



More than one sweet tabaiba: disentangling the systematics of the succulent dendroid shrub *Euphorbia balsamifera*

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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.

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3 **More than one sweet tabaiba: disentangling the systematics**
4 **of the succulent dendroid shrub *Euphorbia balsamifera***
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8 Short Title: More than one sweet tabaiba (*Euphorbia*)
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25 **Abstract** The sweet tabaiba (*Euphorbia balsamifera*
26 Ait.) is one of the classical examples of the disjunct
27 biogeographic pattern known as Rand Flora. This species is
28 currently circumscribed to comprise two subspecies,
29 *Euphorbia balsamifera* subsp. *balsamifera* and *E.*
30 *balsamifera* subsp. *adenensis* (Deflers) P.R.O. Bally, with
31 their respective areas of distribution separated by a gap
32 of about 2000 km across central-east Africa. We use
33 multiple sources of evidence including phylogenomics,
34 morphometrics, lineage ages, and climatic niche analysis
35 to disentangle the confusing taxonomy around this
36 charismatic *Euphorbia* lineage. Based on our integrative
37 approach, we reestablish the two current subspecies to the
38 rank of species (*E. balsamifera* Ait., *E. adenensis*
39 Deflers) and resurrect the long forgotten *E. sepium* N.E.
40 Br., a commonly used species in the western Sub-Saharan
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3 and Sahelian regions. The taxonomic treatment presented
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5 here includes an identification key, updated morphological
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7 descriptions, and lectotypification of several names.
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12 **Key words:** divergence times, *Euphorbia*, Euphorbiaceae,
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14 Macaronesia, phylogenomics, Rand Flora, Sahara, Sahel,
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16 taxonomy.
17

18 19 **1 Introduction**

20
21 Incomplete or poor taxonomic knowledge can bias our
22
23 understanding of evolutionary and biogeographic patterns,
24
25 which in turn can hamper biodiversity conservation and
26
27 management efforts, especially for endemic taxa and
28
29 cryptic species (Brito, 2004; Statler et al., 2007).
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31 Molecular phylogenetics has greatly contributed to
32
33 overcome the so called taxonomic impediment (de Carvalho
34
35 et al., 2005) by improving classification schemes that
36
37 foster further studies at different taxonomic levels
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39 (e.g., Olmstead et al., 2009; van Ee et al., 2011; LPWG
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41 2013; Jiménez-Mejías et al., 2016; Soreng et al., 2017;
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43 Xiao & Simpson 2017). In addition, information from
44
45 molecular phylogenetics and DNA barcoding (Hubert & Hanner
46
47 2015; Rannala 2015; Lavinia et al., 2017) in combination
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49 with other sources of data is being used more and more for
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51 species discovery and taxonomic delimitation in different
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53 groups (e.g., Smith et al., 2007; Cheek et al., 2016;
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55 Alors et al., 2016; Nugnes et al., 2017; Souza et al.,
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3 2017). More recently, the rapid consolidation of high
4
5 throughput sequencing (HTS) techniques coupled with novel
6
7 analytical tools is providing massive amounts of sequence
8
9 data, which can potentially resolve recalcitrant regions
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11 of the tree of life (but see Olmstead & Bedoya, 2019).
12
13 Phylogenomics (i.e., phylogenetics using genome-scale
14
15 datasets) can also contribute to clarify long standing
16
17 taxonomic controversies, and even more in the context of
18
19 an integrative taxonomic approach (e.g., Prata et al.,
20
21 2018; Frajman et al., 2019).
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26 While working on the evolution of Rand Flora lineages
27
28 of *Euphorbia* (Villaverde et al., 2018), we stumbled upon
29
30 the taxonomic uncertainty surrounding *Euphorbia*
31
32 *balsamifera* Ait. This species belongs to *Euphorbia* section
33
34 *Balsamis* Webb & Berthelot, a clade in *E.* subgenus
35
36 *Athymalus* Neck. ex Rchb. (Peirson et al., 2013). The
37
38 species, as presently circumscribed (*E. balsamifera* sensu
39
40 lato), comprises two subspecies: *E. balsamifera* subsp.
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42 *balsamifera* and *E. balsamifera* subsp. *adenensis* (Deflers)
43
44 P.R.O. Bally (Govaerts et al., 2000; Peirson et al.,
45
46 2013), which are congruent with two disjunct areas
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48 separated by a gap of more than 2000 km across central
49
50 Africa (Fig. 1).
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52
53 *Euphorbia balsamifera* s.l. is popularly known as "tabaiba
54
55 dulce" (sweet tabaiba) in the Canary Islands, but it has
56
57 many other common names across its entire geographic
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3 range. It is a dioecious, pachycaul, succulent dendroid
4
5 shrub adapted to extreme thermal habitats and growing on
6
7 rocky to sandy substrates. Pachycaul succulence is a
8
9 specific condition in which water storage occurs in non-
10
11 photosynthetic parenchyma derived from the vascular
12
13 cambium (Hearn et al., 2013) and represents a quite
14
15 distinct condition from the great majority of
16
17 succulent *Euphorbia*, which involves significant water
18
19 storage parenchyma in the cortex and a persistent,
20
21 photosynthetic periderm.
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26 As many species in the genus, *Euphorbia balsamifera*
27
28 s.l. has been traditionally used by humans as food (Sahel;
29
30 latex is boiled and eaten as a gelatine), medicine (Sahel,
31
32 Western Sahara, Morocco), chewing gum, and cork for wine
33
34 bottles (Canary Islands). In the African Sahel, the
35
36 species is propagated from cuttings to build living fences
37
38 that provide sand stabilization, erosion control, and
39
40 protection of crops from livestock (Dolbear 2016).
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45 There are other *Euphorbia* species, distantly related
46
47 to *E. balsamifera*, that are also called tabaibas. They
48
49 belong to *E.* section *Aphyllis*, a clade of 23 Macaronesian-
50
51 African dendroid shrubs in a different subgenus—*E.*
52
53 subgenus *Esula*—(Barres et al., 2011, 2017; Riina et al.,
54
55 2013). The fact that *E. balsamifera* s.l. is the only
56
57 "sweet" of the tabaibas probably has to do with the
58
59 apparent lack of bitterness of its latex in comparison
60

