichadenia* and *E. pseudotuberosa*, in *E. platycephala* (all widely distributed in southern tropical Africa) and in *E. ecklonii*, *E. silenifolia* and *E. tuberosa* from the GCFR.

(iii) the spiny, cactoid form in which the angled stem and branches are armed with stout spines (Fig. 1G, M–P). This last growth-form is taken to an extreme in *E. meloformis* (Fig. 1N) and *E. obesa*, where the whole plant is reduced to a single, spherical (or short and thickly cylindrical) stem that grows close to the ground and is supported by a fairly insubstantial root system. In these highly succulent species, *E. meloformis* is “armed” with particularly soft and pliable short-shoots that dry out and somewhat camouflage the plant (rather than protecting it with spines), while *E. obesa* lacks persistent short-shoots entirely and is camouflaged by subtle markings on the surface that closely match the shadows under dwarf shrubs and the stones among which it grows.

It should be noted that all three of these modifications are present in *Euphorbia* subg. *Euphorbia*, though they are absent in the other two subgenera. *Euphorbia* sect. *Euphorbia* contains a few “medusoid” species such as *E. schizacantha* Pax and relatives, several geophytic species such as *E. meenae* S. Carter and relatives, and a large number of cactoid succulents. The only other known instances in the genus of the highly reduced, globose growth form of *E. meloformis* and *E. obesa* also occur in *E.* sect. *Euphorbia*, in *E. gymnocalycioides* M.G. Gilbert & S. Carter, *E. piscidermis* M.G. Gilbert and *E. turbiniformis* Chiov. Apart from the geophytic forms, this diversity in *E.* subg. *Euphorbia* is concentrated in Ethiopia, Kenya and Somalia.

Spines. – Spines are found widely in *Euphorbia*. In *E.* subg. *Chamaesyce* spines are present mainly as hardened tips to the branches (*E. spinea* N.E. Br.), and in *E.* subg. *Euphorbia* spines mainly take the form of special structures associated with the bases of the leaves known as “spine-shields” (Uhlarz, 1974; Bruyns & al., 2006). In the basal grade of *E.* subg. *Athymalus*, spines may develop at the tips of branches in *E.* sect. *Lyciopsis* (as in *E. cuneata*), but otherwise spines are generally absent from these groups. Members of *E.* sect. *Anthacanthae*, on the other hand, are very often spiny and appear to exhibit considerable diversity in the nature of the spines (Fig. 1G, M–P). Spine-tipped branches also occur in this section (as in *E. lignosa*), but what appear to be different kinds of spines are the result of a higher order of modified branches that again are spine-tipped, as described below.

In many of the highly succulent species a third level of branching occurs (above that of the stem and the morphologically similar or thinner branches), namely short-shoots arising in the axils of the tubercles on the stem and branches. These short-shoots are often tuberculate like the stem and branches

but are generally much more slender (in many species they are scarcely succulent or not succulent at all) and are usually terminated by a cyathium (i.e., a peduncle). After flowering these shoots may persist as hard stalks and form a “protective armor” of somewhat spine-like structures (though they are never sharp-tipped). Among the “medusoid” species these are typical in species such as *E. arida*, *E. crassipes* and *E. fasciculata*. Similarly, in many members of *E.* subsect. *Florispiniae*, the fertile short-shoots persist as hard stalks but are not sharp-tipped. In a further development, exclusive to *E.* subsect. *Florispiniae* and *E. schoenlandii* of *E.* subsect. *Medusea*, sterile short-shoots are also produced in the axils of many of the tubercles (Fig. 1O, P). These are slender and non-succulent (usually only one per axil except in *E. polygona*) and are initially soft, bearing several minute leaf rudiments that rapidly drop off, after which the shoot hardens and the tip becomes sharp (often extremely so). Each of these short-shoots then terminates in a spine and so we find here a form of the spine-tipped branch that is present more widely in the subgenus. The main difference between the fertile short-shoots and the sterile ones is the presence of cyathia and the increase in size of the “bracts” near the apex in the former. A further unique modification of this arrangement occurs in *E. stellispina*, in which each short-shoot is made up of a shaft with a rosette of spinelets at the apex, each arising in the axil of a tiny bract (Fig. 1M). The shaft itself remains blunt-tipped.

■ CONCLUSIONS

Euphorbia subg. *Athymalus* is the smallest of the four main lineages of *Euphorbia* and is the only one that is absent from the New World and from most of Asia. Its earliest diverging member occurs in Madagascar and is an unusual tree-like species with large fruits and seeds, and dimorphic, unisexual cyathia. Other members of the basal grade within the subgenus include shrubs or small trees, many with smooth or exfoliating bark. There are also annual to perennial leafy herbs and a few pencil-stemmed succulent shrubs that are mostly confined to the Arabian Peninsula. The subgenus contains a remarkable diversity of succulent forms, particularly within *E.* sect. *Anthacanthae*. Spines are found in several distinct groups in the subgenus but all appear to be hardened branch-tips and no other structures give rise to spines within the subgenus. The cyathia show considerable diversity in their size, but except in some of the earlier diverging lineages, they are all radially symmetric. They exhibit a wide range in the shape of the glands and a series of crenulate, pectinate or finger-like outgrowths on their outer margins is a common feature of this subgenus. Dioecy is present in several clades and is often accompanied by some sexual dimorphism. This subgenus has many species (especially in the most species-rich clade in the subgenus, *E.* sect. *Anthacanthae*) that are endemic to the western part of southern Africa, and it appears to be one of many groups (including several others that are rich in succulents) that have diversified in response to recent changes in climatic regimes and aridification in the southwestern edge of the continent.

■ TAXONOMIC TREATMENT

Here we present a new taxonomic treatment of *Euphorbia* subg. *Athymalus* based principally on the results of our phylogenetic analyses. For each section we provide types, synonymy, a brief description, a list of included species, geographical distribution and a brief discussion. Those species sampled here or in previously published studies are listed in **bold italics**, whereas others whose membership in a particular section is inferred from morphological or geographical criteria are listed in *italics* only. Names below the rank of species have been omitted from the lists, but a complete database of names and synonyms is available online (Riina & Berry, 2013b).

There are also some species not sampled in any of the molecular analyses to date, which probably belong in *Euphorbia* subg. *Athymalus* but are of uncertain position within our sections. These include *E. asclepiadea* Milne-Redh. (Angola), *E. linearibracteata* L.C. Leach (Angola) and *E. erythrocephala* P.R.O. Bally & Milne-Redh. (Zimbabwe), three similar species with narrowly lanceolate leaves and tuberous roots. Other species that also appear to belong to *E.* subg. *Athymalus* are *E. arrecta* N.E. Br. (Tanzania, Zambia), *E. carinifolia* N.E. Br. (Angola), *E. dilobadena* S. Carter (Tanzania), *E. erantes* R.A. Dyer & Milne-Redh. (Zambia), *E. kouandenensis* Beille ex A. Chev. (western tropical Africa), *E. ledermanniana* Pax & K. Hoffm. (Chad), *E. parifolia* N.E. Br. (Angola), *E. radiifera* L.C. Leach (Angola) and *E. taboraensis* A. Hüssl. (Tanzania).

***Euphorbia* subg. *Athymalus* Neck. ex Rchb., Consp. Regn. Veg. 1: 194. 1829 ≡ *Athymalus* (Neck. ex Rchb.) Raf., Fl. Tellur. 4: 112. 1838 – Type (designated here): *E. tridentata* Lam.**

- = *Anthacantha* Lem. (see under *E.* sect. *Anthacanthae*)
- = *Dactylanthes* Haw. (see under *E.* subsect. *Dactylanthes*)
- = *Euphorbia* subg. *Rhizanthium* (Boiss.) Wheeler (see under *E.* ser. *Rhizanthium*)
- = *Euphorbia* subg. *Trichadenia* (Pax) S. Carter (see under *E.* subsect. *Dactylanthes*)
- = *Lyciopsis* (Boiss.) Schweinf. ≡ *E.* subg. *Lyciopsis* (Boiss.) Wheeler (see under *E.* sect. *Lyciopsis*)
- = *Medusea* Haw. (see under *E.* subsect. *Medusea*)
- = *Treisia* Haw. (see under *E.* ser. *Treisia*)

Annual or perennial herbs, geophytes, shrubs, small trees, pencil- or tuberculate-stemmed succulents, sometimes spiny with spines developing from tips of branches or from sterile short-shoots on branches. Leaves alternate or spiral, ovate to lanceolate and sometimes reduced to minute rudiments, mostly deciduous and often rapidly caducous; stipules sometimes present and glandular (filiform). Synflorescences axillary (often arising in axils of tubercles towards apices of stem and branches) or terminal on a short to long bracteate peduncle, peduncles simple to dichotomously branching, often with alternate or opposite bracts arising on small tubercles, bracts often differently shaped from leaves and often much larger just beneath cyathium, further peduncles with terminal cyathia sometimes developing from axils of uppermost bracts. Cyathia sometimes dimorphic, bisexual or unisexual; glands (1–)4–5(–9), ranging from tubular

with finely toothed margins to elliptic and flat with entire, crenulate, pectinate or deeply toothed outer margins, marginal teeth sometimes modified into differently colored finger-like and branched outgrowths. Capsule deeply to obtusely 3-lobed to spherical, smooth to verrucose, glabrous to pilose, 2.5–40 mm diam., walls mostly thin but occasionally thick and lignescent, sessile to exserted. Seeds 1–3 per capsule, pyramidal-conical with acute apex to ellipsoidal or ± spherical, grey to nearly black, smooth to tuberculate or verrucose, ecarunculate.

Morphologically, this is a very diverse group within *Euphorbia*. Several parallel morphological developments between this subgenus and others, as well as the broad variation in many features across the subgenus, make it difficult to place some species in this group and also hinder the construction of a key to the sections. On the other hand, many species are readily placed here. This applies especially to those from southern Africa that have succulent, often angled stems, with the leaves on tubercles and often with spines derived from sterile short-shoots. In all species in the subgenus the seeds lack a caruncle (Morawetz & al., 2009; Wagner & al., 2010, 2011), but this alone does not define the subgenus since some members of the other three subgenera have seeds that also may lack caruncles.

While Steinmann & Porter (2002) informally named this subgenus “Clade A”, Bruyns & al. (2006) formally recognized this group as *Euphorbia* subg. *Rhizanthium* (Boiss.) Wheeler (1943), the basionym (*E.* sect. *Rhizanthium*) being published by Boissier in 1862. However, *E.* subg. *Rhizanthium* is not the earliest name for this taxon, since Reichenbach (1829) previously had validly published *E.* subg. *Athymalus*, based on the description of *Athymalus* by Necker (1790) (Necker’s publication has since been suppressed). Although Wheeler (1943: 460) provided strong arguments to associate the name *Athymalus* with *E. tridentata* Lam. (then known as *E. anacantha* Aiton), and this is supported by the illustration that accompanied Necker’s description (t. 29, fig. 1a, b, which was copied from Danty d’Isnard (1720: pl. 11, p. 398); see our Fig. 6), *Athymalus* was never formally typified. We have therefore chosen *E. tridentata* as the type for this name.

