



Research Article

More than one sweet tabaiba: Disentangling the systematics of the succulent dendroid shrub *Euphorbia balsamifera*Ricarda Riina^{1*} , Tamara Villaverde^{1,2} , Mario Rincón-Barrado¹ , Julià Molero³, and Isabel Sanmartín^{1*} ¹Real Jardín Botánico (RJB-CSIC), Plaza de Murillo 2, Madrid 28014, Spain²Departamento de Biología y Geología, Universidad de Almería, Ctra. Sacramento s/n. 04120 Almería, Spain³Departament de Biologia, Sanitat i Medi Ambient, Facultat de Farmàcia (GREB-IRBio), Universitat de Barcelona, Barcelona 08028, Spain

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Abstract The sweet tabaiba (*Euphorbia balsamifera* Ait.) is one of the classical examples of the disjunct biogeographic pattern known as Rand Flora. This species is currently circumscribed to comprise two subspecies, *Euphorbia balsamifera* subsp. *balsamifera* and *E. balsamifera* subsp. *adenensis* (Deflers) P.R.O. Bally, with their respective areas of distribution separated by a gap of about 2000 km across Central-East Africa. We use multiple sources of evidence including phylogenomics, morphometrics, lineage ages, and climatic niche analysis to disentangle the confusing taxonomy around this charismatic *Euphorbia* lineage. Based on our integrative approach, we reestablish the two current subspecies to the rank of species (*E. balsamifera* Ait., *E. adenensis* Deflers) and resurrect the long forgotten *E. sepium* N.E. Br., a commonly used species in the western Sub-Saharan and Sahelian regions. The taxonomic treatment presented here includes an identification key, updated morphological descriptions, and lectotypification of several names.

Key words: divergence times, *Euphorbia*, Euphorbiaceae, Macaronesia, phylogenomics, Rand Flora, Sahara, Sahel, taxonomy.

1 Introduction

Incomplete or poor taxonomic knowledge can bias our understanding of evolutionary and biogeographic patterns, which in turn can hamper biodiversity conservation and management efforts, especially for endemic taxa and cryptic species (Brito, 2004; Sattler et al., 2007). Molecular phylogenetics has greatly contributed to overcome the so-called taxonomic impediment (De Carvalho et al., 2005) by improving classification schemes that foster further studies at different taxonomic levels (e.g., Olmstead et al., 2009; Van Ee et al., 2011; LPWG, 2013; Jiménez-Mejías et al., 2016; Soreng et al., 2017; Xiao & Simpson, 2017). In addition, information from molecular phylogenetics and DNA barcoding (Hubert & Hanner, 2015; Rannala, 2015; Lavinia et al., 2017) in combination with other sources of data is being used more and more for species discovery and taxonomic delimitation in different groups (e.g., Smith et al., 2007; Alors et al., 2016; Cheek et al., 2016; Nugnes et al., 2017; Sousa et al., 2017). More recently, the rapid consolidation of high throughput sequencing (HTS) techniques coupled with novel analytical tools is providing massive amounts of sequence data, which can potentially resolve recalcitrant regions of the tree of life (but see Olmstead & Bedoya, 2019). Phylogenomics (i.e., phylogenetics using genome-scale datasets) can also contribute to clarify long-standing taxonomic controversies, and even

more in the context of an integrative taxonomic approach (e.g., Prata et al., 2018; Frajman et al., 2019).

While working on the evolution of Rand Flora lineages of *Euphorbia* (Villaverde et al., 2018), we stumbled upon the taxonomic uncertainty surrounding *Euphorbia balsamifera* Ait. This species belongs to *Euphorbia* section *Balsamis* Webb & Berthelot, a clade in *E.* subgenus *Athymalus* Neck. ex Rchb. (Peirson et al., 2013). The species, as presently circumscribed (*E. balsamifera* sensu lato), comprises two subspecies: *E. balsamifera* subsp. *balsamifera* and *E. balsamifera* subsp. *adenensis* (Deflers) P.R.O. Bally (Govaerts et al., 2000; Peirson et al., 2013), which are congruent with two disjunct areas separated by a gap of more than 2000 km across Central Africa (Fig. 1).

Euphorbia balsamifera s.l. is popularly known as “tabaiba dulce” (sweet tabaiba) in the Canary Islands, but it has many other common names across its entire geographic range. It is a dioecious, pachycaul, succulent dendroid shrub adapted to extreme thermal habitats and growing on rocky to sandy substrates. Pachycaul succulence is a specific condition in which water storage occurs in nonphotosynthetic parenchyma derived from the vascular cambium (Hearn et al., 2013) and represents a quite distinct condition from the great majority of succulent *Euphorbia*, which involves significant water storage parenchyma in the cortex and a persistent, photosynthetic periderm.

As many species in the genus, *Euphorbia balsamifera* s.l. has been traditionally used by humans as food (Sahel;

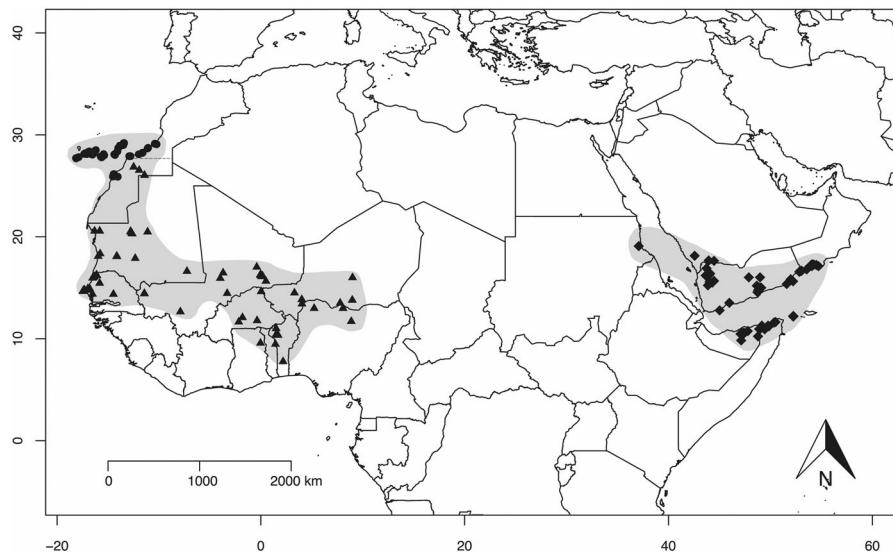


Fig. 1. Map showing georeferenced collections of the three species proposed in this study: *Euphorbia adenensis* (diamonds), *E. balsamifera* s.s. (circles), and *E. sepium* (triangles). The two shaded areas reflect the former taxonomic circumscription recognizing a single species (*E. balsamifera* s.l.) with two subspecies (subsp. *balsamifera* on the west and subsp. *adenensis* on the east).

latex is boiled and eaten as a gelatine), medicine (Sahel, Western Sahara, Morocco), chewing gum, and cork for wine bottles (Canary Islands). In the African Sahel, the species is propagated from cuttings to build living fences that provide sand stabilization, erosion control, and protection of crops from livestock (Dolbear, 2016).

There are other *Euphorbia* species, distantly related to *E. balsamifera*, that are also called tabaibas. They belong to *E.* section *Aphyllis*, a clade of 23 Macaronesian-African dendroid shrubs in a different subgenus—*E.* subgenus *Esula*—(Barres et al., 2011, 2017; Riina et al., 2013). The fact that *E. balsamifera* s.l. is the only “sweet” of the tabaibas probably has to do with the apparent lack of bitterness of its latex in comparison with tabaiba species in *E.* section *Aphyllis*. The milky latex of most *Euphorbia* species can be toxic and may cause skin and eye inflammation of different degrees, depending on the species (Webster, 1986; Eke et al., 2000; Vasas et al., 2012; Otang et al., 2014).

The two subspecies of *E. balsamifera* currently accepted correspond to former taxa at the species level, namely *E. balsamifera* Ait. and *E. adenensis* Defflers (Bally, 1965). On the contrary, populations of *E. balsamifera* s.l. from the west-central Africa were recognized in the past under two different names—*E. sepium* N.E.Br. and *E. rogeri* N.E.Br.—but they were later reduced to the subspecies level as *E. balsamifera* subsp. *sepium* with *E. rogeri* under its synonymy (Maire, 1938). Both *sepium* names are currently considered synonyms of *E. balsamifera* subsp. *balsamifera* (Govaerts et al., 2000; Peirson et al., 2013).