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2
3 with tabaiba species in *E.* section *Aphyllis*. The milky
4
5 latex of most *Euphorbia* species can be toxic, and may
6
7 cause skin and eye inflammation of different degrees
8
9 depending on the species (Webster 1986; Eke et al., 2000;
10
11 Vasas et al., 2012; Otang et al., 2014).

12
13
14 The two subspecies of *E. balsamifera* currently
15
16 accepted correspond to former taxa at the species level,
17
18 namely *E. balsamifera* Ait. and *E. adenensis* Deflers (Bally
19
20 1965). On the other hand, populations of *E. balsamifera*
21
22 s.l. from the west-central Africa were recognized in the
23
24 past under two different names—*E. sepium* N.E.Br. and *E.*
25
26 *rogeri* N.E.Br.—but they were later reduced to the
27
28 subspecies level as *E. balsamifera* subsp. *sepium* with *E.*
29
30 *rogeri* under its synonymy (Maire 1938). Both *sepium* names
31
32 are currently considered synonyms of *E. balsamifera* subsp.
33
34 *balsamifera* (Govaerts et al., 2000; Peirson et al., 2013).

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37 In a study focused on the karyological evolution of
38
39 Macaronesian dendroid *Euphorbia*, Molero et al., (2002), in
40
41 disagreement with Govaerts et al., (2000), recognized
42
43 three taxa at the rank of subspecies, accepting *E.*
44
45 *balsamifera* subsp. *sepium* along with the other two
46
47 subspecies. However, Govaerts' view of the group prevailed
48
49 and was later adopted by Peirson et al., (2013) in their
50
51 sectional classification of *E.* subgenus *Athymalus* using a
52
53 phylogenetic framework. Unfortunately, accessions
54
55 representing typical localities of *E.* subsp. *sepium* were
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3 not sampled in that work, which only included samples of
4
5 subsp. *balsamifera* from the Canary Islands, and subsp.
6
7 *adenensis* from Oman (Peirson et al., 2013).
8
9

10 In a recent phylogenomic study, Villaverde et al.
11
12 (2018) used DNA sequences from exons of 296 orthologous
13
14 low-copy-nuclear loci representing most sections of
15
16 *Euphorbia* subgenus *Athymalus* and a relatively good
17
18 population sampling across the entire range of *Euphorbia*
19
20 *balsamifera* s.l. to analyse phylogenetic relationships
21
22 within this enigmatic species. They recovered three well-
23
24 supported clades, which were tentatively labeled in their
25
26 paper as *E. balsamifera* subsp. *adenensis*, *E. balsamifera*
27
28 subsp. *balsamifera*, and *E. balsamifera* subsp. *sepium*
29
30 (Villaverde et al., 2018). Here, we use an integrative
31
32 approach that combines evidence from phylogenomics and
33
34 lineage divergence times generated by Villaverde et al.
35
36 (2018) with information from morphology, morphometrics,
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38 occurrence data, and climate niche analysis to revise and
39
40 update the taxonomy of *Euphorbia balsamifera*.
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48 **2 Materials and Methods**

49 **2.1 Phylogenomics and divergence times**

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52 Phylogenetic information on the studied taxa and
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54 related lineages within *Euphorbia* subgenus *Athymalus*, as
55
56 well as estimates of divergence times, are based on the
57
58 study of Villaverde et al. (2018).
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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 in Supporting Information includes all specimen records filtered and curated from the original row-set of data downloaded from GBIF (<http://doi.org/10.15468/dl.0qiyuu>) 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 (R Core Team 2015; Hijmans et al., 2013).

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 minutes (~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

1
2
3 applying the `ecospat.grid.clim.dyn` function of the `ecospat`
4 package (Di Cola et al., 2017). We calculated the
5
6 differences in occurrence densities between pairs of the
7
8 three taxa (`ecospat.niche.overlap` function) and used the
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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 the 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 the 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

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3 the native niches of two different species (e.g., species
4 A and B), and adapted the concepts applied in that field
5 to our case as follows (species A represents the "exotic
6 range" and species B the "native range"): *niche stability*
7 is the proportion of the niche of species A overlapping
8 with the niche of species B, *niche unfilling* is the
9 proportion of niche B non-overlapping with niche A, and
10 finally, *niche expansion* is the proportion of niche A non-
11 overlapping with niche B.
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26 **2.4 Leaf morphometrics**