Diversity and distribution. – With 80 of the 148 species occurring in southern Africa, this is where the subgenus is most diverse and where all of the highly succulent members occur (belonging to *E.* sect. *Anthacanthae*). A secondary center of diversity is located in the Horn of Africa (in Somalia, the Oga-den region of Ethiopia and the Socotran Archipelago), where 24 species are endemic. These mainly belong to *E.* sect. *Lyciopsis* and sect. *Somalica*. Although this region is also known for its high diversity in succulents (Bally, 1959; Davis & al., 1994), only partly succulent species of *E.* subg. *Athymalus* occur there. A few species are present in the southern Arabian Peninsula, and *E. larica* extends into western Iran. *Euphorbia balsamifera* is particularly widespread, with *E. balsamifera* subsp. *balsamifera* occurring in Macaronesia (the Canary Islands) and West Africa and with *E. balsamifera* subsp. *adenensis* (Deflers) P.R.O. Bally disjunctly distributed in Sudan (Red Sea Hills), Somalia, the southern Arabian Peninsula and Abd-al-Kuri in the Socotran Archipelago. Finally, *E. antso* is the only species occurring in and restricted to Madagascar.

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

- 1 Annual or short-lived perennial herbs with persistent leaves, not succulent with photosynthetic and tuberculate stems and branches 2
- 1 Perennial herbs, leafy shrubs, trees or geophytes with persistent leaves, or succulent with photosynthetic and tuberculate stems and branches with leaves often reduced to minute caducous rudiments 3
- 2 Leaves with serrate margins 4. *E.* sect. *Crotonoides*
- 2 Leaves with entire margins ... 2. *E.* sect. *Pseudacalypha*
- 3 Succulent or semi-succulent herbs or shrubs, often with much reduced and rapidly caducous leaves, often with green photosynthetic and tuberculate stems and branches 4
- 3 Woody or semi-succulent shrubs or trees or geophytes, leafy (mostly deciduous), with grey, yellow or brown, sometimes peeling bark (usually neither green nor photosynthetic), stems and branches not tuberculate 6
- 4 Plants small, 3–30 cm tall; cyathia with 1–4 ± tubular cyathial glands, usually pubescent on the outside; seeds conical-pyramidal, usually with one or more encircling ridges 2. *E.* sect. *Pseudacalypha*

- 4 Plants large, to 3 m tall; cyathia with 4 or 5 ± flat, generally glabrous cyathial glands; seeds ellipsoid or ovoid and without encircling ridges 5
- 5 Pencil-stemmed succulent shrubs from southern Arabian Peninsula to Iran 6. *E.* sect. *Balsamis*
- 5 Pencil-stemmed succulent shrubs from southern Africa, or variously medusoid, cactoid, meloform or shrubby succulent with tuberculate and often angled stems and branches, often bearing spine-like sterile short-shoots 7. *E.* sect. *Anthacanthae*
- 6 Synflorescence with a single central pistillate cyathium surrounded by 3–6 long-pedunculate staminate cyathia, style undivided at tip, capsule 1- or 2-locular and 3–4 cm diam.; from W & SW Madagascar 1. *E.* sect. *Antso*
- 6 Synflorescence of mostly bisexual cyathia, style divided towards tip into three diverging arms, capsule 3-locular and less than 2 cm diam.; from sub-Saharan Africa, Macaronesia and southern Arabian Peninsula 7
- 7 Cyme-bracts similar in shape to the leaves 6. *E.* sect. *Balsamis*
- 7 Cyme-bracts different in shape to the leaves 8
- 8 Woody herbs, shrubs to trees, often with peeling yellow or brown papery bark, cyme-bracts much smaller than leaves and scarious, or larger, spatulate and brightly colored .. 3. *E.* sect. *Lyciopsis*
- 8 Semi-succulent herbs with swollen rootstock to shrubs or trees with thickened and pliable branches, cyme-bracts larger than leaves (sometimes shorter and broader) but neither spatulate nor brightly colored 9
- 9 Trees or shrubs with thick stems covered with smooth grey bark, rays of pseudo-umbels producing one cyathium, cyme-bracts scarious and soon falling 5. *E.* sect. *Somalica*
- 9 Trees or shrubs with semi-succulent stems (rarely with smooth grey bark) or perennial herbs with fleshy rootstock and annual stems and branches, rays of pseudo-umbels usually producing a succession of cyathia, cyme-bracts leafy and persistent 7. *E.* sect. *Anthacanthae*

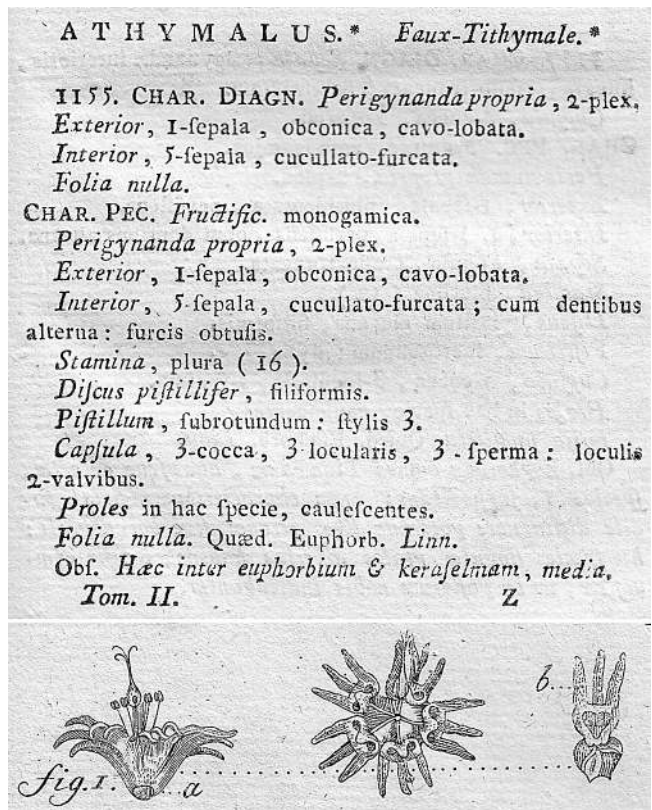


Fig. 6. The description of *Athymalus* by Necker (1790) that was used by Reichenbach (1829) to establish *E.* subg. *Athymalus*. At the base we have inserted Necker's tabula 29, fig. 1a and b (copied from Danty d'Isnard (1720: pl. 11, p. 398), which illustrated his description of *Athymalus*. The drawing corresponds closely to cyathia of *E. tridentata* Lam., which was known and cultivated in Europe at the time.

1. *Euphorbia* sect. *Antso* P.E. Berry, sect. nov. – Type: *Euphorbia antso* Denis.

Monoecious semi-succulent shrubs to trees, 4–15 m tall, sometimes with slightly bottle-shaped trunk, many-branched above, with smooth and grey bark (Fig. 1A). Leaves spiral, lanceolate-elliptic, entire and not undulate, sessile and not arising on tubercles, deciduous, stipules absent. Synflorescences terminal, surrounded by a rosette of 5–8 leaf-like bracts (usually whitish towards the base), with central sessile pistillate cyathium (maturing first) surrounded by 3–6 long-pedunculate staminate cyathia (Fig. 1B). Pistillate cyathium 4–6 mm diam., campanulate, with 5 horseshoe-shaped, deeply concave bilabiate glands, ovary rugose and pilose, style undivided; staminate cyathia ca. 3 mm diam., subtended by 2 conspicuous greenish-white, basally fused, narrowly triangular-lanceolate, apically and obliquely recurved bracts, urceolate, with 2 (rarely 3) horseshoe-shaped, deeply concave, entire glands. Capsule spherical, verrucose and somewhat ridged, glabrous, 2–3.5 cm diam., 1- or 2-locular by abortion, walls 2–3 mm thick and

lignescens, exserted. Seeds 1 (2) per capsule, subspherical, brown, smooth, ± 1 cm diam. (Fig. 1Q).

Species included. – 1: *E. antso* Denis.

Distribution and habitat. – Western and southwestern Madagascar (Toliara Region), in semiarid, deciduous forests and scrub, often on soils derived from limestone, from sea level to 500 m.

Etymology. – The epithet “*antso*” is derived from a local name for the species (Denis, 1921). Denis (1921) first proposed that *E. antso* was an aberrant member of *E. sect. Goniosstema* (in *E. subg. Euphorbia*), whereas Léandri (1957) placed it in *E. sect. Denisophorbia* (also belonging to *E. subg. Euphorbia*). Since it appears that *E. antso* has never been properly lectotypified, a lectotype is selected below.

Euphorbia antso Denis, *Euphorb. Iles Austr. Afr.*: 45. 1921 – **Lectotype (designated here):** MADAGASCAR. Toliara: Forêt de Maronfondelia près Morondava, *H. Perrier de la Bathie 9843* (P No. P00077946!, isolectotype: P No. P00220628!). Denis (1921) listed two syntypes, namely *Perrier de la Bathie 9843* and *Perrier de la Bathie 9784*. The sheet of no. 9843 chosen here as lectotype was annotated by Denis as “type”.

2. ***Euphorbia* sect. *Pseudacalypha*** Boiss. in Candolle, *Prodr.* 15(2): 10, 98. 1862 – Type (designated by Wheeler, 1943: 483): *E. acalyphoides* Hochst.

Monoecious annual herbs or small, sometimes tuberous perennial herbs to 10 cm tall often with succulent, sometimes tuberculate stems. Leaves alternate, ovate to linear-lanceolate, petiolate, entire or undulate, shortly petiolate and sometimes arising at apices of conical tubercles, often deciduous; stipules glandular or as subulate filaments. Synflorescences axillary or in 3-rayed terminal umbels, branching dichotomously (bracts opposite in synflorescences, usually similar to leaves). Cyathia all similar and bisexual, 1.5–4 mm diam.; glands 1–4, entire or finely toothed, spreading or erect and tubular, usually puberulous on outer surface. Capsule obtusely to deeply 3-lobed, smooth, \pm pubescent, 2.5–7 mm diam., 3-locular, walls less than 0.5 mm thick, exserted. Seeds 3 per capsule, conical to pyramidal, apex acute and base truncate, ventral face with 1 or 2 horizontal constrictions (and 2 or 3 corresponding sometimes faint ridges), smooth to verrucose, 1.5–4 mm long.