In a study focused on the karyological evolution of Macaronesian dendroid *Euphorbia*, Molero et al. (2002), in disagreement with Govaerts et al. (2000), recognized three taxa at the rank of subspecies, accepting *E. balsamifera* subsp. *sepium* along with the other two subspecies. However, Govaerts’ view of the group prevailed and was

later adopted by Peirson et al. (2013) in their sectional classification of *E.* subgenus *Athymalus* using a phylogenetic framework. Unfortunately, accessions representing typical localities of *E.* subsp. *sepium* were not sampled in that work, which only included samples of subsp. *balsamifera* from the Canary Islands, and subsp. *adenensis* from Oman (Peirson et al., 2013).

In a recent phylogenomic study, Villaverde et al. (2018) used DNA sequences from exons of 296 orthologous low-copy-nuclear loci representing most sections of *Euphorbia* subgenus *Athymalus* and a relatively good population sampling across the entire range of *Euphorbia balsamifera* s.l. to analyse phylogenetic relationships within this enigmatic species. They recovered three well-supported clades, which were tentatively labeled in their paper as *E. balsamifera* subsp. *adenensis*, *E. balsamifera* subsp. *balsamifera*, and *E. balsamifera* subsp. *sepium* (Villaverde et al., 2018). Here, we use an integrative approach that combines evidence from phylogenomics and lineage divergence times generated by Villaverde et al. (2018) with information from morphology, morphometrics, occurrence data, and climate niche analysis to revise and update the taxonomy of *Euphorbia balsamifera*.

2 Material and Methods

2.1 Phylogenomics and divergence times

Phylogenetic information on the studied taxa and related lineages within *Euphorbia* subgenus *Athymalus*, as well as estimates of divergence times, is based on the study of Villaverde et al. (2018).

2.2 Species occurrences and morphological study

Taxon occurrence information was obtained from herbarium specimen labels. When geographic coordinates were not

available from collection labels, if possible, specimens were georeferenced using Google Maps depending on the locality data recorded. Table S1 includes all specimen records filtered and curated from the original row-set of data downloaded from GBIF (<https://doi.org/10.15468/dl.oqiyuu>) plus records from other sources (i.e., herbarium collections not available in GBIF). This dataset (Table S1) was used to create the updated distribution map of the studied taxa using the *Dismo* Package in R (Hijmans et al., 2013; R Core Team, 2015).

A comparative morphological study of *Euphorbia balsamifera* s.l. was conducted using specimens from the following herbaria: B, BCN, BM, DAKAR, E, FR, FT, G, GM, K, L, LPA, P, M, MA, MPU, RAB, U, UPS, W, WAG (acronyms follow Index Herbariorum, available at <https://sweetgum.nybg.org/science/ih/>). In addition, we checked types and other historic collections available online via JSTOR Global Plants and virtual herbarium collections. Lectotypifications were made, when necessary, following the rules of the International Code of Nomenclature for algae, fungi, and plants (Turland et al., 2018).

2.3 Climatic niche analysis

Occurrence data points (see above) of the putative species analysed here are listed in Table S1. We downloaded the 19 bioclimatic variables from the WorldClim dataset website (<http://worldclim.org/version2>) at 2.5 arc min (~5 km; Hijmans et al., 2005). To understand the climatic differences among the three species, we performed niche comparison analysis using the *ecospat* package (Di Cola et al., 2017) in R version 3.4.1 (R Core Team, 2017). A PCA was built using the data of the 19 bioclimatic variables within the environmental space, which was defined based on the species distribution ranges (Fig. 1) as follows: *E. balsamifera* from W 9.01° to W 18.15° and N 25.9° to N 31.55°; *E. sepium* from W 17° to E 17.5° and N 7.75° to N 26.9°; and *E. adenensis* from E 37.06° to E 54.8° and N 9.7° to N 19.08°.

The environmental space delimited above was divided into a grid of 100 × 100 cells, as in Broennimann et al. (2012). To correct for sampling bias and environmental availability and to ensure that the results were independent of the grid resolution, we measured the frequency of species occurrences for each combination of environmental conditions in each grid cell of the environmental space using a kernel smoother function applying the *ecospat.grid.clim.dyn* function of the *ecospat* package (Di Cola et al., 2017). We calculated the differences in occurrence densities between pairs of the three taxa (*ecospat.niche.overlap* function) and used Schöner's D metric to calculate the degree of overlap (from no overlap to complete overlap, i.e., from 0 to 1).

To assess the similarity of the three niches (using pairwise comparisons), we performed a test of niche equivalency (Warren et al., 2008; Broennimann et al., 2012) with 100 random permutations of occurrences between the two species in the comparison (*ecospat.niche.equivalency.test* function). To evaluate whether two niches were more or less similar than expected by chance, we performed a similarity test through 100 random shifts of these niches within the available conditions in each of the species environmental space (*ecospat.niche.similarity.test* function). In both analyses, we tested for niche conservation and niche divergence (i.e., alternative “greater” and “lower”). Finally, we determined

the niche expansion, stability, and niche unfilling (Petitpierre et al., 2012) using the *ecospat.niche.dyn.index* function.

This niche comparison approach is commonly used in the field of biological invasions to compare the native and the exotic niches of the same species (Guisan et al., 2014). In our case, we borrowed this procedure to compare the native niches of two different species (e.g., species A and B), and adapted the concepts applied in that field to our case as follows (species A represents the “exotic range” and species B the “native range”): *niche stability* is the proportion of the niche of species A overlapping with the niche of species B, *niche unfilling* is the proportion of niche B non-overlapping with niche A, and finally, *niche expansion* is the proportion of niche A nonoverlapping with niche B.

2.4 Leaf morphometrics

To provide a quantitative assessment of the relevance of leaf morphology, a character traditionally used in the taxonomy of *Euphorbia balsamifera* s.l., the following measurements were performed selecting three leaves per specimen: leaf maximum length, leaf maximum width, length from the leaf base to the point of leaf maximum width, and mucron length. We selected mature leaves from young branches below the fourth internode (from the apex) whenever possible. For each measurement, the average of the three leaves measured was taken to represent a given specimen. We measured 29 specimens of subsp. *balsamifera*, 29 of subsp. *sepium*, and 22 of subsp. *adenensis* (80 specimens in total; see Table S2), aiming to cover the geographic range and morphological variability of the three taxa. The type specimen of *E. sepium* was included in the analyses; other types were visually inspected but not included in the analyses due to the poor quality of specimens. Finding suitable specimens of subsp. *adenensis* was particularly challenging because many specimens were poorly preserved (i.e., leafless specimens or just with a few apical leaves remaining), and also because this taxon is not well represented in herbaria. Differences in leaf size and shape among the three taxa were visualized using boxplots and principal component analysis (PCA). Statistical analyses on each variable (leaf measures) were performed using univariate (analysis of variance [ANOVA]) and multiple variance (MANOVA) analyses. All analyses were performed in the R statistical environment v. 3.6 (R Core Team, 2015).

3 Results

3.1 Phylogenomics and lineage ages

The phylogenetic tree, based on 296 nuclear exon loci and a relatively dense population sampling (110 individuals) covering the vast geographic range of *Euphorbia balsamifera* s.l. (Villaverde et al., 2018), recovered three highly supported clades (Fig. 2) recognized here at the species level as *E. adenensis*, *E. balsamifera* s.s., and *E. sepium* (see Taxonomic treatment below). *Euphorbia sepium* was recovered sister to the clade of *E. adenensis*-*E. balsamifera*. Age estimates differ among the three lineages, with *E. sepium* diverging at approximately 11 Ma (stem age) in the late Miocene and with a crown age of ~7 Ma. Divergence between *E. adenensis* and