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28 To provide a quantitative assessment of the relevance
29 of leaf morphology, a character traditionally used in the
30 taxonomy of *Euphorbia balsamifera* s.l., the following
31 measurements were performed selecting three leaves per
32 specimen: leaf maximum length, leaf maximum width, length
33 from the leaf base to the point of leaf maximum width, and
34 mucron length. We selected mature leaves from young
35 branches below the fourth internode (from the apex)
36 whenever possible. For each measurement, the average of
37 the three leaves measured was taken to represent a given
38 specimen. We measured 29 specimens of subsp. *balsamifera*,
39 29 of subsp. *sepium*, and 22 of subsp. *adenensis* (80
40 specimens in total; see Table S2), aiming to cover the
41 geographic range and morphological variability of the
42 three taxa. The type specimen of *E. sepium* was included in
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3 the analyses; other types were visually inspected but not
4 included in the analyses due to the poor quality of
5 specimens. Finding suitable specimens of subsp. *adenensis*
6 was particularly challenging because many specimens were
7 poorly preserved (i.e., leafless specimens or just with a
8 few apical leaves remaining), and also because this taxon
9 is not well represented in herbaria. Differences in leaf
10 size and shape among the three taxa were visualized using
11 boxplots and Principal Component Analysis (PCA).
12 Statistical analyses on each variable (leaf measures) were
13 performed using univariate (ANOVA) and multiple variance
14 (MANOVA) analyses. All analyses were performed in the R
15 statistical environment v. 3.6 (R Core Team, 2015).
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35 **3 Results**

36 **3.1 Phylogenomics and lineage ages**

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38 The phylogenetic tree, based on 296 nuclear exon loci
39 and a relatively dense population sampling (110
40 individuals) covering the vast geographic range of
41 *Euphorbia balsamifera* s.l. (Villaverde et al., 2018),
42 recovered three highly supported clades (Fig. 2)
43 recognized here at the species level as *E. adenensis*, *E.*
44 *balsamifera* s.s., and *E. sepium* (see Taxonomic treatment
45 below). *Euphorbia sepium* was recovered sister to the clade
46 of *E. adenensis*-*E. balsamifera*. Age estimates differ among
47 the three lineages, with *E. sepium* diverging at
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3 approximately 11 Ma (stem age) in the late Miocene and
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5 with a crown age of ~7 Ma. Divergence between *E. adenensis*
6
7 and *E. balsamifera* dates back to the early Pliocene (~5
8
9 Ma), with crown ages of ~4 and ~3 Ma, respectively (Fig.
10
11
12 2).

17 3.2 Updating species geographic ranges

19 The distribution ranges of the studied species do not
20
21 overlap (Fig. 1): *E. balsamifera* s.s. occurs in
22
23 Macaronesia (all islands in the Canary Archipelago) and in
24
25 several sparse and isolated patches along the SW coast of
26
27 Morocco and N coast of Western Sahara, reaching its
28
29 southernmost distribution around 26 latitude N, 30 km
30
31 south of Boujdour (Western Sahara). The more continental
32
33 of the three species, *E. sepium*, occurs in western sub-
34
35 Saharan Africa and western Sahel, with collection records
36
37 in Western Sahara, Mauritania, Senegal, Mali, Burkina
38
39 Faso, Benin, Togo, Nigeria, and W Niger. The most
40
41 northwestern known populations of *E. sepium* in northern
42
43 Western Sahara are separated by ca. 190 km from the *E.*
44
45 *balsamifera* s.s. localities along the African Atlantic
46
47 coast. Finally, the geographic range of *E. adenensis*,
48
49 separated from the easternmost localities of *E. sepium* (W
50
51 Niger) by more than 2000 km, spans from the coast of E
52
53 Africa to the southern Arabian Peninsula, with collection
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55 records from the NE coast of Sudan (two records), N
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3 Somalia, SW corner of Saudi Arabia, Yemen, and Oman, and
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5 the island of Abd al Kuri in the Socotra Archipelago. All
6
7 the herbarium specimens used to update the geographic
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9 distribution of the three species (Fig. 1) are listed in
10
11 the taxonomic treatment below and in Supporting
12
13 Information Table S1.
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19 3.3 Climatic niche assessment

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21 Our results indicate a low overlapping of climatic
22
23 niches among the three species (Schöner's $D < 0.30$, Table
24
25 1, Fig. 3). The lowest overlapping niche values are among
26
27 *E. sepium* and the other two species ($D < 0.10$, Table 1).
28
29 Also, the results of the equivalency test comparing *E.*
30
31 *sepium* and *E. balsamifera* niches showed that the
32
33 overlapping is significantly smaller than the null
34
35 distribution (Table 2). The similarity test did not
36
37 indicate any difference from a random model between *E.*
38
39 *sepium* and each of the other two species (Table 2).
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42
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44 Niche overlap between *Euphorbia balsamifera* and *E.*
45
46 *adenensis* is also low (Schöner's $D = 0.27$; Table 1), while
47
48 the equivalency test indicated that these species do not
49
50 share the same climatic conditions (Table 2).
51
52 Nevertheless, the similarity test indicated that there are
53
54 significant similarities between the two niches (p-values
55
56 < 0.05 ; Table 2). Besides, *E. balsamifera* and *E. sepium*
57
58 niches have almost no overlap ($D = 0.004$; Table 1) and are
59
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3 less close to each other than expected in a random model
4
5 (equivalency test p-value = 0.009; Table 2). The *E.*
6
7 *adenensis* niche is more similar than expected in a random
8
9 model to the *E. balsamifera* niche (p-value = 0.019; Table
10
11 2). In sum, the similarity and equivalency tests indicated
12
13 that the niches of *E. adenensis* and *E. balsamifera* are not
14
15 significantly equivalent, neither significantly similar
16
17 nor equivalent to the *E. sepium* niche.
18
19