Species included. – 11: *E. acalyphoides* Hochst., *E. adenchila* S. Carter, *E. etuberculosa* P.R.O. Bally & S. Carter, *E. globulicaulis* S. Carter, *E. hadramautica* Baker, *E. longituberculosa* Hochst. ex Boiss., *E. napoides* Pax, *E. orbiculifolia* S. Carter, *E. perangustifolia* S. Carter, *E. scyphadena* S. Carter, *E. systyla* Edgew.

Distribution and habitat. – Most species in this section are restricted to northeast Africa (Ethiopia, Somalia, Sudan) and the southern Arabian Peninsula (Oman, Yemen); the widespread *E. acalyphoides* also occurs in Angola, Egypt, Kenya and Tanzania; the non-succulent species occur in open, disturbed habitats, while the thicker-stemmed species (such as *E. hadramautica* and *E. longituberculosa*) inhabit rocky terrain, sheltered among stones or under small shrubs; from sea level to 1800 m.

Boissier (1862) established *E. sect. Pseudacalypha* with three species, *E. acalyphoides*, *E. crotonoides* and *E. systyla*. These are all similar-looking leafy herbs, but *E. crotonoides*, which has leaves with serrate margins, is now placed in *E. sect. Crotonoides* (see below). Boissier (1862) initially placed the more succulent, tuberculate-stemmed *E. longituberculosa* in *E. sect. Euphorbium* Boiss. The extreme morphological forms of this section, such as the leafy, annual *E. acalyphoides* and the small, tuberculate, perennial *E. hadramautica* (Fig. 1C), are connected by intermediates among the other species. All share the distinctive horizontal ridges encircling the seeds (see Fig. 1T).

3. ***Euphorbia* sect. *Lyciopsis*** Boiss. in Candolle, *Prodr.* 15(2): 10, 97. 1862 \equiv *Lyciopsis* (Boiss.) Schweinf., *Beitr. Fl. Aethiop.* 1: 37. 1867, non Spach 1835, nom. illeg. \equiv *E. subg. Lyciopsis* (Boiss.) Wheeler in *Amer. Midland Naturalist* 30: 483. 1943 – Type: *E. cuneata* Vahl.

\equiv *Euphorbia* sect. *Bongium* Baill. in Candolle, *Prodr.* 15(2): 1264. 1862 – Type: *E. bongensis* Kotschy & Peyr. ex Boiss.

Monoecious subwoody herbs, shrubs to small trees, 0.1–5 m tall, branch tips sometimes spinose, stems and older branches often with shiny yellow or brown, peeling papery bark, sometimes with a thickened, underground stem. Leaves alternate, lanceolate to obovate, entire and not undulate, shortly petiolate to sessile, glabrous to pubescent, deciduous and mainly on young growth; stipules glandular to shortly filamentous or sharply pointed. Synflorescences terminal or axillary in several-branched umbels or with a solitary cyathium, bracts scarious or leaf-like. Cyathia all similar and bisexual, 4–10 mm diam.; glands (1)4–5(–8), saucer-shaped or funnel-shaped, entire, 2-lipped or fringed to pectinate. Capsule obtusely 3-lobed, smooth, glabrous to pubescent, 4.5–8 mm diam., 3-locular, walls less than 0.5 mm thick, subsessile (pedicellate). Seeds 3 per capsule, spherical to turbinate, grey to brown, smooth, 1.8–3 mm long.

Species included. – 19: *E. betulicortex* M.G. Gilbert, *E. bongensis* Kotschy & Peyr. ex Boiss., *E. cuneata* Vahl, *E. doloensis* M.G. Gilbert, *E. dumensis* S. Carter, *E. gypsophila* S. Carter, *E. handeniensis* S. Carter, *E. intricata* S. Carter, *E. jatrophioides* Pax, *E. joyae* P.R.O. Bally & S. Carter, *E. kaessneri* Pax, *E. kelleri* Pax, *E. lavicola* S. Carter, *E. leucochlamys* Chiov., *E. matabelensis* Pax, *E. oatesii* Rolfe, *E. smithii* S. Carter, *E. tripartita* S. Carter, *E. uniglans* M.G. Gilbert.

Distribution and habitat. – West-central to eastern and northeastern Africa and the Arabian Peninsula (Oman, Saudi Arabia, Yemen, Socotra), most species concentrated in eastern and northeastern Africa from Ethiopia and Somalia to Kenya and Tanzania, with *E. matabelensis* extending into Angola, Botswana and Namibia; dry stony areas among deciduous shrubs and trees, with several endemic species in the Horn of Africa occurring on gypsum, limestones, granites, or sand dunes, from sea level to 2100 m.

4. ***Euphorbia* sect. *Crotonoides*** Bruyns & P.E. Berry, **sect. nov.** – Type: *E. crotonoides* Boiss.

Monoecious erect, branching annual herbs reaching 0.5–1.5 m tall, stem sometimes woody or slightly fleshy above, usually

with hairs at least on young growth. Leaves alternate, lanceolate to ovate, serrate, usually pubescent, petiolate, often deciduous; stipules glandular and red to purple. Synflorescences axillary or in 3-branched terminal umbels, branching dichotomously many times but often with only one ray developing at each fork, bracts opposite and usually similar to leaves. Cyathia all similar and bisexual, 2.5–4 mm diam.; glands 4, entire, spreading. Capsule subglobose to obtusely 3-lobed, smooth, pubescent, 4–7 mm diam., 3-locular, walls less than 0.5 mm thick, exserted. Seeds 3 per capsule, ovoid or conical with rounded or pointed apex, ± angled, with 2–4 transverse ridges and sulcae, pitted to finely verrucose, grey to black, 3–4.5 mm long.

Species included. – 8: *E. benthamii* Hiern, *E. caperonioides* R.A. Dyer & P.G. Meyer, *E. crotonoides* Boiss., *E. insarmentosa* P.G. Mey. *E. lophiosperma* S. Carter, *E. lutosa* S. Carter, *E. sarmentosa* Welw. ex Pax, *E. systyloides* Pax.

Distribution and habitat. – Southern to eastern Africa, in Angola, Botswana, Namibia, South Africa, Zimbabwe, Malawi, Zambia, Tanzania, Kenya, Sudan and Ethiopia; on grassy hillsides, in leaf-litter under trees in dry open woodlands, on sand or loam, sometimes in disturbed patches, 200–3000 m.

Species from this group were previously placed in *E.* sect. *Pseudacalypha* (Boissier, 1862), with which they share the similarly distinctive seed shape (Fig. 1S, T). All species in this section, however, have leaves with at least somewhat serrate margins (Fig. 1D). This is a much more homogenous group of species than *E.* sect. *Pseudacalypha*.

5. *Euphorbia* sect. *Somalica* S. Carter in Kew Bull. 40: 817. 1985 – Type: *E. scheffleri* Pax.

Monoecious softly woody shrubs to small trees, 0.2–8 m tall with grey bark, branches reddish-brown. Leaves alternate, ovate to obovate, entire, shortly petiolate, usually deciduous; stipules glandular. Synflorescences pseudo-umbellate with 3–6 unbranched rays around central cyathium (rays rarely absent), bracts often subquadrate and ± leaf-like. Cyathia all similar and bisexual, (8)10–18 mm diam.; glands 5 (6), outer margins crenulate or with finger-like processes, rarely entire. Capsule globose, smooth to longitudinally ridged, glabrous to pubescent, 10–25 mm diam., 3-locular, walls less than 1 mm thick, subsessile. Seeds 3 per capsule, ovoid, somewhat laterally compressed, grey to brown, smooth, 4–6 mm long.

Species included. – 13: *E. appendiculata* P.R.O. Bally & S. Carter, *E. carinulata* P.R.O. Bally & S. Carter, *E. giumboensis* A. Hässl., *E. grosseri* Pax, *E. hamaderoensis* A.G. Mill., *E. kiritensis* P.R.O. Bally & S. Carter, *E. marie-cladieae* Rzepecky, *E. nogalensis* (A. Hässl.) S. Carter, *E. obcordata* Balf. f., *E. scheffleri* Pax, *E. sennii* Chiov., *E. socotrana* Balf. f., *E. somalensis* Pax.

Distribution and habitat. – Eastern Africa (Tanzania, Kenya, Ethiopia, Somalia) and Yemen (Socotra); dry, largely deciduous bushland in open flats, on slopes of rocky hills and escarpments, from near sea level to 1000 m.

6. *Euphorbia* sect. *Balsamis* Webb & Berthelot, Hist. Nat. Iles Canaries 3(2): 253: 1847 – Type: *E. balsamifera* Aiton.
Monoecious bisexual shrubs to small trees with pliable

semi-succulent densely dichotomous branches and grey to green (then photosynthetic) bark (often red on young growth), 0.2–3 m tall. Leaves alternate and often clustered towards branch apices, narrowly lanceolate to small and narrowly deltate, entire, (sub)sessile, deciduous to ephemeral; stipules sometimes present as small dark glands. Synflorescences with 4–6 short unbranched rays around a terminal cyathium or reduced to a terminal cyathium, bracts similar to leaves or broader. Cyathia all similar and usually bisexual, 3.5–7(–20) mm diam.; glands (4) 5, elliptical to rounded, outer margins entire (with filiform processes in *E. meuleniana*). Capsule subglobose to obtusely 3-angled, smooth, glabrous to pubescent, 5–10(–12) mm diam., 3-locular, subsessile to exserted. Seeds 3 per capsule, subglobose to turbinate, brown, smooth to rugose, 3–5 mm long.

Species included. – 9: *E. balsamifera* Aiton, *E. dhofarensis* S. Carter, *E. larica* Boiss., *E. masirahensis* Ghaz., *E. meuleniana* O. Schwartz, *E. rubriseminalis* S. Carter. There are several unsampled species from Somalia and Ethiopia that may also belong in this section, if their similarities to *E. meuleniana* are an indication; these include *E. noxia* Pax, *E. ogadenensis* P.R.O. Bally & S. Carter and *E. thulinii* S. Carter.

Distribution and habitat. – Most species are restricted to the southern Arabian Peninsula (*E. larica* extends eastwards into Iran). In contrast, *E. balsamifera* is widespread, occurring in Sudan (Red Sea Hills), Somalia, southern Arabian Peninsula and the Socotran Archipelago (Abd al Kuri only), as well as in West Africa and the Canary Islands. Species grow on dry stony slopes or stony flat plains and they sometimes form the dominant component of the otherwise very scanty vegetation; from sea level to 2000 m.

Euphorbia larica (Fig. 1F), *E. masirahensis* and *E. rubriseminalis* are pencil-stemmed shrubs with rapidly caducous, relatively small leaves that bear considerable resemblance to some members of the other three subgenera of *Euphorbia*. Our phylogeny suggests that these three species may have evolved from ancestors that resembled the leafy species *E. balsamifera* and *E. meuleniana*. The disjunct distribution of *E. balsamifera* is unusual. The eastern populations are currently treated as a distinct subspecies, *E. balsamifera* subsp. *adenensis*.