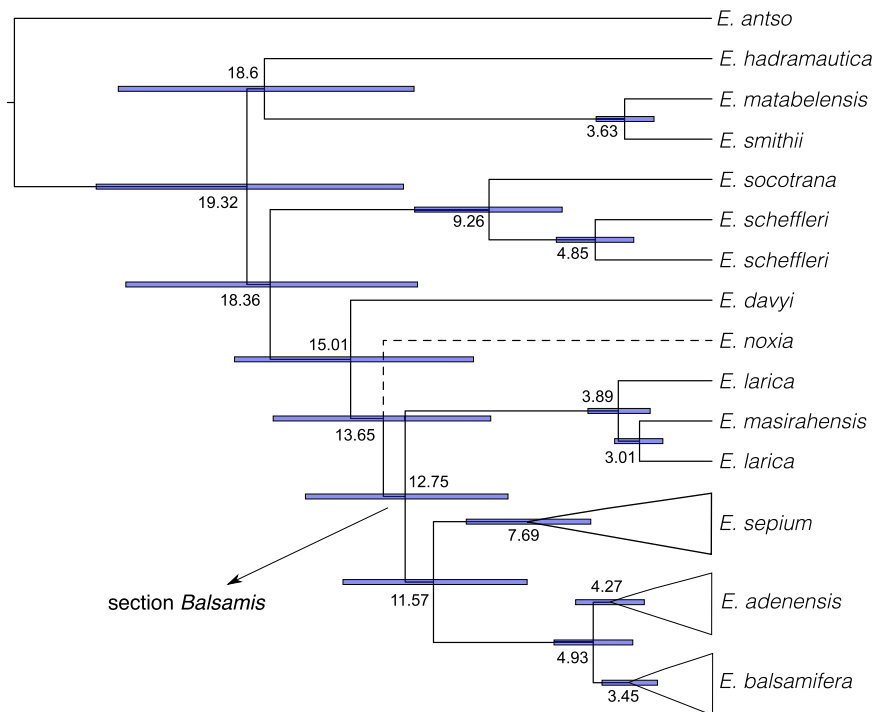


Fig. 2. Maximum clade credibility (MCC) tree of *Euphorbia* subgenus *Athymalus* based on 296 exons of the nuclear genome (Villaverde et al., 2018). The arrow indicates section *Balsamis* which includes the three well-supported clades corresponding to *E. adenensis* (19 accessions), *E. balsamifera* (81 accessions), and *E. sepium* (10 accessions). Bayesian estimates of divergence times are given at each node above branches; clade support (posterior probabilities, PP) is 1 for all nodes in the tree except for the node leading to *E. noxia* (dashed line, 0.82 PP). Node bars represent the 95% highest posterior density intervals of the divergence time estimates using a strict clock analysis. Figure modified from Villaverde et al. (2018, fig. 4A).

E. balsamifera dates back to the early Pliocene (~5 Ma), with crown ages of ~4 and ~3 Ma, respectively (Fig. 2).

3.2 Updating species geographic ranges

The distribution ranges of the studied species do not overlap (Fig. 1): *E. balsamifera* s.s. occurs in Macaronesia (all islands in the Canary Archipelago) and in several sparse and isolated patches along the SW coast of Morocco and N coast of Western Sahara, reaching its southernmost distribution around 26 latitude N, 30 km south of Boujdour (Western Sahara). The more continental of the three species, *E. sepium*, occurs in western sub-Saharan Africa and the western Sahel, with collection records in Western Sahara, Mauritania, Senegal, Mali, Burkina Faso, Ghana, Benin, Togo, Nigeria, and W Niger. The most northwestern known populations of *E. sepium* in northern Western Sahara are separated by ca. 190 km from the *E. balsamifera* s.s. localities along the African Atlantic coast. Finally, the geographic range of *E. adenensis*, separated from the easternmost localities of *E. sepium* (W Niger) by more than 2000 km, spans from the coast of E Africa to the southern Arabian Peninsula, with collection records from the NE coast of Sudan (two records), N Somalia, SW corner of Saudi Arabia, Yemen, and Oman, and the island of Abd al Kuri in the Socotra Archipelago. All the herbarium specimens used to update the geographic distribution of the

three species (Fig. 1) are listed in the taxonomic treatment below and in Table S1.

3.3 Climatic niche assessment

Our results indicate a low overlapping of climatic niches among the three species (Schöner's $D < 0.30$; Fig. 3; Table 1). The lowest overlapping niche values are among *E. sepium* and the other two species ($D < 0.10$; Table 1). Also, the results of the equivalency test comparing *E. sepium* and *E. balsamifera* niches showed that the overlapping is significantly smaller than the null distribution (Table 2). The similarity test did not indicate any difference from a random model between *E. sepium* and each of the other two species (Table 2).

Niche overlap between *Euphorbia balsamifera* and *E. adenensis* is also low (Schöner's $D = 0.27$; Table 1), while the equivalency test indicated that these species do not share the same climatic conditions (Table 2). Nevertheless, the similarity test indicated that there are significant similarities between the two niches (P -values < 0.05 ; Table 2). Besides, *E. balsamifera* and *E. sepium* niches have almost no overlap ($D = 0.004$; Table 1) and are less close to each other than expected in a random model (equivalency test P -value = 0.009; Table 2). The *E. adenensis* niche is more similar than expected in a random model to the *E. balsamifera* niche (P -value = 0.019; Table 2). In sum, the similarity and equivalency tests indicated that the niches of *E. adenensis* and *E. balsamifera* are not significantly

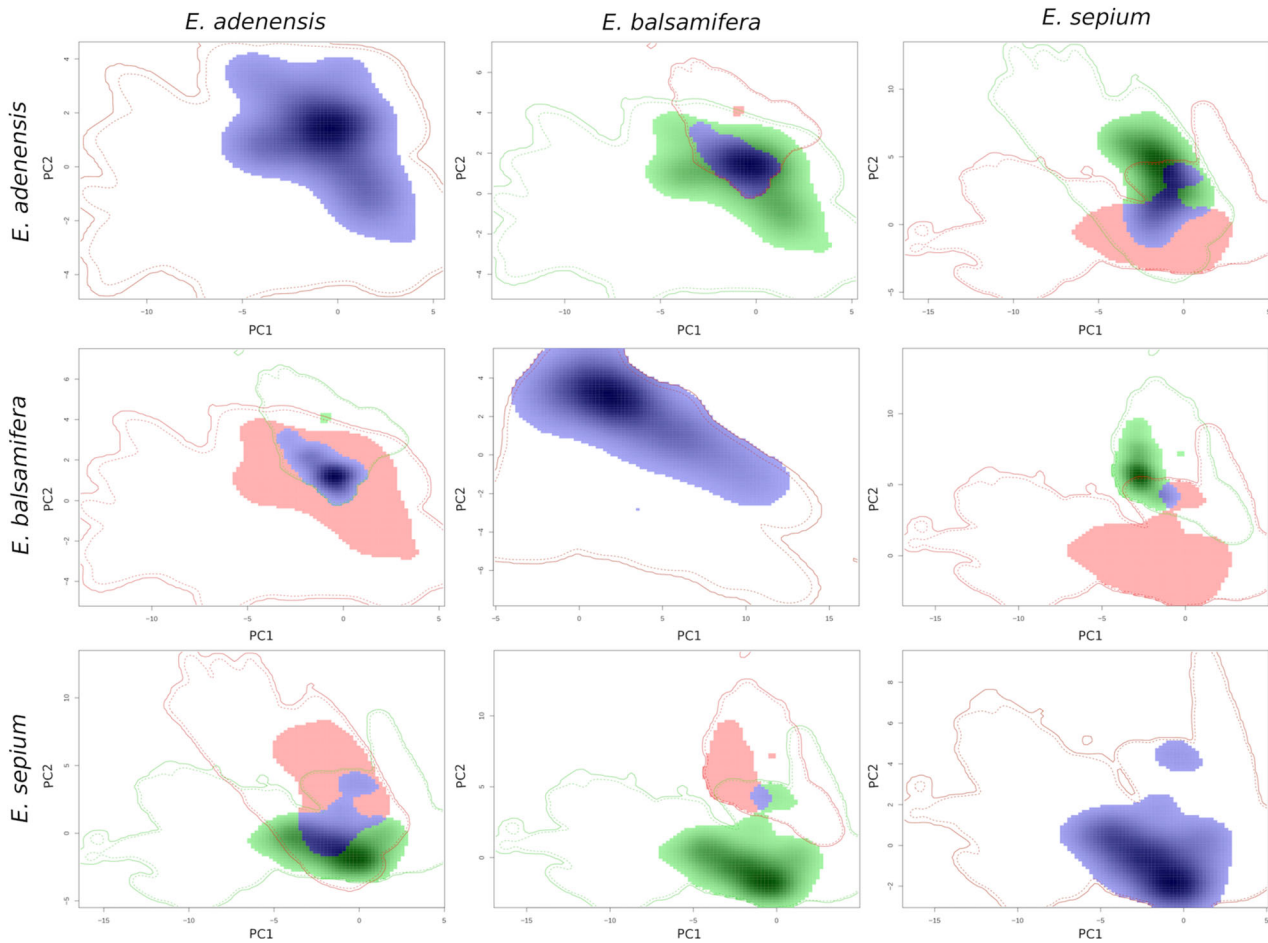


Fig. 3. Comparison of climatic niches among the three species of *Euphorbia* recognized here: *E. adenensis*, *E. balsamifera*, and *E. sepium*. Cells along the diagonal from the upper left to bottom right show the niche occupied by each species, and the other cells represent composed niche overlap of species pairs. Colors indicate niche expansion (green), niche stability (blue), and niche unfilling (red). Solid lines enclose all available environments for each range; dashed lines represent the 90th percentile of the background environment for the paired species ranges.

equivalent, neither significantly similar nor equivalent to the *E. sepium* niche.