20
21 The values of niche expansion, niche unfilling and
22
23 niche stability are summarized in Table 3 and visualized
24
25 in Figure 3. The niches of *E. balsamifera* and *E. adenensis*
26
27 show the highest values of niche stability or overlap ($\sigma =$
28
29 0.88 and 0.99; Table 3, Fig. 3), and they also exhibit the
30
31 lowest values of niche expansion and unfilling (0 and
32
33 0.12; Table 3, Fig. 3). The niche stability (overlap)
34
35 between *E. sepium* and *E. adenensis* is twice as high ($\sigma =$
36
37 0.74) as the overlap with *E. balsamifera* ($\sigma = 0.36$) (Table
38
39 3, Fig. 3). Finally, the highest values of niche expansion
40
41 ($\epsilon = 0.63$) were found between *E. sepium* and *E. balsamifera*,
42
43 while the highest niche unfilling value ($\nu = 0.64$) was
44
45 reported in comparisons between *E. balsamifera* and *E.*
46
47 *sepium* (Table 3, Fig. 3).
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54 In the PCA analysis of all climatic variables
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56 associated to occurrences of the three putative species
57
58 (Fig. 4), *Euphorbia sepium* appears segregated from the
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2
3 other two species along the first axis (PC1), which was
4 correlated with temperature-related bioclimatic variables,
5 such as annual mean temperature (bio1) and mean
6 temperature of coldest quarter (bio11, Table S2 and Fig.
7 4), indicating that *E. sepium* is more tolerant to higher
8 temperatures than *E. balsamifera* and *E. adenensis*. In
9 contrast, *E. sepium* shows a high variation (variance)
10 along the second axis, PC2, which is mainly associated
11 with precipitation variables (annual precipitation, bio12)
12 and temperature seasonality (bio4). *Euphorbia adenensis*
13 and *E. balsamifera* shows a lesser degree of segregation
14 (i.e., they exhibit similar climatic tolerances),
15 especially along PC2. The two species, however, appear
16 slightly segregated along PC1, with *E. adenensis* showing
17 tolerance to higher temperatures than in *E. balsamifera*
18 (Fig. 4).

3.4 Leaf Morphometrics

41
42
43 Leaf length, mucron, and leaf shape (assessed as the
44 ratio between maximum length and maximum width) differ
45 significantly between the three taxa, but *Euphorbia sepium*
46 shows the largest difference for all the measured
47 variables (Fig. 5A, 5C-E, Table 4). Only maximum leaf
48 width is not significantly different (Table 4), with the
49 box-plots of the three species showing a broad overlap for
50 this variable (Fig. 5B).

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3 In the PCA, the first two components (PC1, PC2)
4
5 **account** for approximately 62% and 27% of the observed
6
7 variance, respectively. Characters contributing
8
9 significantly to the first component axis PC1 were leaf
10
11 maximum length, leaf length from base to widest part, and
12
13 mucron length, whereas leaf width **is** the variable
14
15 contributing the most (94%) to the second axis PC2. The
16
17 scatter plot shows a clear separation between *E. adenensis*
18
19 and *E. sepium* along PC1, but *E. balsamifera* fills the gap
20
21 between the two species and partially overlaps with both
22
23 of them, especially with *E. sepium*. PC2 shows significant
24
25 overlapping among the three species (Fig. 5F).
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32 **4 Discussion**

33
34 **Phylogenetic trees** are important when addressing
35
36 biological questions in an evolutionary context, but they
37
38 are also essential to refine taxonomic knowledge. We used
39
40 the most robust phylogenetic tree of *Euphorbia* section
41
42 *Balsamis* built to date (Villaverde et al., 2018), and
43
44 complemented it with additional sources of evidence to
45
46 support the reestablishment of three lineages at the rank
47
48 of species. The newly reinstated taxa (*E. adenensis*, *E.*
49
50 *balsamifera*, and *E. sepium*) were previously treated under
51
52 the former *E. balsamifera* s.l., either as subspecies or
53
54 under synonymy (see **taxonomic** treatment).
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3 Our approach is consistent with studies arguing
4
5 against establishing species limits based solely on
6
7 genomic data (e.g., Solís-Lemus et al., 2015; Sukumaran &
8
9 Knowles 2017). Similar integrative studies have been
10
11 successful resolving the taxonomy of problematic groups at
12
13 the species level (e.g., Denham et al., 2019; Li et al.,
14
15 2019; Perkins 2019; Yang et al., 2019), but they are still
16
17 scarce in plants, and even more those integrating
18
19 phylogenomics, divergence time estimations, and
20
21 phylogeography with morphology and climate niche analysis
22
23 (e.g., Frajman et al., 2019). Generating large amounts of
24
25 genomic data continues to be expensive and the steps from
26
27 taxon sampling to tree inference are considerably longer
28
29 and bioinformatically more demanding than just generating
30
31 and analyzing a small set of genes. In addition, placing
32
33 the resulting phylogeny in a morphological and ecological
34
35 context using quantitative techniques is also time-
36
37 consuming and requires expert knowledge on the focal group
38
39 (Giribet, 2015).
40
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46 Based on a previous work (Villaverde et al., 2018),
47
48 we recovered three distinct clades within *Euphorbia*
49
50 *balsamifera* s.l. Ten individuals of *Euphorbia sepium* were
51
52 clustered with strong support as a monophyletic lineage
53
54 sister to the clade formed by *E. adenensis* and *E.*
55
56 *balsamifera*. This nuclear topology (Fig. 2) was also fully
57
58 congruent with the chloroplast phylogeny (not shown)
59
60