The accessions of *E. dhofarensis* reported by Barres & al. (2011), Bruyns & al. (2011) and Dorsey & al. (2013) were misidentified and are from a species belonging to *E.* subg. *Euphorbia*, perhaps *E. uzumuk* S. Carter & J.R.I. Wood or a related species.

7. *Euphorbia* sect. *Anthacanthae* Lem. in Ill. Hort. 2: Misc. 69. 1855 ≡ *Anthacantha* Lem. in Ill. Hort. 2: Misc. 69. 1855 ≡ *E.* subsect. *Anthacanthae* (Lem.) Pax & K. Hoffm. in Engler & Prantl, Nat. Pflanzenfam., ed. 2, 19c: 216. 1931 – Type (designated by Wheeler, 1943: 485): *E. heptagona* L. – “*Euphorbia* subg. *Anthacantha*” R. Turner, Euphorbias, A Gardener’s Guide: 67. 1995. Not validly published, the page of publication of the intended basionym, *Anthacantha* Lem. not cited (Art. 41.5).

Monoecious or dioecious succulent shrubs, sometimes consisting of a cylindrical tuberculate stem with a tuft of leaves at its apex, dwarf succulents (occasionally small trees with pliable semi-succulent branches) or geophytes, usually with green

(or grey-green) photosynthetic bark, stem and branches often tuberculate, often armed with spines developing from persistent hardened short-shoots arising in axils of tubercles. Leaves alternate to spiral, narrowly lanceolate (ovate) and often reduced to minute rudiments, entire, often sessile and often arising at the apices of conical tubercles (these often arranged or fused vertically into 4–20 straight or spiral angles or rows along stems and branches), deciduous to ephemeral; stipules absent (rarely present as minute glands). Synflorescences usually solitary in axils of tubercles, often reduced to a single cyathium terminating a short (rarely to 10 cm long) sometimes tuberculate peduncle (peduncles sometimes branching among uppermost bracts to bear further cyathia), sometimes a solitary peduncle terminating stem or branches (possibly with other cyathia arising in axils of uppermost bracts), sometimes consisting of many-rayed false umbels branching in axils of upper bracts, bracts leaf-like or enlarged but often much reduced. Cyathia all similar and bisexual or unisexual (staminate cyathia up to twice the diameter of pistillate cyathia), 2.5–30 mm diam.; glands 4–5(8), outer margins entire to crenulate or with 2- to many finger-like, sometimes branched projections. Capsule obtusely 3-angled, smooth (with slight ridges), glabrous to pubescent, 5–18 mm diam., 3-locular, walls less than 0.5 mm thick, sessile or subsessile (exserted on pedicel to 15 mm long). Seeds 3 per capsule, turbinate to globose, often with 2–4 longitudinal ridges, pale to dark brown, smooth to verrucose, 1.5–5.5 mm long.

Species included. – 87 (for further synonymy see Bruyns, 2012; Riina & Berry, 2013b).

Distribution and habitat. – This is by far the largest section within the subgenus, with 76 out of the 87 recognized species found in southern Africa and the remaining 11 species very sparsely distributed over the rest of sub-Saharan Africa; bare, dry, stony plains with little other vegetation to deep Kalahari sand among scattered clumps of grass and trees to among *fynbos* vegetation on nutrient-poor sandy soils in the Cape Floristic Region (Bruyns, 2000), sometimes on steep rocky slopes and sometimes in shallow soils on flattish granite or sandstone outcrops, from sea level to 2700 m.

Both molecular and morphological characters support the division of *E. sect. Anthacanthae* into five subsections (Figs. 3, 5).

Key to the subsections of *Euphorbia* sect. *Anthacanthae*

- 1 Geophytes, with rosettes of leaves at ground level 7b. *E. subsect. Florispinae*
- 1 Shrubs, trees or dwarf succulents, if geophytic then with annual stems above ground 2
- 2 Geophytes, with fleshy subterranean tuber and annual branches above ground 3
- 2 Non-geophytic shrubs or herbs, with branches above ground (sometimes small but not annual) 4
- 3 Cyathial glands with obscurely crenulate outer margins ... 7a. *E. subsect. Platycephalae*
- 3 Cyathial glands with many finger-like, often forked processes on outer margins 7c. *E. subsect. Dactylanthes*
- 4 Plants semi-succulent or somewhat woody with grey

- non-photosynthetic bark on stems and branches, leaves prominent and deciduous but not arising on tubercles and leaving scars directly on stems and branches 7a. *E. subsect. Platycephalae*
- 4 Plants succulent with green or grey-green photosynthetic stems and branches (with shiny grey-brown non-photosynthetic bark in *E. quadrata*), leaves soon deciduous and often minute, always borne on distinct tubercles (small but clearly present in *E. quadrata*), tubercles often arranged into straight or spiral rows or fused into angles along the stems 5
- 5 Cyathia unisexual 6
- 5 Cyathia bisexual 7
- 6 Stems and branches with ± prominent tubercles in rows or with indistinct tubercles fused into 4–20 often prominent angles; branches usually with many sterile short-shoots each arising in the axil of a tubercle and often developing into spines 7b. *E. subsect. Florispinae*
- 6 Stems and branches with prominent tubercles randomly arranged or roughly organized into 3 rows (occasionally tubercles indistinct but then not fused into rows) 7d. *E. subsect. Pseudeuphorbium*
- 7 Some branches elongating and terminated by cyathium on short peduncle, peduncles (at least near their bases) indistinguishable from branches 8
- 7 Cyathia on peduncles arising in axils of tubercles on branches and not terminating some branches, peduncles different in appearance to branches 9
- 8 Plants highly rhizomatous or slender and scandent from a turnip-shaped tuber (*E. bruynsii*), with green branches and often prominent tubercles on branches bearing leaves or leaf-rudiments that persist for most of growing season (forming a very dense mound of short bright green branches in *E. polycephala*), often with finger-like processes on outer margins of cyathial glands corrugated above, inner margins of glands folded outwards over base of gland (absent in *E. bruynsii*) 7c. *E. subsect. Dactylanthes*
- 8 Plants not rhizomatous (if with much swollen rootstock then with shiny grey-brown non-photosynthetic bark and small tubercles on branches in *E. quadrata*) often with pencil-shaped grey-green branches and very indistinct tubercles bearing fleeting leaves or leaf-rudiments 7d. *E. subsect. Pseudeuphorbium*
- 9 Plants with thickened, coarsely tuberculate stem with more finely tuberculate and much more slender branches arising near its apex (occasionally plant densely mound-like or shrubby with stem not visible: *E. braunsii*, *E. clavarioides*) 7e. *E. subsect. Medusea*
- 9 Plants consisting of a single erect cylindrical, tuberculate stem rarely with few to many branches, tubercles on stem and branches all of similar size, branches of similar thickness to stem 10
- 10 Cyathial glands with entire to very finely crenulate outer margins; peduncles 0.1–18 cm long 7b. *E. subsect. Florispinae*
- 10 Cyathial glands with deeply toothed outer margins; peduncles 3–20 cm long 11

- 11 Plants with prominent tuft of deciduous leaves at apex of stem (and branches, if present); peduncle with conspicuous deltate bracts 20–40 mm broad 7d. *E.* subsect. ***Pseudeuphorbium***
- 11 Plants with ephemeral and relatively inconspicuous leaves at apex of stem; peduncle with linear to ± spatulate inconspicuous bracts 1–4 mm broad 7e. *E.* subsect. ***Medusea***

7a. *Euphorbia* subsect. ***Platycephalae*** Bruyns, **subsect. nov.**
– Type: *E. platycephala* Pax.

Monoecious semi-succulent trees (to 9 m) or ± woody shrubs, sometimes geophytes with fleshy rootstock and slightly fleshy annual stem and branches, larger species with grey non-photosynthetic bark, stem and branches not tuberculate, spineless. Leaves alternate, narrow, entire, sessile, deciduous, stipules present as minute glands or filaments. Synflorescences usually solitary in axils or in terminal many-rayed false umbels branching further in axils of upper bracts. Cyathia all similar and bisexual, 7–30 mm diam.; glands 4–5, outer margins crenulate or with 6–12 finger-like, sometimes branched projections. Capsule subspherical or obtusely to deeply 3-angled, smooth, often pubescent, 8–18 mm diam., exerted on pedicel 2.5–15 mm long. Seeds globose to subglobose, smooth to wrinkled.

Species included. – 10: *E. cervicornu* Baill., *E. friesiorum* (A. Hässl.) S. Carter, *E. grantii* Oliv., *E. macrophylla* Pax, *E. maritae* Rauh, *E. omariana* M.G. Gilbert, *E. papillosicapsa* L.C. Leach, *E. platycephala* Pax, *E. pseudograntii* Pax, *E. specksii* Rauh.

Distribution and habitat. – Widespread in sub-Saharan Africa from Botswana and Zimbabwe to West Africa and to Ethiopia; seasonally wet flats among trees, open woodland on stony hillsides, sandy soil to black cotton soil and hard clays, 500–1800 m.

This group differs from most others in *E.* sect. *Anthacanthae* by the lack of tubercles on the stems and branches, the non-photosynthetic though semi-succulent branches in the larger species and the many-rayed, umbel-like synflorescences with prominent bracts. While such prominent and obviously bracteate synflorescences find close parallels in *E. monteiroi* and *E. wildii* of *E.* subsect. *Pseudeuphorbium*, these two species differ by their much more succulent, tuberculate stems with strong photosynthetic abilities.

7b. *Euphorbia* subsect. ***Florispinae*** Haw. in Philos. Mag. Ann. Chem. 1: 275. 1827 – Type: *E. stellispina* Haw.

Monoecious or dioecious succulent shrubs sometimes consisting of a cylindrical tuberculate stem with a tuft of leaves at its apex, dwarf succulents or geophytes, usually with green photosynthetic bark, stem and branches mostly tuberculate, often armed with spines developing from persistent hardened sterile peduncles arising in axils of tubercles. Leaves spiral, mostly narrow and linear, occasionally ovate, entire, mostly sessile, deciduous and often reduced to minute ephemeral rudiments, arising at apex of conical tubercles (these mostly fused vertically into 4–20 straight or spiral angles along stem and branches); stipules absent. Synflorescences usually solitary

in axils of tubercles often reduced to a single cyathium terminating the short (rarely to 10 cm long), sometimes tuberculate peduncle (peduncle sometimes branching among uppermost bracts to bear further cyathia). Cyathia all similar and bisexual or unisexual with males usually larger than females, 2.5–10 mm diam.; glands 4–5, outer margins entire to finely crenulate. Capsule obtusely 3-angled, smooth, glabrous (pubescent), 5–8 mm diam., ± sessile. Seeds faintly ridged to round, usually smooth (slightly pitted).

Species included. – 27.