The values of niche expansion, niche unfilling and niche stability are summarized in Table 3 and visualized in Fig. 3. The niches of *E. balsamifera* and *E. adenensis* show the highest values of niche stability or overlap ($\sigma = 0.88$ and 0.99 ; Fig. 3; Table 3), and they also exhibit the lowest values of niche expansion and unfilling (0 and 0.12 ; Fig. 3; Table 3). The niche stability (overlap) between *E. sepium* and *E. adenensis* is twice as high ($\sigma = 0.74$) as

the overlap with *E. balsamifera* ($\sigma = 0.36$) (Fig. 3; Table 3). Finally, the highest values of niche expansion ($\epsilon = 0.63$) were found between *E. sepium* and *E. balsamifera*, while the highest niche unfilling value ($\nu = 0.64$) was reported in comparisons between *E. balsamifera* and *E. sepium* (Fig. 3; Table 3).

In the PCA analysis of all climatic variables associated with occurrences of the three putative species (Fig. 4), *Euphorbia sepium* appears segregated from the other two species along the first axis (PC1), which was correlated with temperature-related bioclimatic variables, such as annual mean temperature (bio1) and mean temperature of coldest quarter (bio11; Fig. 4; Table S2), indicating that *E. sepium* is more tolerant to higher temperatures than *E. balsamifera* and *E. adenensis*. In contrast, *E. sepium* shows a high variation (variance) along the second axis, PC2, which is mainly associated with precipitation variables (annual precipitation, bio12) and temperature seasonality (bio4). *Euphorbia adenensis* and *E. balsamifera* shows a lesser degree of segregation (i.e., they exhibit similar climatic tolerances), especially along PC2. The two species, however, appear slightly segregated along PC1, with *E. adenensis* showing tolerance to higher temperatures than in *E. balsamifera* (Fig. 4).

Table 1 Values of niche overlap (Schöner's D) obtained for each species pair-wise comparison of the studied *Euphorbia* taxa

	<i>E. adenensis</i>	<i>E. balsamifera</i>	<i>E. sepium</i>
<i>E. adenensis</i>	1	0.271	0.071
<i>E. balsamifera</i>	0.271	1	0.004
<i>E. sepium</i>	0.071	0.004	1

Schöner's D varies between 0 (no niche overlap) and 1 (complete niche overlap).

Table 2 Results of the niche equivalency and similarity tests shown as *P*-values per each species pairwise comparison

	Equivalency					
	<i>E. adenensis</i>		<i>E. balsamifera</i>		<i>E. sepium</i>	
	Greater	Lower	Greater	Lower	Greater	Lower
<i>E. adenensis</i>	–	–	0.386	0.624	0.148	0.841
<i>E. balsamifera</i>	0.366	0.554	–	–	1	0.009
<i>E. sepium</i>	0.139	0.832	1	0.009	–	–

	Similarity					
	<i>E. adenensis</i>		<i>E. balsamifera</i>		<i>E. sepium</i>	
	Greater	Lower	Greater	Lower	Greater	Lower
<i>E. adenensis</i>	–	–	0.019	0.99	0.445	0.624
<i>E. balsamifera</i>	0.029	1	–	–	0.544	0.653
<i>E. sepium</i>	0.624	0.346	0.723	0.366	–	–

The null hypothesis is that two given niches are not more (“greater”) or less (“lower”) equivalent or similar than expected by chance (random niches). Significant *P*-values (<0.05) are in bold. *E.*, *Euphorbia*.

Table 3 Values of niche expansion (ϵ), niche stability (σ), and niche unfilling (ν) for the species’ niche pairwise comparisons (see Fig. 4)

	<i>E. adenensis</i>			<i>E. balsamifera</i>			<i>E. sepium</i>		
	ϵ	σ	ν	ϵ	σ	ν	ϵ	σ	ν
<i>E. adenensis</i>	–	–	–	0.001	0.999	0.121	0.552	0.447	0.264
<i>E. balsamifera</i>	0.121	0.879	0.001	–	–	–	0.465	0.535	0.637
<i>E. sepium</i>	0.265	0.735	0.552	0.637	0.363	0.465	–	–	–

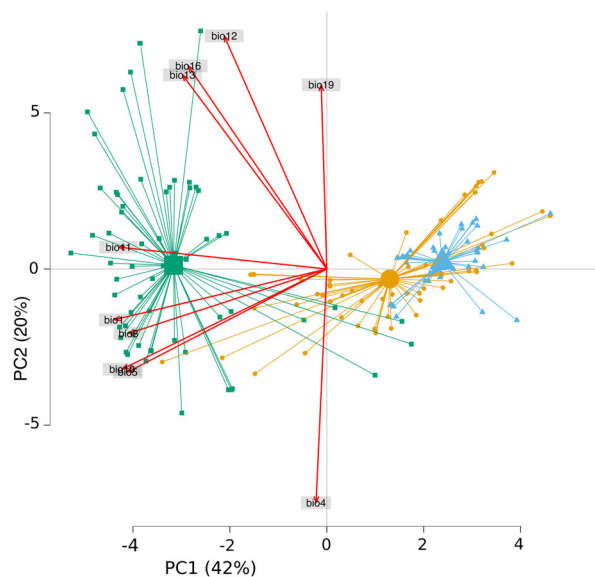


Fig. 4. Principal component analysis (PCA) scatterplot, including within-group centroid, of the first two principal components based on 19 bioclimatic variables associated with occurrence points of the three proposed *Euphorbia* species: orange circle (*E. adenensis*), blue triangle (*E. balsamifera*), green square (*E. sepium*).

3.4 Leaf morphometrics

Leaf length, mucron, and leaf shape (assessed as the ratio between maximum length and maximum width) differ significantly between the three taxa, but *Euphorbia sepium* shows the largest difference for all the measured variables (Figs. 5A, 5C–5E; Table 4). Only maximum leaf width is not significantly different (Table 4), with the box-plots of the three species showing a broad overlap for this variable (Fig. 5B).

In the PCA, the first two components (PC1, PC2) account for approximately 62% and 27% of the observed variance, respectively. Characters contributing significantly to the first component axis PC1 were leaf maximum length, leaf length from base to widest part, and mucron length, whereas leaf width is the variable contributing the most (94%) to the second axis PC2. The scatter plot shows a clear separation between *E. adenensis* and *E. sepium* along PC1, but *E. balsamifera* fills the gap between the two species and partially overlaps with both of them, especially with *E. sepium*. PC2 shows significant overlapping among the three species (Fig. 5F).

4 Discussion

Phylogenetic trees are important when addressing biological questions in an evolutionary context, but they are also