1
2
3 obtained by Villaverde et al., (2018). Each lineage was
4 represented by 10 or more individuals spread across the
5 entire geographic range, which is desirable when
6 addressing species relationships at the species level
7 where incomplete lineage sorting may have an impact on
8 phylogenetic resolution (Naciri & Linder 2015).
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Estimated divergence times for the origin of these
three taxa (5 to 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 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,

1
2
3 agrees well with results from Pokorny et al. (2015; ~3.8
4 Ma) and coincides with a period of global climate warming,
5 the mid-Pliocene Warm Period (Zachos et al., 2008), and
6 increased aridification in Africa (Senut et al., 2009).
7 Clade age and geographic disjunction are in alignment with
8 the climatic vicariance/extinction hypothesis (Mairal et
9 al., 2017), which posits that species' failure to adapt to
10 the new more xeric environments, in combination with niche
11 conservatism, contributed to the geographic isolation of
12 populations in the eastern and western margins of Africa
13 and led to the generation of the allopatric Rand Flora
14 lineages.
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30 The much older split of *E. sepium* (~11 Ma) predates
31 the formation of the Sahara Desert (~8 Ma, Senut et al.,
32 2009). This taxon exhibits a much more widespread and
33 inland distribution, as well as a wider climatic niche
34 than either *E. adenensis* or *E. balsamifera* (Fig. 3). Our
35 study places the divergence of *E. sepium* in the late
36 Miocene (Tortonian), a period characterized by lower
37 temperatures and wetter environments (Mairal et al.,
38 2017); it is thus possible that ecological vicariance—the
39 appearance of a hostile environment—is involved also in
40 the origin of this clade.
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54 The climatic niche analysis showed that the three
55 species have different climatic niches, especially *E.*
56
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59
60 *sepium*. This species' niche barely overlaps with any of

1
2
3 the other two species, and equivalency tests showed that
4
5 the bioclimatic conditions where this species occurs are
6
7 more different than expected by chance when compared with
8
9 *E. balsamifera* or *E. adenensis*. However, this difference
10
11 is greater between *E. sepium* and *E. balsamifera*, because
12
13 their expansion and unfilling values are higher than those
14
15 of the other two species pairwise comparisons (Table 3,
16
17 Fig. 3). Differences between *E. balsamifera* and *E.*
18
19 *adenensis* niches are not as remarkable, although niche
20
21 overlap is comparatively low (Schönen'D = 0.271; Table 1)
22
23 and there is low conservation according to the equivalency
24
25 test (Table 2). However, similarity among these niches is
26
27 higher than expected for a random comparison, and the
28
29 stability value is high (Table 3). The niche equivalency
30
31 test is considered very conservative (Aguirre-Gutiérrez et
32
33 al., 2015), and even if there is a part of both taxa that
34
35 dwell in an equivalent niche, this can result in not
36
37 rejecting the null distribution when their means are
38
39 different. However, similarity between them may be
40
41 accepted (Glennon et al., 2014).

42
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44 The allopatric distribution of the three taxa,
45
46 particularly the large gap between the sister *E.*
47
48 *balsamifera* and *E. adenensis*, also supports the
49
50 reinstatement of the three lineages as separate species.
51
52 The enormous distance (> 2000 km) separating these two
53
54 species makes gene flow between them unlikely. Even if
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1
2
3 they are morphologically very similar and perhaps
4
5 potentially able to hybridize, isolation by distance will
6
7 continue to increase genetic divergence and decrease the
8
9 possibility of gene flow over time (Sexton et al., 2014).
10
11 The much larger distribution area of *Euphorbia sepium*
12
13 compared with the other two species, could be in part the
14
15 result of human activities due to the common use of this
16
17 species across the Sahel for live-fencing to protect
18
19 crops, avoid soil erosion, and keep livestock out of
20
21 fields (Dolbear 2016).
22
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24

25
26 We show that morphological data, particularly leaf
27
28 shape and size (Fig. 4), is useful to distinguish
29
30 *Euphorbia sepium* from the other two species. As expected
31
32 by their closest phylogenetic relationship, the
33
34 morphological separation between *E. adenensis* and *E.*
35
36 *balsamifera* is not that clear-cut. The most useful
37
38 characters distinguishing these two taxa are leaf shape
39
40 and plant stature. The length of the style fusion and the
41
42 density of capsule **indumentum** have also been used to
43
44 distinguish these species, but they are not taxonomically
45
46 as useful (see Taxonomic Treatment). A palynological
47
48 survey (Perez & Roca-Salinas 1977) reported differences in
49
50 pollen size between the two species, larger grains in *E.*
51
52 *balsamifera* (47.3–55 μm) than in *E. adenensis* (34.32–40.92
53
54 μm), but slight differences in exine ornamentation. As far
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3 as we know, there are no palynological data available for
4
5 *E. sepium*.