Distribution and habitat. – Lesotho, South Africa, Swaziland; stony slopes to gravelly flats, semi-arid areas to locally dry spots in moist grassland, mostly in dwarf scrub on hard loam often with many other succulents, *E. pulvinata* in shallow soils overlaying flat pavements of rock or on rocky slopes in grassland, sometimes very common and then forming a major component of scanty semi-arid shrubland, 10–2100 m.

This subsection consists of four groups that are morphologically quite distinctive. Although we have been unable to establish either their monophyly or the relationships among them, they are groups of considerable horticultural interest and are sufficiently characteristic that they can be recognized here as four distinct series.

Key to the series of *Euphorbia* subsect. *Florispinae*

- 1 Plants bearing bisexual cyathia 7b-4. *E.* ser. ***Treisia***
- 1 Plants bearing unisexual cyathia only 2
- 2 Geophytes, with only leaves appearing above ground 7b-3. *E.* ser. ***Rhizanthium***
- 2 Not geophytes, with stems and branches at least reaching the ground surface, usually shrub-forming 3
- 3 Plants with conspicuous leaves in growing season, tubercles arranged into obscure rows but not fused into angles along stems and branches, fertile peduncles with 2–3 ± prominent bracts immediately beneath and exceeding cyathium 7b-1. *E.* ser. ***Hystrix***
- 3 Plants mostly with much reduced leaf-rudiments only (though cf. *E. pulvinata*), tubercles fused into angles along stems and branches, fertile peduncles rarely with 2–3 slightly larger bracts immediately beneath cyathium and these rarely exceeding cyathium 7b-2. *E.* ser. ***Meleuphorbia***

7b-1. *Euphorbia* ser. ***Hystrix*** Bruyns, **ser. nov.** – Type: *E. hystrix* Jacq. (= *E. loricata* Lam.).

These shrubby species are characterized by their tuberculate stem and branches where the tubercles are arranged into obscure rows (but not fused into angles). They have soft, quite conspicuous, deciduous leaves that last for much of the growing season. They usually possess persistent, sterile short-shoots (spiny in *E. loricata*; not spiny in *E. multifolia*; weak and slender in *E. oxystegia*; absent in *E. bupleurifolia*). The fertile peduncle has two or three fairly prominent bracts at the tip that immediately subtend and usually considerably exceed the cyathium. These are lacking on the sterile short-shoots. Cyathia are unisexual and the plants dioecious.

Species included. – 4: *E. bupleurifolia* Jacq., *E. loricata* Lam., *E. multifolia* A.C. White, R.A. Dyer & B. Sloane, *E. oxystegia* Boiss.

All species are found in South Africa only, with only *E. bupleurifolia* occurring outside the Greater Cape Floristic Region, in the Eastern Cape and KwaZulu-Natal.

7b-2. *Euphorbia* ser. *Meleuphorbia* (A. Berger) Bruyns, **stat. nov.** ≡ *E. sect. Meleuphorbia* A. Berger, Sukkul. Euphorb.: 10, 101. 1906 ≡ *E. subsect. Meleuphorbia* (A. Berger) Pax & K. Hoffm. in Engler & Prantl, Nat. Pflanzenfam., ed. 2, 19c: 216. 1931 – Type (designated by Pax, 1921: 161): *E. meloformis* Aiton.

In this group the stem and the branches (mostly not distinct from each other, except for *E. nesemannii* and *E. pseudoglobosa*) usually form a shrub and are covered with tubercles that are joined into distinct angles along the branches and the stem (Fig. 1G, M–O). Except in *E. pulvinata*, the leaves are minute and rapidly fall off. The plants are generally armed with stout spines that are also derived (as above) from slender, non-succulent short-shoots that arise in the axils of the tubercles (here usually only one per axil, but sometimes more in *E. polygona*). Such short-shoots are initially soft and bear several minute leaf-rudiments (usually referred to as “bracts”) that rapidly drop off, after which the shoot hardens and dries into a formidable, persistent spine. Unlike in the first group, the cyathia are not surrounded by larger bracts at the tip of the peduncle (except in *E. pulvinata*). The cyathia are unisexual and all species are dioecious (rarely bisexual plants occur), with the male cyathia usually about twice the diameter of the females.

Species included. – 15: *E. cumulata* R.A. Dyer, *E. ferox* Marloth, *E. heptagona* L., *E. jansenvillensis* Nel, *E. mamillaris* L., *E. meloformis* Aiton, *E. nesemannii* R.A. Dyer, *E. obesa* Hook. f., *E. pentagona* Haw., *E. pillansii* N.E. Br., *E. polygona* Haw., *E. pseudoglobosa* Marloth, *E. pulvinata* Marloth, *E. stellispina* Haw., *E. susannae* Marloth.

Of the species here, *E. polygona* may form very large, cactoid shrubs reaching 2 m tall (Fig. 1G). Others form shrubs of intermediate size, as in *E. heptagona*, while yet others (like *E. pseudoglobosa* and *E. susannae*) have a nearly geophytic habit where the stem and branches are almost entirely subterranean, with only their apices protruding above the ground. In this group, the development of spines is not diagnostic. They are intermittently present in *E. polygona* (there are regions where all the plants are spineless), and there are also a few species (*E. jansenvillensis*, *E. pseudoglobosa* and *E. susannae*) in which the spines do not develop at all.

Species of this group mainly occur in South Africa and most of them are found in the southern part of the Greater Cape Floristic Region, on the Little Karoo, the Worcester-Robertson Karoo and the southern coastal plain. From here they extend eastward beyond its margins into the Great Karoo and Eastern Cape. *Euphorbia pulvinata* is the only widespread species, extending into the tropical parts of South Africa and the small, mountainous countries of Lesotho and Swaziland.

7b-3. *Euphorbia* ser. *Rhizanthium* (Boiss.) Bruyns, **stat. nov.** ≡ *E. sect. Rhizanthium* Boiss. in Candolle, Prodr. 15(2): 10, 92. 1862 ≡ *E. subsect. Rhizanthium* (Boiss.) Denis, Euphorb. Iles Austr. Afr.: 41, 66. 1921 – Type (designated by Wheeler, 1943: 488): *E. tuberosa* L.

These species are geophytes, with scarcely tuberculate subterranean stems and branches in *E. tuberosa* (the other two species lack branches). They have soft, conspicuous, petiolate, deciduous leaves that persist for much of the growing season and are often pressed to the ground. They lack persistent short-shoots, the cyathia are unisexual and the plants are dioecious.

Species included. – 3: *E. ecklonii* (Klotzch & Garcke) Baill., *E. silenifolia* (Haw.) Sweet, *E. tuberosa* L.

All species are restricted to South Africa, with only *E. silenifolia* extending outside the Greater Cape Floristic Region into the Eastern Cape.

7b-4. *Euphorbia* ser. *Treisia* (Haw.) Bruyns, **stat. nov.** ≡ *Treisia* Haw., Syn. Pl. Succ.: 131. 1812 ≡ *E. sect. Treisia* (Haw.) Baill., Étude Euphorb.: 284. 1858 ≡ *E. subsect. Treisia* (Haw.) Benth. & Hook. f., Gen Pl. 3(1): 260. 1880 – Type (designated by Wheeler, 1943: 474): *T. clava* (Jacq.) Haw. (≡ *E. clava* Jacq.).

These species are mainly single-stemmed succulents (rarely branching into a shrub, as in *E. pubiglans*; in the others mainly if damaged) with cylindrical, densely tuberculate stems and a small slender rootstock. They have soft, conspicuous, deciduous leaves that persist for much of the growing season, arising in a dense tuft around the apex of the stem. Persistent sterile short-shoots are absent, and while the peduncles sometimes dry out and remain, they do not become spiny. Each peduncle has 2–3 fairly prominent bracts at the tip that immediately subtend and somewhat exceed the cyathium. The cyathia are bisexual and the plants monoecious.

Species included. – 5: *E. bubalina* Boiss., *E. clandestina* Jacq., *E. clava* Jacq., *E. cylindrica* A.C. White, R.A. Dyer & B. Sloane, *E. pubiglans* N.E. Br.

All species are found in South Africa only. *Euphorbia clandestina*, *E. clava*, *E. cylindrica* and *E. pubiglans* occur within the Greater Cape Floristic Region (three of them are endemic to it), while *E. clava* also occurs in the Eastern Cape and *E. bubalina* from the Eastern Cape to northern KwaZulu-Natal.

7c. *Euphorbia* subsect. *Dactylanthes* (Haw.) Pax & K. Hoffm. in Engler & Prantl, Nat. Pflanzenfam., ed. 2, 19c: 216. 1931 ≡ *Dactylanthes* Haw., Syn. Pl. Succ.: 132. 1812 ≡ *E. sect. Dactylanthes* (Haw.) A. Berger, Sukkul. Euphorb.: 10, 104. 1906 – Type (designated by Wheeler, 1943: 463): *Dactylanthes anacantha* (Aiton) Haw. (≡ *E. anacantha* Aiton = *E. tridentata* Lam.).
= *Euphorbia* sect. *Trichadenia* Pax in Engler, Veg. Erde 9 Pflanzenwelt Afrikas 3(2): 152. 1921 ≡ *E. subg. Trichadenia* (Pax) S. Carter in Kew Bull. 40: 816. 1985 – Type (designated by Hässler 1931: 318, 322): *E. trichadenia* Pax.
= *Euphorbia* sect. *Euphorbium* Boiss. in Candolle, Prodr. 15(2): 10, 85. 1862 – Type (designated by Wheeler, 1943: 485): *E. anacantha* Aiton.

Monoecious small, rhizomatous to large mound-forming succulents with short tuberculate stem and branches mostly arising from tubers or underground rhizomes or geophytes, spineless. Leaves loosely spiral, narrowly lanceolate, entire, sessile, deciduous, often reduced to minute ephemeral rudiments arising at apex of conical tubercles (these arranged vertically into loosely spiral rows along stem and branches); stipules absent. Synflorescence a solitary peduncle terminating stem or branches, with small leaf-like bracts (sometimes with other cyathia arising in axils of uppermost bracts). Cyathia all similar and bisexual, 5–19 mm diam.; glands 4–5, usually heavily reticulated-corrugated above, usually with rectangular-truncate inner margin recurved over basal part of gland, outer margins divided into several spreading finger-like, irregularly reticulated-corrugated processes, rarely only slightly indented and almost entire. Capsule obtusely 3-angled, smooth, glabrous, 5–8 mm diam., slightly exserted. Seeds usually without ridges, smooth to finely papillate.

Species included. – 8: *E. bruynsii* L.C. Leach, *E. globosa* (Haw.) Sims, *E. patula* Mill., *E. polycephala* Marloth, *E. pseudotuberosa* Pax, *E. trichadenia* Pax, *E. tridentata* Lam., *E. wilmaniae* Marloth.