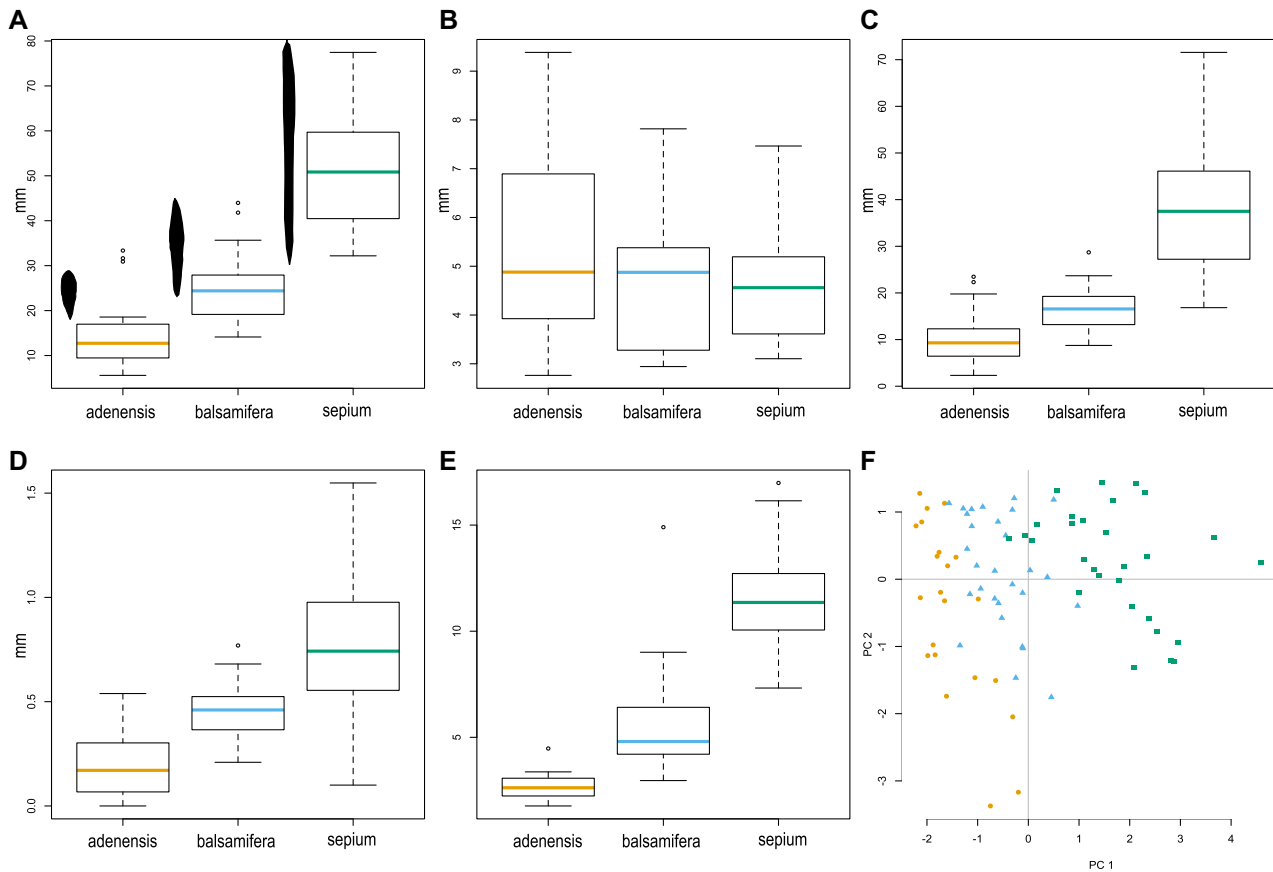


Fig. 5. Box-whisker plots and principal component analysis (PCA) of leaf size measurements of *Euphorbia* specimens ($n = 80$) from *E. adenensis* (yellow), *E. balsamifera* (blue), and *E. sepium* (green). Each box represents the interquartile range, which contains 50% of the values and the median (horizontal line across the box); the whiskers are the lines that extend from the box to the highest and lowest values, excluding outliers (o). **A**, Leaf length, including a silhouette of the average leaf shape and size for each species. **B**, Leaf maximum width. **C**, Length from leaf base to the point of maximum width. **D**, Mucron length. **E**, Ratio between leaf length (**A**) and leaf maximum width (**B**). **F**, Scatter plot of the first two components of the PCA based on the five leaf measurements. Row data are provided in Table S3.

essential to refine taxonomic knowledge. We used the most robust phylogenetic tree of *Euphorbia* section *Balsamis* built to date (Villaverde et al., 2018), and complemented it with additional sources of evidence to support the reestablishment of three lineages at the rank of species. The newly reinstated taxa (*E. adenensis*, *E. balsamifera*, and *E. sepium*) were previously treated under the former *E. balsamifera* s.l., either as subspecies or under synonymy (see taxonomic treatment).

Our approach is consistent with studies arguing against establishing species limits based solely on genomic data (e.g., Solís-Lemus et al., 2015; Sukumaran & Knowles, 2017). Similar integrative studies have been successful resolving the taxonomy of problematic groups at the species level (e.g., Denham et al., 2019; Li et al., 2019; Perkins 2019; Yang et al., 2019), but they are still scarce in plants, and even more those integrating phylogenomics, divergence time estimations, and phylogeography with morphology and climate niche analysis (e.g., Frajman et al., 2019). Generating large amounts of genomic data continues to be expensive, and the steps from taxon sampling to tree inference are considerably longer and bioinformatically more demanding than just generating and analyzing a small set of genes. In addition, placing the resulting

phylogeny in a morphological and ecological context using quantitative techniques is also time-consuming and requires expert knowledge on the focal group (Giribet, 2015).

Based on a previous work (Villaverde et al., 2018), we recovered three distinct clades within *Euphorbia balsamifera* s.l. Ten individuals of *Euphorbia sepium* were clustered with strong support as a monophyletic lineage sister to the clade formed by *E. adenensis* and *E. balsamifera*. This nuclear topology (Fig. 2) was also fully congruent with the chloroplast phylogeny (not shown) obtained by Villaverde et al. (2018). Each lineage was represented by 10 or more individuals spread across the entire geographic range, which is desirable when addressing species relationships at the species level where incomplete lineage sorting may have an impact on phylogenetic resolution (Naciri & Linder, 2015).

Estimated divergence times for the origin of these three taxa (5–11 Ma; Fig. 2) provide further evidence for considering these lineages at the rank of species. It has been suggested that clade age should not be used as a single criterion (Lücking, 2019) for classification at high taxonomic ranks (e.g., families, genera), but it can be considered as another element within an integrative approach at the



Fig. 6. Representative field images of the three species. *Euphorbia adenensis*: **A**, Plant growing in stony desert, Oman. **B**, Male cyathium. **C**, Female cyathium. **D**, Habitat, Oman. **E**, Young female cyathium. **F**, Mature capsule. *Euphorbia balsamifera*: **G**, Population on volcanic rocks, El Hierro Island (Canaries). **H**, Male cyathium. **I**, Female cyathium. **J**, Plant in sandy substrate, coast of NW Africa. **K**, Developing ovary. **L**, Mature capsule. *Euphorbia sepium*: **M**, Population in a desert wadi, Western Sahara. **N**, Male cyathium. **O**, Female cyathium. **P**, Live fence, NE Senegal. **Q**, Detail of the long narrow leaves. **R**, Almost mature capsule with persistent styles. Photos: Flickr public domain (A, B, C), C. Dolbeare (P), C. Lemmel (M, N, Q), D. Marquina Reyes (K), J. Mesa (L), J.J. Morawetz (D, E, F), J.P. Peltier, www.teline.fr (H, I, J), R. Riina (O, R), T. Villaverde (G).

Table 4 Univariate (ANOVA) and multivariate (MANOVA) analysis of variance conducted on leaf size measurements of *Euphorbia* specimens ($n = 80$) from three species (*E. adenensis*, *E. balsamifera*, and *E. sepium*)

Leaf measurement	F-test	Significance
Maximum length (A)	106.20	S
Maximum width (B)	2.322	NS
Length from base to maximum width (C)	70.81	S
Mucron length (D)	35.42	S
MANOVA (A–D)	15.207	S
Ratio A/B (F)	133.9	S

Letters A–D correspond to the box plots in Fig. 5. ANOVA, analysis of variance; NS, not significant; S, significant ($P < 0.001$).

lowest ranks (e.g., species). However, divergence times can vary greatly across large plant genera like *Euphorbia* (Horn et al., 2014), going from recent radiations (i.e., species-rich and relatively young groups) to older clades with various degrees of species richness. For example, Frajman & Schönswetter (2017) dated time divergences within a small clade (6 spp.) of eastern Mediterranean *Euphorbia* (*E. sect. Pithyusa*) to the mid-late Pleistocene (<1.5 Mya), which contrasts with the much older age of the split between *E. balsamifera* and *E. adenensis* (~5 Ma; Fig. 2).

The age of divergence between the disjunct *E. balsamifera* and *E. adenensis*, on each side of Africa, agrees well with results from Pokorny et al. (2015; ~3.8 Ma) and coincides with a period of global climate warming, the mid-Pliocene Warm Period (Zachos et al., 2008), and increased aridification in Africa (Senut et al., 2009). Clade age and geographic disjunction are in alignment with the climatic vicariance/extinction hypothesis (Mairal et al., 2017), which posits that species' failure to adapt to the new more xeric environments, in combination with niche conservatism, contributed to the geographic isolation of populations in the eastern and western margins of Africa and led to the generation of the allopatric Rand Flora lineages.

The much older split of *E. sepium* (~11 Ma) predates the formation of the Sahara Desert (~8 Ma; Senut et al., 2009). This taxon exhibits a much more widespread and inland distribution, as well as a wider climatic niche than either *E. adenensis* or *E. balsamifera* (Fig. 3). Our study places the divergence of *E. sepium* in the late Miocene (Tortonian), a period characterized by lower temperatures and wetter environments (Mairal et al., 2017); it is, thus, possible that ecological vicariance—the appearance of a hostile environment—is involved also in the origin of this clade.

The climatic niche analysis showed that the three species have different climatic niches, especially *E. sepium*. This species' niche barely overlaps with any of the other two species, and equivalency tests showed that the bioclimatic conditions where this species occurs are more different than expected by chance when compared with *E. balsamifera* or *E. adenensis*. However, this difference is greater between *E. sepium* and *E. balsamifera*, because their expansion and unfilling values are higher than those of the other two species pairwise comparisons (Fig. 3; Table 3). Differences

between *E. balsamifera* and *E. adenensis* niches are not as remarkable, although niche overlap is comparatively low (Schönen'D = 0.271; Table 1) and there is low conservation according to the equivalency test (Table 2). However, similarity among these niches is higher than expected for a random comparison, and the stability value is high (Table 3). The niche equivalency test is considered very conservative (Aguirre-Gutiérrez et al., 2015), and even if there is a part of both taxa that dwell in an equivalent niche, this can result in not rejecting the null distribution when their means are different. However, the similarity between them may be accepted (Glennon et al., 2014).