6
7 The criterion of reciprocal monophyly, along with the
8
9 relatively old stem ages exhibited by the three taxa,
10
11 compared to those in other *Euphorbia* lineages (Horn et
12
13 al., 2014) and within subgenus *Athymalus* (Villaverde et
14
15 al., 2018), would be enough to satisfy the unified species
16
17 concept proposed by De Queiroz (2007), i.e. species as
18
19 separately evolving metapopulation lineages. Nevertheless,
20
21 we have shown here that there is additional evidence,
22
23 including differences in leaf shape/size and climatic
24
25 tolerances, to support the establishment of three species
26
27 of sweet tabaiba.

28
29 The integration of phylogenomic data with evidence
30
31 from morphology, distribution ranges, divergence times,
32
33 and climatic niches, allows us to settle the long-standing
34
35 confusing taxonomy around the former *Euphorbia balsamifera*
36
37 s.l. Our results are consistent with the recognition of
38
39 three taxa at the species level: *E. adenensis*, *E.*
40
41 *balsamifera*, and *E. sepium*. The reinstatement of the
42
43 widespread *E. sepium* from synonymy uncovers a highly
44
45 distinct species, whose divergence predates the formation
46
47 of the Sahara Desert as well as the split between *E.*
48
49 *adenensis* and *E. balsamifera*.

59 **5 Taxonomic Treatment**

5.1 Identification key to the studied species of *Euphorbia*

1 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

1' 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

2 Stem leaves lanceolate to linear-lanceolate, 14.1-
44.9(50) x 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

2' Stem leaves linear, (32.2)40.5-77.5(100) x 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. (Fig. 6A-F)***Euphorbia balsamifera* subsp. *adenensis* (Deflers) P.R.O.

Bally, *Candollea* ~~20: 31, 34.~~ 1965. - *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; isolectotype MPU014212!); Yemen, presqu'ile d'Aden, vallée de Kiosaf, 8 Mar 1885, Deflers s.n. (MPU014216!).

Compact dendroid shrubs, 0.6-0.9(1.2) m tall, usually dioecious, much branched; upper branches (0.8)2-3(6) cm long, succulent. Rhytidome whitish-cream, pearly white. Stem leaves 5.6-33.4 x 2.8-9.4 mm, obovate-oblong; apex obtuse to rounded, sometimes minutely mucronate, mucron 0-0.5 mm long; subcyathial leaves similar in length but wider than cauline leaves, obovate-spatulate. Cyathia solitary, terminal; involucre broadly cupuliform, 2.6-3.4 x 5.4-7.8 mm; glands 5, green-yellowish, transversally oblong, 0.23-0.42 x 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) x (6)7.6-9(11) mm, globose, rugulose, glabrous, rarely glabrescent.

1
2
3 Seeds ecarunculate, 2.9–3.8 x 2.5–3 x 2.6–3.2 mm, ovoid-
4
5 subglobose to globose; hilar zone with an angle of 25–30°.
6

7 **Distribution and habitat:** *Euphorbia adenensis* occurs in
8
9 eastern Africa (Somalia, east coast of Sudan), the
10
11 southern Arabian Peninsula (Yemen, Oman), and Abd-al-Kuri
12
13 island (Socotra), between 150 and 1900 m elevation (Fig.
14
15
16 1).

17
18
19 **Common names:** “mark, scar of blow” (Soqotri) (Miller &
20
21 Morris, 2004).
22