Distribution and habitat. – Angola, South Africa, Botswana, Zimbabwe; stony areas among trees sometimes in shallow soils or in dwarf scrub on hard loam, sometimes with other succulents, often in crevices on pavements of calcrete or in crevices in low shale outcrops, 50–1500 m.

This subsection consists of two geophytic, essentially non-succulent species (*E. pseudotuberosa*, *E. trichadenia*) from the summer-rainfall (partly tropical) parts of southern Africa and Angola that are weakly supported sister species to the remainder (Fig. 3). The others are all similar succulents with greatly reduced leaves and a characteristic growth-habit. They are typically found in various semi-arid (“karroid”) areas of South Africa, also mainly receiving summer rainfall. In these, the often highly rhizomatous plant arises from a thick central rootstock that is sometimes expanded into a tuber. The stem and many small branches form a large mound (*E. polycephala*) or many small clusters connected by rhizomes beneath the soil (as in *E. tridentata*), or the plant can also be scandent in other bushlets (*E. bruynsii*). *Euphorbia bruynsii* is unique in the subsection for its particularly small and slender cyathia, the small cyathial glands that have almost entire outer margins and the absence of recurved inner margins on the glands. The female flower is also not exserted to the extent of the other species.

7d. *Euphorbia* subsect. *Pseudeuphorbium* Pax in Engler & Prantl, Nat. Pflanzenfam. 3(5): 107. 1891 ≡ *E. sect. Pseudeuphorbium* (Pax) A. Berger, Sukkul. Euphorb.: 10, 115. 1906 – Type: *E. marlothii* Pax (= *E. monteiroi* Hook. f.).

= *E. subsect. Lignosae* (Pax & K. Hoffm.) Pax & K. Hoffm. in Engler & Prantl, Nat. Pflanzenfam., ed. 2, 19c: 213. 1931 ≡ *E. sect. Lignosae* Pax & K. Hoffm. in Engler, Veg. Erde 9 Pflanzenwelt Afrikas 3(2): 150. 1921 – Type: *E. lignosa* Marloth.

Monoecious or dioecious partly to highly succulent shrubs, rarely consisting of a cylindrical tuberculate stem with a tuft of leaves at its apex, or small trees to 3 m or dwarf rhizomatous succulents, usually with green or grey-green photosynthetic bark, stem and branches tuberculate, tips of branches occasionally developing into spines but otherwise plant spineless. Leaves alternate to spiral, narrow, entire, ± sessile, deciduous and occasionally reduced to minute ephemeral rudiments, arising at apex of small to conspicuous conical tubercles arranged very loosely into slightly spiral rows along stem and branches; stipules absent. Synflorescences usually solitary in axils of tubercles, often reduced to a single cyathium on short to elongated faintly tuberculate peduncle (peduncle sometimes branching among uppermost bracts), sometimes a solitary peduncle terminating stem or branches (possibly with other cyathia arising in axils of uppermost bracts), sometimes consisting of many-rayed false umbels branching dichotomously. Cyathia all similar and bisexual or unisexual and males larger than females, 2.5–16 mm diam.; glands 4–5, outer margins entire to divided into many finger-like projections. Capsule obtusely 3-angled, smooth, glabrous to pubescent, 5–13 mm diam., subsessile (exserted on pedicel to 10 mm long). Seeds subglobose to turbinate with 2–4 ridges, finely papillate to pitted or verrucose.

Species included. – 10: *E. celata* R.A. Dyer, *E. dregeana* E. Mey. ex Boiss., *E. gariiepina* Boiss., *E. hamata* (Haw.) Sweet, *E. indurescens* L.C. Leach, *E. lignosa* Marloth, *E. monteiroi* Hook. f., *E. pedemontana* L.C. Leach, *E. quadrata* Nel, *E. wildii* L.C. Leach.

Distribution and habitat. – Angola, Namibia, Botswana, South Africa and Zimbabwe; stony to very rocky steep slopes to gravelly flats, sometimes in shallow soils or in dwarf scrub on stony ground with hard loam, often common in predominantly succulent scrub and occasionally dominant (*E. dregeana*), 50–2600 m.

This subsection is vegetatively very diverse, ranging from dwarf, rhizomatous succulents (*E. celata*) to pencil-stemmed shrubs both small (*E. gariiepina*, *E. indurescens*, *E. lignosa*) and large (*E. dregeana*) and to single-stemmed cylindrical or sparingly branched succulents up to 3 m tall (with a tuft of deciduous leaves at the apices of the stem and branches in *E. monteiroi* and *E. wildii*). This group appears to have evolved in two distinct regions, with one subclade occurring only in arid parts of the Greater Cape Floristic Region (with winter rainfall and dry summers) and the other in the summer rainfall regions of Namibia and South Africa, extending into Angola and Zimbabwe. Several species have cyathia arising on short peduncles that terminate the branch or stem, but in others they arise on longer, conspicuously bracteate peduncles from the axils of the tubercles (*E. monteiroi*, *E. wildii*). In most species (excluding *E. celata*, *E. indurescens*, *E. lignosa* and *E. quadrata*), the cyathia are encircled by a whorl of conspicuous bracts that are much broader than the cyathium and that are sometimes brightly colored. The cyathia vary from small and unisexual (*E. celata*, *E. gariiepina*) to broad and bisexual in the others and are sometimes dark red (*E. monteiroi*). *Euphorbia quadrata* is the most unusual species here since it does not have green,

photosynthetic bark on the stem and branches and, indeed, is the least succulent of all the species, with somewhat pliable branches and conspicuous but ephemeral leaves. Its most succulent part is the swollen, tuberous rootstock.

7e. *Euphorbia* subsect. *Medusea* (Haw.) Pax & K. Hoffm. in Engler & Prantl, Nat. Pflanzenfam., ed. 2, 19c: 216. 1931 ≡ *Medusea* Haw., Syn. Pl. Succ.: 133. 1812 ≡ *E.* sect. *Medusea* (Haw.) Baill. in Étude Euphorb.: 284. 1858 – Type (designated by Wheeler 1943: 469): *Medusea major* (Aiton) Haw. (≡ *E. caput-medusae* var. *major* Aiton = *E. caput-medusae* L.).

= *E.* subsect. *Pseudomedusea* (A. Berger ex Pax) Pax & K. Hoffm. in Engler & Prantl, Nat. Pflanzenfam., ed. 2, 19c: 216. 1931 ≡ *E.* sect. *Pseudomedusea* A. Berger, Sukkul. Euphorb.: 11, 118. 1906 – Type: *E. procumbens* Mill.

Monoecious succulent shrubs or dwarf succulents with a thick, mostly subterranean, flat-topped stem (sometimes giving rise to several swollen roots well beneath the surface) and more slender deciduous branches radiating from near the apex of the main shoot (occasionally a single thick cylindrical stem), with green photosynthetic bark, stem and branches tuberculate, spineless (except in *E. schoenlandii*) but sometimes with persistent woody remains of fertile (rarely also some sterile ones cf. *E. arida*) peduncles in axils of tubercles (these long in *E. fasciculata* and *E. restituta*). Leaves spiral, narrow, entire, sessile, rapidly caducous and usually reduced to minute rudiments, arising at apex of conical tubercles (these arranged vertically into many spiral rows along stem and branches); stipules absent. Synflorescences solitary in axils of tubercles, reduced to a single cyathium terminating a short, finely tuberculate peduncle (peduncle to 15 cm long and branching among uppermost bracts to bear further cyathia only in *E. fasciculata* and *E. restituta*). Cyathia all similar and bisexual, 2.5–15 mm diam.; glands 4–5, outer margins crenulate or with 2–many finger-like, sometimes branched projections. Capsule obtusely 3-angled, smooth to somewhat ridged along edges, glabrous to sparsely pubescent, 5–12 mm diam., subsessile (rarely exerted on pedicel to 5 mm long). Seeds 4-angled (rarely not angled), papillate to coarsely tuberculate.

Species included. – 32: *E. albipollinifera* L.C. Leach, *E. arida* N.E. Br., *E. brakdamensis* N.E. Br., *E. braunsii* N.E. Br., *E. brevirama* N.E. Br., *E. caput-medusae* L., *E. clavarioides* Boiss., *E. colliculina* A.C. White, R.A. Dyer & B. Sloane, *E. crassipes* Marloth, *E. davyi* N.E. Br., *E. decepta* N.E. Br., *E. duseimata* R.A. Dyer, *E. esculenta* Marloth, *E. fasciculata* Thunb., *E. filiflora* Marloth, *E. flanaganii* N.E. Br., *E. fortuita* A.C. White, R.A. Dyer & B. Sloane, *E. friedrichiae* Dinter, *E. gerstneriana* Bruyns, *E. hallii* R.A. Dyer, *E. huttonae* N.E. Br., *E. hypogaea* Marloth, *E. inermis* Mill., *E. maleolens* E. Phillips, *E. melanohydrata* Nel, *E. multiceps* A. Berger, *E. namaquensis* N.E. Br., *E. namibensis* Marloth, *E. pentops* A.C. White, R.A. Dyer & B. Sloane, *E. procumbens* Mill., *E. restituta* N.E. Br., *E. schoenlandii* Pax.

Distribution and habitat. – Botswana, Lesotho, Namibia, South Africa, Swaziland, Zimbabwe; stony slopes to gravelly flats, arid to semi-arid areas to locally dry spots in moist

grassland, from dwarf scrub on hard, stony loam with many other succulents to among scattered trees and clumps of grass on Kalahari sand or shallow soils overlaying basalt in grassland, from very inconspicuous dwarf succulents to conspicuous, very common plants that are a major component of scanty, semi-arid shrubland, 10–2700 m.

This subsection includes all the well-known “medusoid” succulents, characterized by a thick, wedge-shaped, flat-topped, coarsely tuberculate stem from which a mass of snake-like, more finely tuberculate branches spread out, each of which arises in the axil of a tubercle on the stem (Fig. 1P). In typical “medusoid” plants, the stem varies from projecting partly above the ground (as often in *E. esculenta*) to wholly subterranean (as in *E. gerstneriana*), and plants with such underground stems can be geophytic, in the sense that the whole plant readily survives the dry season with all the branches removed. While the “medusoid” form is typified most clearly by the widespread and quite variable *E. caput-medusae* (where individuals may exceed 1 m in diameter), there are also much smaller species such as *E. procumbens*, in which the whole plant may be only 5 cm in diameter.

Our phylogeny and previous ones (Bruyns & al., 2006, 2011; Zimmermann & al., 2010) have shown that other species that are not as clearly “medusoid” as those mentioned above also belong in this subsection. Of note is *E. hallii*, with its conspicuous stem, slender, very ephemeral branches and considerable, tuberous rootstock. A further vegetatively disparate group is *E. fasciculata*, *E. restituta* and *E. schoenlandii*, all restricted to coastal parts of Namaqualand (Greater Cape Floristic Region) in western South Africa that receive winter rainfall. The rootstock in these species is small compared to the size of the plant. In *E. fasciculata* and *E. schoenlandii* the plant is again reduced to a single, cylindrical stem (though the characteristic tuft of leaves at its apex is inconspicuous), and *E. schoenlandii* is the only species in the subsection that is armed with spines derived from dried-out, sterile short-shoots. The top of the plant is partly protected by many persistent dried-out remains of the peduncles in *E. fasciculata* and *E. restituta*, but these are not sharp-tipped and never become spiny.