The allopatric distribution of the three taxa, particularly the large gap between the sister *E. balsamifera* and *E. adenensis*, also supports the reinstatement of the three lineages as separate species. The enormous distance (>2000 km) separating these two species makes gene flow between them unlikely. Even if they are morphologically very similar and perhaps potentially able to hybridize, isolation by distance will continue to increase genetic divergence and decrease the possibility of gene flow over time (Sexton et al., 2014). The much larger distribution area of *Euphorbia sepium* compared with the other two species could be in part the result of human activities due to the common use of this species across the Sahel for live-fencing to protect crops, avoid soil erosion, and keep livestock out of fields (Dolbear, 2016).

We show that morphological data, particularly leaf shape and size (Fig. 4), is useful to distinguish *E. sepium* from the other two species. As expected by their closest phylogenetic relationship, the morphological separation between *E. adenensis* and *E. balsamifera* is not that clear-cut. The most useful characters distinguishing these two taxa are leaf shape and plant stature. The length of the style fusion and the density of capsule indumentum have also been used to distinguish these species, but they are not taxonomically as useful (see Taxonomic Treatment). A palynological survey (Perez & Roca-Salinas, 1977) reported differences in pollen size between the two species, larger grains in *E. balsamifera* (47.3–55 μm) than in *E. adenensis* (34.32–40.92 μm), but slight differences in exine ornamentation. As far as we know, there are no palynological data available for *E. sepium*.

The criterion of reciprocal monophyly, along with the relatively old stem ages exhibited by the three taxa, compared to those in other *Euphorbia* lineages (Horn et al., 2014) and within subgenus *Athymalus* (Villaverde et al., 2018), would be enough to satisfy the unified species concept proposed by De Queiroz (2007), that is, species as separately evolving metapopulation lineages. Nevertheless, we have shown here that there is additional evidence, including differences in leaf shape/size and climatic tolerances, to support the establishment of three species of sweet tabaiba.

The integration of phylogenomic data with evidence from morphology, distribution ranges, divergence times, and climatic niches, allows us to settle the long-standing confusing taxonomy around the former *Euphorbia balsamifera* s.l. Our results are consistent with the recognition of three taxa at the species level: *E. adenensis*, *E. balsamifera*, and *E. sepium*. The reinstatement of the widespread *E. sepium* from synonymy uncovers a highly distinct species, whose divergence predates the formation of the Sahara Desert as well as the split between *E. adenensis* and *E. balsamifera*.

5 Taxonomic Treatment

5.1 Identification key to the studied species of *Euphorbia*

- 1a. Compact dendroid shrubs, adult plants usually <1 m tall. Leaves obovate-oblong. Styles fused along the lower half of their length. Capsules glabrous, rarely glabrescent. Distributed in eastern Africa (Somalia, east coast of Sudan) and the southern Arabian Peninsula (Yemen, Oman) and Abd-al-Kuri island (Socotra)..... *E. adenensis*
- 1b. Open dendroid shrubs, adult plants usually >1 m tall. Leaves lanceolate or linear. Styles fused along the lower quarter or less of their length. Capsules pubescent. Distributed in western Africa and the Canary Islands..... 2
- 2a. **Stem leaves lanceolate to linear-lanceolate**, 14.1–44.9(50) × 2.9–10(12) mm; mucron 0.3–0.6 mm long, when present. **Ovary and capsule slightly pubescent, sometimes glabrescent**. Widespread in the Canary Islands with a few sparse populations along the coast of southern Morocco and northern Western Sahara..... *E. balsamifera*
- 2b. **Stem leaves linear**, (32.2)40.5–77.5(100) × 3.1–7.4 mm; mucron (0.1)1–1.5(2) mm long. **Ovary and capsule densely pubescent, never glabrous**. Occurring in southern areas of the Sahara desert and across Western Sahel..... *E. sepium*

5.2 *Euphorbia adenensis* Deflers, Bull. Soc. Bot. France 34: 67. 1887. (Figs. 6A–6F)

Euphorbia balsamifera subsp. *adenensis* (Deflers) P.R.O. Bally, Candollea 29: 390. 1974. – *Tithymalus adenensis* (Deflers) J. Sojak, Cas. Nar. Muz. 140: 170, 1972. Syntypes: Yemen, Aden, Scham-Scham near Semaphore, Goldmore Valley, 7 May 1886, Deflers s.n. (lectotype MPU014213!, designated here; isotype MPU014212!); Yemen, presqu'île d'Aden, vallée de Kiosaf, 8 Mar 1885, Deflers s.n. (MPU014216!).

Compact dendroid shrubs are 0.6–0.9(1.2) m tall, usually dioecious, much branched; upper branches are (0.8)2–3(6) cm long, succulent. Rhytidome whitish-cream, pearly white. Stem leaves are 5.6–33.4 × 2.8–9.4 mm, obovate-oblong; apex obtuse to rounded, sometimes minutely mucronate, mucron 0–0.5 mm long; subcyathial leaves are similar in length but wider than cauline leaves, obovate-spatulate. Cyathia solitary, terminal; involucre broadly cupuliform, 2.6–3.4 × 5.4–7.8 mm; glands 5, green-yellowish, transversally oblong, 0.23–0.42 × 0.14–0.22 mm; ovary smooth, glabrous, rarely glabrescent; styles 1.8–2.5 mm, fused half of their length, 0.9–1.2 mm from the base, tips bifid, stigmatic lobes 0.2–0.4 mm long. Capsule (5)6.5–8.6(10) × (6) 7.6–9(11) mm, globose, rugulose, glabrous, rarely glabrescent. Seeds ecarunculate, 2.9–3.8 × 2.5–3 × 2.6–3.2 mm, ovoid-subglobose to globose; hilar zone with an angle of 25–30°.

Distribution and habitat: *Euphorbia adenensis* occurs in eastern Africa (Somalia, east coast of Sudan), the southern Arabian Peninsula (Yemen, Oman), and Abd-al-Kuri island (Socotra), between 150 and 1900 m elevation (Fig. 1).

Common names: “mark, scar of blow” (Soqotri) (Miller & Morris, 2004).

Specimens examined (see Table S1 for additional information): **OMAN:** J.T. Bent 197 (K); P. Hein & N. Kilian s.n. (B100430939); R.M. Lawton 1892 (K); J.R. Maconochie 2877 (K); J.R. Maconochie 3011 (K); J.R. Maconochie 3545 (K); A.G. Miller 2201 (E00445559, K); A.G. Miller 2350 (E0445557, K); A.G. Miller 7513 (E00445555, K); A.G. Miller 7514 (E00445562, K); J.J. Morawetz 325 (K); J.J. Morawetz

346 (MICH); A. Radcliffe-Smith 5173 (K). **SAUDI ARABIA:** I.S. Collenette 1428 (K); I.S. Collenette 1615 (E00221064); A.K. Nasher H42 (E00221063). **SOMALIA:** P.R.O. Bally 10360 (G, K 5193); P.R.O. Bally 10858 (G, K); P.R.O. Bally 11007 (G, K); P.R.O. Bally & R. Melville 15951 (K); R. Bavazzano & J. Lavranos s.n. (FT); J.J. Beckett 773 (K); S.B. Boaler 86 (K); S. Carter 940 (K); C.N. Collenette 74 (K); J.B. Gillett & R.W. Watson 23477 (K); P.E. Glover & Gilliland 555 (BM); O.J. Hansen & H. Heemstra 6216 (K); C.F. Hemming 1605 (K); C.F. Hemming 1973 (FT, K); C.F. Hemming & R.M. Watson 3039 (K); J. Lavranos, S. Carter & al. 24766 (K); E. Peck E266 (G, K); M. Thulin 4242 (K); M. Thulin & M.A. Warfa 5875 (UPS); M. Thulin & M.A. Warfa 6097 (UPS). **SUDAN:** S. Carter 1881 (K); Sahni & Kaamil 699 (K). **YEMEN:** S. Birdwood 104 (K); E. Bisset 218 (K); L. Boulos & A.M. Rowashed 17088 (E00445574, K); J.S. Collenette 8955 (K, 60195); Deflers s.n. (MPU014212, MPU014213, MPU014216); K.J. Gordon 592A (E00445561); L. Guarino & L. Balaidi H68 (E00445563); P. Hein 314 (B100430940); P. Hein 3560 (B1004330941); P. Hein 6331 (B100430938); P. Hein 6709 (B100430948); P. Hein 6780 (B100430945); P. Hein 6880 (B100430947); P. Hein 7816 (B100430946); P. Hein 4881a (W20160006061); C.F. Hemming 523 (K); K.J.V. A25 (K); K.J.V. A30 (K); N. Kilian 4421 (B100451739); N. Kilian 4538 (B100430943); N. Kilian 5097 (B100430942); N. Kilian 6350 (B100430949); N. Kilian 6394 (B10430944); N. Kilian s.n. (B100430941); J.J. Lavranos 15714 (E00445558); J.J. Lavranos 16012 (E00445556); A.G. Miller 3158 (E00445553, K); A.G. Miller. M8073 (E00445564, K); J. Molero s.n. (BCN44902); J. Molero s.n. (BCN44901); J. Molero s.n. (BCN44900); J. Molero s.n. (BCN44899); Ogilvie-Grant & Forbes Expedition 75 (E00239518); Ogilvie-Grant & Forbes Expedition 89 (E00239517, K); A. Radcliffe-Smith & S.J. Henchie 4770 (K); N. Sanadiki 41 (K); N. Sanadiki s.n. (E); N. Sanadiki s.n. (E00445560); G. Schweinfurth 132 (G, K); A.R. Smith & J. Lavranos 52 (K); A.R. Smith & J. Lavranos 666 (K); M. Thulin, B.-A., Beier & M.A. Hussein 9585 (UPS); Wakefield Expedition 3 (K); J. Waring 121 (K); D. Wood Y1115 (E00445554).