23 **Specimens examined** (see Table S1 for additional
24
25 information): **OMAN:** J.T. Bent 197 (K); P. Hein & N. Kilian
26
27 s.n. (B100430939); R.M. Lawton 1892 (K); J.R. Maconochie
28
29 2877 (K); J.R. Maconochie 3011 (K); J.R. Maconochie 3545
30
31 (K); A.G. Miller 2201 (E00445559, K); A.G. Miller 2350
32
33 (E0445557, K); A.G. Miller 7513 (E00445555, K); A.G.
34
35 Miller 7514 (E00445562, K); J.J. Morawetz 325 (K); J.J.
36
37 Morawetz 346 (MICH); A. Radcliffe-Smith 5173 (K). **SAUDI**
38
39 **ARABIA:** I.S. Collenette 1428 (K); I.S. Collenette 1615
40
41 (E00221064); A.K. Nasher H42 (E00221063). **SOMALIA:** P.R.O.
42
43 Bally 10360 (G, K 5193); P.R.O. Bally 10858 (G, K); P.R.O.
44
45 Bally 11007 (G, K); P.R.O. Bally & R. Melville 15951 (K);
46
47 R. Bavazzano & J. Lavranos s.n. (FT); J.J. Beckett 773
48
49 (K); S.B. Boaler 86 (K); S. Carter 940 (K); C.N.
50
51 Collenette 74 (K); J.B. Gillett & R.W. Watson 23477 (K);
52
53 P.E. Glover & Gilliland 555 (BM); O.J. Hansen & H.
54
55 Heemstra 6216 (K); C.F. Hemming 1605 (K); C.F. Hemming
56
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2
3 1973 (FT, K); C.F. Hemming & R.M. Watson 3039 (K); J.
4
5 Lavranos, S. Carter & al. 24766 (K); E. Peck E266 (G, K);
6
7 M. Thulin 4242 (K); M. Thulin & M.A. Warfa 5875 (UPS); M.
8
9 Thulin & M.A. Warfa 6097 (UPS). **SUDAN**: S. Carter 1881 (K);
10
11 Sahni & Kaamil 699 (K). **YEMEN**: S. Birdwood 104 (K); E.
12
13 Bisset 218 (K); L. Boulos & A.M. Rowaished 17088
14
15 (E00445574, K); J.S. Collenette 8955 (K, 60195); Deflers
16
17 s.n. (MPU014212, MPU014213, MPU014216); K.J. Gordon 592A
18
19 (E00445561); L. Guarino & L. Balaidi H68 (E00445563); P.
20
21 Hein 314 (B100430940); P. Hein 3560 (B1004330941); P. Hein
22
23 6331 (B100430938); P. Hein 6709 (B100430948); P. Hein 6780
24
25 (B100430945); P. Hein 6880 (B100430947); P. Hein 7816
26
27 (B100430946); P. Hein 4881a (W20160006061); C.F. Hemming
28
29 523 (K); K.J.V. A25 (K); K.J.V. A30 (K); N. Kilian 4421
30
31 (B100451739); N. Kilian 4538 (B100430943); N. Kilian 5097
32
33 (B100430942); N. Kilian 6350 (B100430949); N. Kilian 6394
34
35 (B10430944); N. Kilian s.n. (B100430941); J.J. Lavranos
36
37 15714 (E00445558); J.J. Lavranos 16012 (E00445556); A.G.
38
39 Miller 3158 (E00445553, K); A.G. Miller. M8073 (E00445564,
40
41 K); J. Molero s.n. (BCN44902); J. Molero s.n. (BCN44901);
42
43 J. Molero s.n. (BCN44900); J. Molero s.n. (BCN44899);
44
45 Ogilvie-Grant & Forbes Expedition 75 (E00239518); Ogilvie-
46
47 Grant & Forbes Expedition 89 (E00239517, K); A. Radcliffe-
48
49 Smith & S.J. Henchie 4770 (K); N. Sanadiki 41 (K); N.
50
51 Sanadiki s.n. (E); N. Sanadiki s.n. (E00445560); G.
52
53 Schweinfurth 132 (G, K); A.R. Smith & J. Lavranos 52 (K);
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2
3 A.R. Smith & J. Lavranos 666 (K); M. Thulin, B.-A., Beier
4
5 & M.A.Hussein 9585 (UPS); Wakefield Expedition 3 (K); J.
6
7 Waring 121 (K); D. Wood Y1115 (E00445554).
8
9

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11
12 **5.3 *Euphorbia balsamifera* Ait., Hort. Kew. 2: 137. 1789.**
13

14 **(Fig. 6G-L)**
15

16 *Tithymalus balsamifer* (Aiton) Haw., Syn. Pl. Succ. 140.
17

18 1812. Type: Canary Islands, Tenerife, 1778, F. Masson
19

20 s.n. (holotype BM000928081!). = *Euphorbia capazii*
21

22 Caball., Trab. Mus. Nac. Ci. Nat., Ser. Bot. No. 30,
23

24 25. 1935. Type: Morocco. Ifni, Cabo Non, 12 Jul 1934,
25

26 A. Caballero s.n. (lectotype MA-01-00074670!,
27

28 designated here).
29
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33

34
35 Open dendroid shrubs, (0.2)0.8–1.5(4) m tall, usually
36
37 dioecious, much branched, erect, sometimes decumbent to
38
39 prostrate in harsher environments; upper branches 2–10(15)
40
41 cm long, succulent. Rhytidome grayish, yellowish-
42
43 ochraceous. Stem leaves 14.1–44.9(50) x 2.9–10(12) mm,
44
45 lanceolate to linear-lanceolate; apex mucronate to
46
47 apiculate, mucron 0.3–0.6 mm long. Cyathia solitary,
48
49 terminal; involucre broadly cupuliform, 2.5–3.5 x 5.2–8 mm;
50
51 glands 5, green-yellowish or orange, transversally oblong,
52
53 0.3–0.5 x 0.1–0.3 mm; ovary smooth, slightly pubescent;
54
55 styles (1.6)1.9–2.3(2.6) mm, fused (0.2)0.3–0.5(0.7) mm
56
57 from the base, tips bifid, stigmatic lobes 0.3–0.5 mm
58
59
60

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2
3 long. Capsule (6)7.5–9(12.5) × (7.4)8.5–11(13.8) mm,
4
5 smooth, globose, punctuated or minutely rugulose, slightly
6
7 pubescent. Seeds ecarunculate, 2.9–4.0 × 2.0–3.25 × 2.0–
8
9 3.5 mm, ovoid-subglobose; hilar zone with an angle of 30–
10
11 45°.
12
13

14 **Distribution and habitat:** *Euphorbia balsamifera* is
15
16 common and usually forms dense populations along the dry
17
18 coastal areas of all Canary islands, and less common and
19
20 forming scattered populations along the coast of south
21
22 Morocco and north Western Sahara, between sea level and
23
24 500 m (Marrero et al., 1999; Fig. 1, Table S1).
25
26

27 **Common names:** "tabaiba dulce", sweet spurge, balsam
28
29 spurge (Canary Islands) (Marrero et al., 1999); "salane",
30
31 "afdir" (Morocco); "lfernan", "azdira" (Western Sahara).
32
33
34