A further variant from the “medusoid” form is in *E. braunsii* and some forms of *E. multiceps*, where the plant forms a small shrub in which the stem is perhaps slightly stouter (occasionally also slightly longer) than the branches but otherwise not distinguishable from them. Our phylogeny is insufficiently resolved to determine whether the “true medusoids” are derived from an ancestor like *E. braunsii*, but this seems likely.

The greatest diversity in this subsection is found inside and on the margins of the Greater Cape Floristic Region receiving winter rainfall (Jürgens, 1991; Born & al., 2007) and in the Nama Karoo Region, where rainfall is bimodal or falls in the summer (Jürgens 1991). Outside these regions the diversity decreases greatly. However, *E. clavarioides* is widely distributed in South Africa, and a few species (*E. davyi*, *E. duseimata* and *E. maleolens*) are also widely distributed, reaching the Kalahari Desert of Botswana and the highlands of Namibia (around Windhoek and in the Waterberg further north).

■ NOMENCLATURAL NOTES

Several changes and corrections relevant to names in *Euphorbia* subg. *Athymalus* are necessary following the synonymy proposed for the southern African species of *Euphorbia* in Bruyns (2012). These are made below.

(1) The number of the type of *E. obesa* was cited in Bruyns (2012) as *MacOwan 3153*, following the information on the JSTOR website. However, a closer examination of the type specimen at K, where the number is not especially clear, and a check of the collection books of MacOwan at PRE, show that this ought to be *MacOwan 3183*, as cited by N.E. Brown (1915).

(2) The two names *E. bubalina* and *E. tugelensis* were maintained as separate species in Bruyns (2012). They were said to differ (White & al., 1941) by their differently shaped bracts subtending the cyathia (abruptly acute or obtuse and apiculate = *E. bubalina*; gradually acute or acuminate = *E. tugelensis*). Koutnik (1984) was the first to point out that these two species may well be the same. An examination of live flowering material of both has shown that these distinctions between them do not hold up and so only one species is recognized here. We therefore have the following new synonymy:

Euphorbia bubalina Boiss., Cent. Euphorb.: 26. 1860 – Holotype: South Africa, Cape, among thorn-bushes near Buffelsrivier, 13 Jan. 1832, *Drège 4615* (P!).
= *E. laxiflora* Kuntze, Revis. Gen. Pl. 3(3): 286. 1898 – Holotype: South Africa, East London, 5 Mar. 1894, *Kuntze s.n.* (NY!; isotype: K!).
= *E. tugelensis* N.E. Br. in Harvey & Sonder, Fl. Cap. 5(2): 335. 1915 – Holotype: South Africa, Natal, near Tugela River, received July 1865, *Gerrard 1626* (K!; isotype: W n.v.).

(3) In Bruyns (2012), *Euphorbia pubiglans* was placed in synonymy under *E. clava*. The two species seem to be frequently muddled and there are many misidentified specimens in South African herbaria. For example, a photograph of *E. pubiglans* appeared under the name *E. clava* in *Euphorbia Journal* 10: 193 (1996). However, the placement of *E. pubiglans* in synonymy is incorrect.

White & al. (1941) maintained *E. pubiglans* as distinct from *E. clava* on the basis of its smaller stature, the more densely crowded, blunt tubercles on the stems, the shorter peduncles with round-tipped bracts under the cyathia and a short pubescence on the spreading cyathial glands. Further distinctions are the frequently shrub-forming habit of *E. pubiglans*, the differently shaped cyathial glands, the much longer styles in *E. clava* (divided only some distance above a lower cylindrical fused part), the more or less glabrous ovary and glabrous male pedicels. The two species actually occur together in several localities around the city of Port Elizabeth in South Africa. They appear to maintain their distinctness by their different flowering times, with *E. pubiglans* flowering at the end of summer and *E. clava* flowering in the spring (P. Bruyns, pers. obs.)

(4) A further synonym of *Euphorbia celata*.

When he described *E. namuskluftensis*, Leach (1983) compared it only to *E. wilmaniae*. Shortly afterwards Leach (1984) described a further new species, *E. miscella*, which he compared only to *E. namuskluftensis* and *E. wilmaniae*.

In Bruyns (1992), it was shown that *E. miscella* was the same as *E. celata*. In Bruyns (2012), *E. namuskluftensis* was maintained as distinct from *E. celata*. This was on the basis that the leaf-rudiments are smaller in the former, the cyathia are longer in *E. celata* and the female flowers have shorter styles in *E. namuskluftensis*, which are divided almost to their bases. One of the main differences was also that Leach (1983: 190) mentioned that the inflorescence was “axillary, at the apex of the branches” in *E. namuskluftensis*. His Fig. 1 shows this possibly for one of the male cyathia illustrated, but the left of the two female cyathia is clearly terminal (the right one being unclear on this point). Cultivated material from the type locality of *E. namuskluftensis* (*Bruyns 2775* at BOL, E, NBG) has, however, shown that the cyathia are terminal at the apex of the branch, as in *E. celata* (except when these are slightly damaged, as may have happened in the plant figured by Leach for the male cyathia). It has also been found that not all the cyathia in *E. namuskluftensis* are as short as shown by Leach (1983), and some are as long as those of *E. celata*. There are therefore inadequate grounds for maintaining the two as distinct. The tiny leaf-rudiments in *E. namuskluftensis* are the smallest found in the broader concept of *E. celata*, corresponding to the fact that this is the most arid spot where *E. celata* occurs. They form a northern extension of the cline in this feature from the largest leaves in the south to the much smaller ones in “*E. miscella*” in the north.

Euphorbia celata R.A. Dyer in Bothalia 11: 278. 1974 – Holotype: South Africa, Vanrhynsdorp distr., Moedverloor, 100 m, 12 May 1973, *Hall 4272* (PRE!).
= *E. namuskluftensis* L.C. Leach in J. S. African Bot. 49: 189. 1983 – Holotype: Namibia, Namuskluft, ±1200 m, Oct. 1978, *Lavranos & Pehlemann 20796* (PRE!; isotype: WIND!).
= *E. miscella* L.C. Leach in J. S. African Bot. 50: 341. 1984 – Holotype: South Africa, Cape, near Lekkersing, 23 Apr. 1982, *Leach & al. 16545* (NBG!; isotype: PRE!).