5.3 *Euphorbia balsamifera* Ait., Hort. Kew. 2: 137. 1789. (Figs. 6G–6L)

Tithymalus balsamifer (Aiton) Haw., Syn. Pl. Succ. 140. 1812. Type: Canary Islands, Tenerife, 1778, F. Masson s.n. (holotype BM000928081!). = *Euphorbia capazii* Caball., Trab. Mus. Nac. Ci. Nat., Ser. Bot. No. 30, 25. 1935. Type: Morocco. Ifni, Cabo Non, 12 Jul 1934, A. Caballero s.n. (lectotype MA-01–00074670!, designated here).

Open dendroid shrubs are (0.2)0.8–1.5(4) m tall, usually dioecious, much branched, erect, sometimes decumbent to prostrate in harsher environments; upper branches are 2–10(15) cm long, succulent. Rhytidome grayish, yellowish-ochraceous. Stem leaves are 14.1–44.9(50) × 2.9–10(12) mm, lanceolate to linear-lanceolate; apex mucronate to apiculate, mucron 0.3–0.6 mm long. Cyathia solitary, terminal; involucre broadly cupuliform, 2.5–3.5 × 5.2–8 mm; glands 5, green-yellowish or orange, transversally oblong, 0.3–0.5 × 0.1–0.3 mm; ovary smooth, slightly pubescent; styles (1.6) 1.9–2.3(2.6) mm, fused (0.2)0.3–0.5(0.7) mm from the base, tips bifid, stigmatic lobes 0.3–0.5 mm long. Capsule (6)

7.5–9(12.5) × (7.4)8.5–11(13.8) mm, smooth, globose, punctuated or minutely rugulose, slightly pubescent. Seeds ecarunculate, 2.9–4.0 × 2.0–3.25 × 2.0–3.5 mm, ovoid-subglobose; hilar zone with an angle of 30–45°.

Distribution and habitat: *Euphorbia balsamifera* is common and usually forms dense populations along the dry coastal areas of all Canary islands, and less common and forming scattered populations along the coast of south Morocco and north Western Sahara, between sea level and 500 m (Marrero et al., 1999; Fig. 1; Table S1).

Common names: “tabaiba dulce”, sweet spurge, balsam spurge (Canary Islands) (Marrero et al., 1999); “salane”, “afdir” (Morocco); “Ifennan”, “azdira” (Western Sahara).

Specimens examined (see Table S1 for additional information): **MOROCCO:** J. Aldasoro, J. Calleja & J. Molero s.n. (BCN126715, BCN126716); A. Caballero s.n. (MPU); J. Fernández Casas & J. Molero 13706 (G00403653); Font-Quer s.n. (BCN); J. Gattefossé s.n. (RAB); J. Gattefossé s.n. (RAB); J. Lepymny, Rungi & Ch. Sauvage 1712 (RAB); R. Maire s.n. (MPU, RAB); R. Maire s.n. (MPU); R. Maire s.n. (MPU); R. Maire s.n. (MPU); Y. Ollivier 39 (MPU); Y. Ollivier s.n. (MPU); Y. Ollivier s.n. (RAB); D. Podlech 40516 (GM, G); D. Podlech 48600 (GM, G); R. Riina & L. Pokorny 1962 (MA); R. Riina & L. Pokorny 1963 (MA); Ch. Sauvage & Essiaf 16132 (RAB); F. Schuhwerk 90/300 (M); Staffford Allen & Son s.n. (K). **SPAIN:** **El Hierro:** J. Molero & A. Rovira s.n. (BCN45956, BCN45957); C.J. Pitard s.n. (P); M. Rincón-Barrado & T. Villaverde 16MRB18 (MA); M. Rincón-Barrado & T. Villaverde 19MRB18 (MA). **Fuerteventura.** I. Álvarez, J. Calvo & B. Ríos JC2074 (MA-768477-1); X. Espadaler s.n. (BCN45989); F. Hekker s.n. (L-0447505); G. Kunkel 11984 (G); M. Rincón-Barrado & T. Villaverde 3MRB18 (MA); M. Rincón-Barrado & T. Villaverde 10MRB18 (MA); M. Rincón-Barrado & T. Villaverde 15MRB18 (MA). **Gran Canaria:** Ch.H. Andreas 6370 (WAG-1800096); E. Asplund s.n. (G, K); J. Bornmüller 2859 (G, P); B. Dorsey 3 (MICH); F.N. Hepper 907 (K); E. Hulten s.n. (S); G. Kunkel 15260 (G); A. Marrero & J. Molero s.n. (BCN45973); A. Marrero, J. Molero & A. Rovira s.n. (BCN129356); Melbold 11749 (M); J. Molero s.n. (BCN45966, BCN45972, BCN45966, BCN45975, BCN45992, BCN45994, BCN45993); J. Molero & A. Rovira s.n. (BCN129349, BCN129350, BCN129351, BCN129357, BCN129358, BCN129364, BCN129366, BCN129367); R.P. Murray s.n. (G, BM); W. Punt s.n. (U-1274933); D.O. Wijnands 623 (WAG-1800093). **Lanzarote:** C. Aedo, L. Medina & A. Quintanar AQ1762 (MA750338); A. Aldridge s.n. (BM); Ch.H. Andreas 6370 (WAG-1800097); Andreas s.n. (M); J. Klackenberg 940401-5 (S); J. Molero & A. Rovira s.n. (BCN126721); M. Rincón-Barrado & T. Villaverde 6MRB18 (MA). **La Gomera:** A. Herrero AH4358.1 (MA); R. Letouzey s.n. (P); L.J.G. van der Maesen 396 (WAG-0158556); J. Molero & A. Rovira s.n. (BCN126717, BCN126718, BCN129352, BCN129353, BCN129355, BCN129362, BCN129363, BCN129365, BCN22672, BCN22673, BCN22674, BCN45960); J. Molero s.n. (BCN45962, BCN45963, BCN45965, BCN45967, BCN45968, BCN45969, BCN45970, BCN45980, BCN45984, BCN45985, BCN45986, BCN45987, BCN45988, BCN45999); R. P. Murray s.n. (K); R. Riina, J. Molero, P.E. Berry 2030 (MA); n.c. n.d. (FR0194912). **La Palma:** J. Molero s.n. (BCN45979); T. Villaverde & E. García-Íñiguez 1TVH17 (MA). **Tenerife:** E. Asplund s.n. (G); E. Bourgeau 472 (BM, G, P, K); E. Bourgeau 1510 (G, P); E. Bourgeau 1810 (G, P, K, BM); BBB. Bresinsky s.n. (M); O.

Burchard 163 (G); A. Carrillo s.n. (BCN39880); B. Cabezudo & S. Talavera n.d. (COFC-95-1, SEV-28116-1); C. Cool 467 (L); T.J. Dinn 196 (K); F. Hekker H254312 (L-0447507); H. Knoche s.n. (MPU, 2 sheets); J.C. Lindeman 7128 (L-3799602); T. Lowe s.n. (BM); N. Lundqvist s.n. (UPS); P. Martínez n.d. (COA); J. Molero s.n. (BCN126720, BCN37836, BCN45959, BCN45961, BCN45962, BCN45967, BCN45968, BCN45984, BCN45985, BCN45986, BCN45991, BCN48883); J. Molero & G. de la Fuente s.n. (BCN45983); J. Molero & A. Rovira s.n. (BCN37827, BCN37828, BCN45970, BCN126719, BCN129354); C.J. Pitard 353 (L, P, WAG); C.J. Pitard 354 (L, P, WAG); C.J. Pitard 6570 (L); R. Riina et al., 2015 (MA); P. Rodrigo n.d. (COA-26937-1); Rolf & Berg n.d. (O-2003110, O-2003111, O-2003109); E.R. Sventenius s.n. (ORT14065, ORT14107, ORT14110); E. Valdés-Bermej 5025EV (MA-250333-1); J.H. Vredereg 324 (WAG-1800092). **WESTERN SAHARA:** Alferez Feliu s.n. (RAB); J. Caujapé & A. Marrero s.n. (LPA, MA); R. Maire 2461 (MPU); A. Marrero & J. Caujapé s.n. (LPA); R. Maire 2536 (MPU); R. Riina & L. Pokorny 1966 (MA); R. Riina & L. Pokorny 1967 (MA); R. Riina & L. Pokorny 1968 (MA).