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■ LITERATURE CITED

- Ali, J.R. & Huber, M.** 2010. Mammalian biodiversity on Madagascar controlled by ocean currents. *Nature* 463: 653–657. <http://dx.doi.org/10.1038/nature08706>
- Arakaki, M., Christin, P.-A., Nyffeler, R., Lendel, A., Eggli, U., Ogburn, R.M., Spriggs, E., Moore, M.J. & Edwards, E.J.** 2011. Contemporaneous and recent radiations of the world's major succulent plant lineages. *Proc. Natl. Acad. Sci. U.S.A.* 108: 8379–8384. <http://dx.doi.org/10.1073/pnas.1100628108>
- Bally, P.R.O.** 1959. *Lithocaulon* Bally (Asclepiadaceae), a new genus from Somaliland. *Candollea* 17: 53–59.
- Barres, L., Vilatersana, R., Moleró, J., Susanna, A. & Galbany-Casals, M.** 2011. Molecular phylogeny of *Euphorbia* subg. *Esula* sect. *Aphyllis* (Euphorbiaceae) inferred from nrDNA and cpDNA markers with biogeographic insights. *Taxon* 60: 705–720.
- Bellstedt, D.U., Van Zyl, L., Marais, E.M., Bytebier, B., De Villiers, C.A., Makwarela, A.M. & Dreyer, L.L.** 2008. Phylogenetic relationships, character evolution and biogeography of southern African members of *Zygophyllum* (Zygophyllaceae) based on three plastid regions. *Molec. Phylog. Evol.* 47: 932–949. <http://dx.doi.org/10.1016/j.ympev.2008.02.019>
- Boissier, E.** 1862. Euphorbieae. Pp. 3–188 in: Candolle, A.P. de (ed.), *Prodromus systematis naturalis regni vegetabilis*, vol. 15(2). Paris: Victor Masson & Fils. <http://dx.doi.org/10.5962/bhl.title.286>
- Born, J., Linder, H.P. & Desmet, P.** 2007. The Greater Cape Floristic Region. *J. Biogeogr.* 34: 147–162. <http://dx.doi.org/10.1111/j.1365-2699.2006.01595.x>
- Brown, N.E.** 1915 (“1925”). *Euphorbia*. Pp. 222–375 in: Thiselton-Dyer, W.T. (ed.), *Flora capensis*, vol. 5(2). London: Reeve. <http://dx.doi.org/10.5962/bhl.title.821>
- Bruyns, P.V.** 1992. Notes on African plants, Euphorbiaceae. Notes on *Euphorbia* species from the northwestern Cape. *Bothalia* 22: 37–42.
- Bruyns, P.V.** 2000. *Euphorbia*. Pp. 455–458 in: Goldblatt, P. & Manning, J. (eds.), *Cape plants*. Strelitzia 9. Pretoria: National Botanical Institute; St. Louis: Missouri Botanical Garden.
- Bruyns, P.V.** 2012. Nomenclature and typification of southern African species of *Euphorbia*. *Bothalia* 42: 217–245.
- Bruyns, P.V., Mapaya, R.J. & Hedderson, T.** 2006. A new subgeneric classification for *Euphorbia* (Euphorbiaceae) in southern Africa based on ITS and *psbA-trnH* sequence data. *Taxon* 55: 397–420. <http://dx.doi.org/10.2307/25065587>
- Bruyns, P.V., Klak, C. & Hanáček, P.** 2011. Age and diversity in Old World succulent species of *Euphorbia* (Euphorbiaceae). *Taxon* 60: 1717–1733.
- Carter, S.** 1988. Euphorbieae. Pp. 409–564 in: Polhill, R.M. (ed.), *Flora of tropical East Africa: Euphorbiaceae*, part 2. Rotterdam: A.A. Balkema.
- Coetzee, J.A.** 1980. Tertiary environmental changes along the southwestern African coast. *Palaeontol. Afr.* 23: 197–203.
- Danty d’Isnard, A.-T.** 1720. Établissement d’un genre de plante appelé Euphorbe; avec le dénombrement de ses espèces, de deux desquelles on donne les descriptions & les figures. *Hist. Acad. Roy. Sci. Mém. Math. Phys. (Paris, 4to)* 1720: 384–399.
- Daru, B.H., Manning, J.C., Boatwright, J.S., Maurin, O., Maclean, N., Schaefer, H., Kuzmina, M. & Van der Bank, M.** 2013. Molecular and morphological analysis of subfamily Alooideae (Asphodelaceae) and the inclusion of *Chortolirion* in *Aloe*. *Taxon* 62: 62–76.
- Davis, S.D., Heywood, V.H. & Hamilton, A.C. (eds.)** 1994. *Centres of plant diversity: A guide and strategy for their conservation*, vol. 1, Europe, Africa, South-west Asia and The Middle East. Cambridge, U.K.: WWF and IUCN.
- Denis, M.** 1921. *Les Euphorbiées des Iles Australes d’Afrique*. Nemours, France: Imprimerie Nemourienne. <http://dx.doi.org/10.5962/bhl.title.36553>
- Dorsey, B.L., Haevermans, T., Aubriot, X., Morawetz, J.J., Riina, R., Steinmann, V.W. & Berry, P.E.** 2013. Phylogenetics, morphological evolution, and classification of *Euphorbia* subgenus *Euphorbia*. *Taxon* 62: 291–315. <http://dx.doi.org/10.12705/622.1>
- Esser, H.-J., Berry, P.E. & Riina, R.** 2009. EupORBia: A global inventory of the spurges. *Blumea* 54: 11–12. <http://dx.doi.org/10.3767/000651909X474023>
- Hässler, A.** 1931. Verwandtschaftliche Gliederung der afrikanischen Euphorbien aus der Sektionen *Trichadenia* Pax und *Rhizanthium* Boiss. *Bot. Not.* 1931: 317–338.
- Hendey, Q.B.** 1981. Geological succession at Langebaanweg, Cape Province and global events of the late Tertiary. *S. African J. Sci.* 77: 33–38.
- Holmes, S. Carter.** 1993. *Euphorbia*. Pp. 323–337 in: Thulin, M. (ed.), *Flora of Somalia*, vol. 1. Kew: Royal Botanic Gardens.
- Horn, J.W., Van Ee, B.W., Morawetz, J.J., Riina, R., Steinmann, V.W., Berry, P.E. & Wurdack, K.J.** 2012. Phylogenetics and the evolution of major structural characters in the giant genus *Euphorbia* L. (Euphorbiaceae). *Molec. Phylog. Evol.* 63: 305–326. <http://dx.doi.org/10.1016/j.ympev.2011.12.022>
- Huelsbeck, J.P. & Ronquist, F.** 2001. MRBAYES: Bayesian inference of phylogenetic trees. *Bioinformatics* 17: 754–755. <http://dx.doi.org/10.1093/bioinformatics/17.8.754>
- Jürgens, N.** 1991. A new approach to the Namib Region I, Phytogeographic subdivision. *Vegetatio* 97: 21–38.
- Jürgens, N.** 1997. Floristic biodiversity and history of African arid regions. *Biodivers. & Conservation* 6: 495–514. <http://dx.doi.org/10.1023/A:1018325026863>
- Katoh, K., Kuma, K.-I., Toh, H. & Miyata, T.** 2005. MAFFT version 5: Improvement in accuracy of multiple sequence alignment. *Nucl. Acids Res.* 33: 511–518. <http://dx.doi.org/10.1093/nar/gki198>
- Klak, C., Reeves, G. & Hedderson, T.A.J.** 2004. Unmatched tempo of evolution in southern African semi-desert ice plants. *Nature* 427: 63–65. <http://dx.doi.org/10.1038/nature02243>
- Koutnik, D.L.** 1984. A brief taxonomy of the *Euphorbia clava-loricata* complex (*Treisia*). *Euphorbia J.* 2: 38–50.
- Leach, L.C.** 1983. A new *Euphorbia* from South West Africa. *J. S. African Bot.* 49: 189–192.
- Leach, L.C.** 1984. A new *Euphorbia* from South Africa. *J. S. African Bot.* 50: 341–345.
- Léandri, J.** 1957. *Euphorbia mandravioky*, nom. nov. et un nom nouveau pour une sous-section du genre Euphorbe. *Bull. Soc. Bot. France* 104: 499–501.
- Maddison, W.P. & Maddison, D.R.** 2011. Mesquite: A modular system for evolutionary analysis, version 2.75. <http://mesquiteproject.org>
- Meve, U. & Liede, S.** 2002. A molecular phylogeny and generic rearrangement of the stapelioid Ceropegieae (Apocynaceae—Asclepiadoideae). *Pl. Syst. Evol.* 234: 171–209. <http://dx.doi.org/10.1007/s00606-002-0220-2>
- Morawetz, J.J., Wagner, B., Riina, R. & Berry, P.E.** 2009. *Euphorbia* Seed Atlas - Part 1. *Euphorbia World* 5(3): 26–29.
- Necker, N.J. de.** 1790. *Elementa Botanica*, vol. 2. Neuwied am Rhein. <http://dx.doi.org/10.5962/bhl.title.4452>
- Partridge, T.C. & Maud, R.R.** 2000. *The Cenozoic of southern Africa*. Oxford: Oxford University Press.

- Pax, F.** 1921. Euphorbiaceae. Pp. 1–168 in: Engler, A. & Prance, O. (eds.), *Die Vegetation der Erde*, vol. 9, *Die Pflanzenwelt Afrikas, insbesondere seiner tropischen Gebiete*, vol. 3(2). Leipzig: Engelmann. <http://dx.doi.org/10.5962/bhl.title.50144>
- Posada, D.** 2008. jModelTest: Phylogenetic model averaging. *Molec. Biol. Evol.* 25: 1253–1256. <http://dx.doi.org/10.1093/molbev/msn083>
- Rambaut, A. & Drummond, A.** 2007. Tracer, version 1.4. Computer program and documentation distributed by the authors. <http://beast.bio.ed.ac.uk/Tracer> (accessed 10 June 2012).
- Reichenbach, H.G.L.** 1829 (“1828”). *Conspectus regni vegetabilis per gradus naturales evoluti*, pars prima. Leipzig.
- Riina, R. & Berry, P.E.** 2013a. *Euphorbia* Planetary Biodiversity Inventory website. http://euphorbiaceae.org/pages/data_portal.html (accessed 23 Apr. 2013).
- Riina, R. & Berry, P.E. (coord.)** 2013b. *Euphorbia* Planetary Biodiversity Inventory database. <http://www.tolkin.org/projects/72> (accessed 23 April 2013).
- Riina, R., Peirson, J.A., Geltman, D.V., Molerio, J., Frajman, B., Pahlevani, A., Barres, L., Morawetz, J.J., Salmaki, Y., Zarré, S., Kryukov, A., Bruyns, P.V. & Berry, P.E.** 2013. A worldwide molecular phylogeny and classification of the leafy spurges, *Euphorbia* subgenus *Esula* (Euphorbiaceae). *Taxon* 62: 316–342. <http://dx.doi.org/10.12705/622.3>
- Ritz, C.M., Zimmermann, N.F.A. & Hellwig, F.H.** 2003. Phylogeny of subsect. *Meleuphorbia* (A. Berger) Pax & Hoffm. (*Euphorbia* L.) reflects the climatic regime in South Africa. *Pl. Syst. Evol.* 241: 245–259. <http://dx.doi.org/10.1007/s00606-003-0064-4>
- Ronquist, F. & Huelsenbeck, J.P.** 2003. MrBayes 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics* 19: 1572–1574. <http://dx.doi.org/10.1093/bioinformatics/btg180>
- Siesser, W. G.** 1980. Late Miocene origin of the Benguela upswelling system off northern Namibia. *Science* 208: 283–285. <http://dx.doi.org/10.1126/science.208.4441.283>
- Simmons, M.P.** 2004. Independence of alignment and tree search. *Molec. Phylog. Evol.* 31: 874–879. <http://dx.doi.org/10.1016/j.ympev.2003.10.008>
- Snijman, D.A.** In press. The Greater Cape Floristic Region, the extra Cape subregion. In: Snijman, D.A. (ed.), *Plants of the Greater Cape Floristic Region*, vol. 2, *The Extra Cape flora*. Strelitzia 30. Cape Town: South African National Biodiversity Institute.
- Stamatakis, A.** 2006. RAxML-VI-HPC: Maximum likelihood-based phylogenetic analyses with thousands of taxa and mixed models. *Bioinformatics* 22: 2688–2690. <http://dx.doi.org/10.1093/bioinformatics/btl446>
- Steinmann, V.W. & Porter, J.M.** 2002. Phylogenetic relationships in Euphorbieae (Euphorbiaceae) based on ITS and *ndhF* sequence data. *Ann. Missouri Bot. Gard.* 89: 453–490. <http://dx.doi.org/10.2307/3298591>
- Swofford, D.L.** 2003. PAUP*: Phylogenetic analysis using parsimony (*and other methods), version 4. Sunderland, Massachusetts: Sinauer.
- Uhlarz, H.** 1974. Entwicklungsgeschichtliche Untersuchungen zur Morphologie der basalen Blatteffigurationen sukkulenter Euphorbien aus den Subsektionen *Diacanthium* Boiss. und *Goniostema* Baill. *Trop. Subtrop. Pflanzenwelt* 9: 571–639.
- Wagner, B., Morawetz, J.J., Riina, R., Berry, P.E., Moller, A. & Becker, R.W.** 2010. *Euphorbia* Seed Atlas - Part 5. *Euphorbia World* 7(1): 11.
- Wagner, B., Morawetz, J.J., Riina, R., Berry, P.E., Moller, A. & Becker, R.W.** 2011. *Euphorbia* Seed Atlas - Part 6. *Euphorbia World* 7(2): 21.
- Wheeler, L.C.** 1943. The genera of living Euphorbieae. *Amer. Midland Naturalist* 30: 456–503. <http://dx.doi.org/10.2307/2421292>
- Wheeler, T.J. & Kececioğlu, J.D.** 2007. Multiple alignments by aligning alignments. *Bioinformatics* 23: i559–i568. <http://dx.doi.org/10.1093/bioinformatics/btm226>
- White, A.C., Dyer, R.A. & Sloan, B.** 1941. *The succulent Euphorbieae*, 2 vols. Pasadena: Abbey Gardens Press.
- Yang, Y., Riina, R., Morawetz, J.J., Haevermans, T., Aubriot, X. & Berry, P.E.** 2012. Molecular phylogenetics and classification of *Euphorbia* subgenus *Chamaesyce* (Euphorbiaceae). *Taxon* 61: 764–789.
- Zimmermann, N.F.A., Ritz, C.M. & Hellwig, F.H.** 2010. Further support for the phylogenetic relationships within *Euphorbia* L. (Euphorbiaceae) from nrITS and *trnL-trnF* IGS sequence data. *Pl. Syst. Evol.* 286: 39–58. <http://dx.doi.org/10.1007/s00606-010-0272-7>