5.4 *Euphorbia sepium* N.E. Br., Fl. Trop. Afr. 6(1): 551. 1911. (Figs. 6M–6Q)

Euphorbia balsamifera subsp. *sepium* (N.E.Br.) Maire in Bull. Soc. Hist. Nat. Afr. Nord 29(26): 450. 1938. Syntypes: Senegal, Sor Island, Brunner 21 (?); Togo, O. Kersting 739 (B, destroyed); northern Nigeria: Katagum District, J.M. Dalziel 320 (lectotype K000252777!, designated here; isolectotype K000252778!). = *E. rogeri* N.E.Br. Fl. Trop. Afr. [Oliver et al.] 6(1.3): 551. 1911. Syntypes: Senegal, Lampsar and Maka, May 1825, Roger s.n. (lectotype K000252776!, designated here); Senegal, 1906, L. Farnar 54 (K000252775!). – *E. balsamifera* Ait. var. *rogeri* (N.E. Br.) Maire in Bull. Soc. Hist. Nat. Afr. Nord 29(26): 450. 1938. – *E. balsamifera* subsp. *rogeri* (N. E. Br.) Guinea in Anales J. Bot. Madrid 8: 399. 1948.

Open dendroid shrubs are (0.8)1.5–3(5) m tall, usually dioecious, much branched, erect; upper branches are 10–20 cm long, semi-succulent. Rhytidome grayish white to pearly white. Stem leaves are (32.2)40.5–77.5(100) × 3.1–7.4 mm, linear; apex obtuse or rounded, mucronate, mucron (0.1)1–1.5(2) mm long; subcyathial leaves are much shorter and wider than cauline leaves, lanceolate, elliptic or obovate-oblong. Cyathia solitary, terminal; involucre broadly conical, 2.5–3.2 × 4.8–7.6 mm; glands 5, yellowish, transversally oblong, 0.1–0.2 × 0.2–0.4 mm; ovary densely pubescent-sericeous; styles 1.2–1.8 mm, fused 0.2–0.5 mm from the base, tips bifid, stigmatic lobes 0.2–0.4 mm long. Capsule (5.8)6.4–7.2(7.5) × (6.7)7.4–8.2(8.4) mm, globose, smooth or rugulose, densely pubescent. Seeds ecarunculate, 2.7–4.0 × 2.5–3.1 × 2.5–3.2 mm, ovoid-subglobose, rarely ellipsoid or subglobose; hilar zone with an angle of 30–40°.

Distribution and habitat: *Euphorbia sepium* is distributed in wadis along a southern belt between the Sahara desert and the Sahel region, at elevations between sea level and 500 m (Fig. 1; Table S1). The species geographic range has likely been modified by the frequent use of this species for live fencing (Fig. 6P) in the Sahel, expanding its natural range further south into the Sahelian savannas.

Common names: “yaro” (Senegal, Nigeria, Brown, 1911); “waiyaro”, “kagua”, “kaguwa”, “katagum” (Nigeria, Holland, 1922).

Specimens examined (see Table S1 for additional information): **BENIN**: A. Chevalier 23620 (P00570817, P00570818); P. Houngnon s.n. (BENIN); J. Krohmer 1985 (FR0018633); Unknown (FR0022735). **BURKINA FASO**: O. Bognounou 428 (P00570820); R. Martin 282 (FR); B. Toutain 776 (P00570821); B. Toutain 2735 (P00570822). **GHANA**: G.K. Akpabla 541 (K). **MALI**: G. Boudet 6643 (P00570823); A. Chevalier 1315 (P00570825, P00570826); A. Chevalier 1316 (P00570827); A. Chevalier 43094 (P00570829); A. Chevalier 43167 (P00570830); A. Chevalier 43180 (P00570824); A. Chevalier 43181 (P00570831); A. Chevalier 43182 (P00570832); J.T. Davey 468 (K); S. de Ganay 148 (P00570834); C. Geerling 2671 (BR16386815, WAG1800090, WAG1800091); F.N. Hepper 3733 (K, P00570828); A. Leclercq 42422 (P00570835); T. Monod 563 (P00570836); M. Wailly 4673 (K, P00570840); M. Wailly 4786 (P00570841); M. Wailly 5148 (P00570842); J. Molero & al. (BCN43587, BCN43588, BCN45977); J. Raynal & A. Raynal 5506 (P00570838). **MAURITANIA**: I. Arvidsson 30 (K); Biologie des Acridiens 23A (P00570814); C. Chatelain CC5259 (G); C. Chatelain CC5260 (G); C. Chatelain CC5261 (G); M. Chudeau s.n. (P00570811, P00570812, P00570813); M. Cludeau (P00570810); J. Codrington 4 (K); Schmitt 28554 (P00570816); A. Marrero s.n. (LPA6573, LPA6574, LPA6723, LPA6724); A. Marrero & M. González Martín s.n. (LPA6526, LPA6527); T. Monod 3969 (P00570815, P00570837). **NIGER**: G. Boudet 5335 (P00570843); A. Chevalier 43622 (P00570844); A. Chevalier 43693 (P00570845, WAG1800088); Coen Foundation 13 (K); Coen Foundation 31 (K); P. de Fabrègues 4358 (P05482482); Gaillard-Mission Tilho s.n. (P00570847, P00570848); D.P.M. Guile s.n. (K); J. B. Hall 18083 (K); J. Koechlin 6554 (P00570849); J. Lowe 3700 (K); K. J. Virgo 12 (K). **NIGERIA**: J.M. Dalziel 320 (K000252777, K000252778); J.M. Dalziel 528 (K); N. Etkin 3 (MO139898); R.W.J. Keay s.n. (K); Sampson 8 (K). **SENEGAL**: J. Audru 2304 (P00570850); J. Audru 3136 (P00570851); E. Bassene s.n. (BCN45976); Brunner 21 (?); O. Caille s.n. (P00570852); O. Caille 25279 (P00570854); A. Chevalier 14610 (P00570853); A. Chevalier 25701 (P00570856); A. Chevalier 25707bis (P00570857); A. Chevalier 34052 (P00570858); L. Farmar 54 (K000252775); F.R. Leprieur s.n. (G); G. Paroisse 43 (P00570859); G.S. Perrottet 128 (P00570860); G.S. Perrottet 741 (G-DC); J. Pujades s.n. (BCN43590); J. Pujades s.n. (BCN43589); J. Raynal & A. Raynal 5762 (P00570861); G. Roberty s.n. (G, 2 sheets); Roger s.n. (K000252776); R. Schnell s.n. (P00570862); F. Stauffer 908 (DAKAR); F. Stauffer 911 (DAKAR); J. Trochain 1543 (P00570863); J. Trochain 4332 (P00570864); M. Wailly 4598 (P00570865). **TOGO**: O. Kersting 739 (B, destroyed). **WESTERN SAHARA**: A. Marrero & J. Caujapé s.n. (LPA32987); R. Riina & L. Pokorny 1969 (MA); R. Riina & L. Pokorny 1970 (MA); Chatelain, C. CC5182 (G).

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Supplementary Material

The following supplementary material is available online for this article at <http://onlinelibrary.wiley.com/doi/10.1111/jse.12656/suppinfo>:

Table S1. List of plant specimens examined for the taxonomic treatment, climatic niche analysis, and distribution map (Fig. 1). Some records were filtered and curated from an original row-set of data downloaded from GBIF (<https://doi.org/10.15468/dl.oqiyuu>) others come from other sources (i.e., herbarium collections not available in GBIF). We include collector name, collection number, herbarium code, locality information from herbarium specimen labels, and estimated geographic coordinates for de novo georeferenced specimens.

Table S2. Descriptor loadings of the first two principal components (PC1, PC2) of the PCA of 19 bioclimatic variables (see Fig. 4).

Table S3. Leaf measurements used for the morphometric analysis (see Table 4; Fig. 5) on 80 selected specimens of *Euphorbia adenensis*, *E. balsamifera*, and *E. sepium*.