35 **Specimens examined** (see Table S1 for additional
36
37 information): **MOROCCO:** J. Aldasoro, J. Calleja & J. Molero
38
39 s.n. (BCN126715, BCN126716); A. Caballero s.n. (MPU); J.
40
41 Fernández Casas & J. Molero 13706 (G00403653); Font-Quer
42
43 s.n. (BCN); J. Gattefossé s.n. (RAB); J. Gattefossé s.n.
44
45 (RAB); J. Lepymny, Rungi & Ch. Sauvage 1712 (RAB); R.
46
47 Maire s.n. (MPU, RAB); R. Maire s.n. (MPU); R. Maire s.n.
48
49 (MPU); R. Maire s.n. (MPU); Y. Ollivier 39 (MPU); Y.
50
51 Ollivier s.n. (MPU); Y. Ollivier s.n. (RAB); D. Podlech
52
53 40516 (GM, G); D. Podlech 48600 (GM, G); R. Riina & L.
54
55 Pokorny 1962 (MA); R. Riina & L. Pokorny 1963 (MA); Ch.
56
57 Sauvage & Essiaf 16132 (RAB); F. Schuhwerk 90/300 (M);
58
59
60

1
2
3 Statfford Allen & Son s.n. (K). **SPAIN: El Hierro:** J.
4
5 Molero & A. Rovira s.n. (BCN45956, BCN45957); C.J. Pitard
6
7 s.n. (P); M. Rincón-Barrado & T. Villaverde 16MRB18 (MA);
8
9 M. Rincón-Barrado & T. Villaverde 19MRB18 (MA).
10
11
12 **Fuerteventura.** I. Álvarez, J. Calvo & B. Ríos JC2074 (MA-
13
14 768477-1); X. Espadaler s.n. (BCN45989); F. Hekker s.n.
15
16 (L-0447505); G. Kunkel 11984 (G); M. Rincón-Barrado & T.
17
18 Villaverde 3MRB18 (MA); M. Rincón-Barrado & T. Villaverde
19
20 10MRB18 (MA); M. Rincón-Barrado & T. Villaverde 15MRB18
21
22 (MA). **Gran Canaria:** Ch.H. Andreas 6370 (WAG-1800096); E.
23
24 Asplund s.n. (G, K); J. Bornmüller 2859 (G, P); B. Dorsey
25
26 3 (MICH); F.N. Hepper 907 (K); E. Hulten s.n. (S); G.
27
28 Kunkel 15260 (G); A. Marrero & J. Molero s.n. (BCN45973);
29
30 A. Marrero, J. Molero & A. Rovira s.n. (BCN129356);
31
32 Melbold 11749 (M); J. Molero s.n. (BCN45966, BCN45972,
33
34 BCN45966, BCN45975, BCN45992, BCN45994, BCN45993); J.
35
36 Molero & A. Rovira s.n. (BCN129349, BCN129350, BCN129351,
37
38 BCN129357, BCN129358, BCN129364, BCN129366, BCN129367);
39
40 R.P. Murray s.n. (G, BM); W. Punt s.n. (U-1274933); D.O.
41
42 Wijnands 623 (WAG-1800093). **Lanzarote:** C. Aedo, L. Medina
43
44 & A. Quintanar AQ1762 (MA750338); A. Aldridge s.n. (BM);
45
46 Ch.H. Andreas 6370 (WAG-1800097); Andreas s.n. (M); J.
47
48 Klackenberg 940401-5 (S); J. Molero & A. Rovira s.n.
49
50 (BCN126721); M. Rincón-Barrado & T. Villaverde 6MRB18
51
52 (MA). **La Gomera:** A. Herrero AH4358.1 (MA); R. Letouzey
53
54 s.n. (P); L.J.G. van der Maesen 396 (WAG-0158556); J.
55
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3 Molero & A. Rovira s.n. (BCN126717, BCN126718, BCN129352,
4 BCN129353, BCN129355, BCN129362, BCN129363, BCN129365,
5 BCN22672, BCN22673, BCN22674, BCN45960); J. Molero s.n.
6 (BCN45962, BCN45963, BCN45965, BCN45967, BCN45968,
7 BCN45969, BCN45970, BCN45980, BCN45984, BCN45985,
8 BCN45986, BCN45987, BCN45988, BCN4599); R. P. Murray s.n.
9 (K); R. Riina, J. Molero, P.E. Berry 2030 (MA); n.c. n.d.
10 (FR0194912). **La Palma:** J. Molero s.n. (BCN45979); T.
11 Villaverde & E. García-Íñiguez 1TVH17 (MA). **Tenerife:** E.
12 Asplund s.n. (G); E. Bourgeau 472 (BM, G, P, K); E.
13 Bourgeau 1510 (G, P); E. Bourgeau 1810 (G, P, K, BM); BBB.
14 Bresinsky s.n. (M); O. Burchard 163 (G); A. Carrillo s.n.
15 (BCN39880); B. Cabezudo & S. Talavera n.d. (COFC-95-1,
16 SEV-28116-1); C. Cool 467 (L); T.J. Dinn 196 (K); F.
17 Hekker H254312 (L-0447507); H. Knoche s.n. (MPU, 2
18 sheets); J.C. Lindeman 7128 (L-3799602); T. Lowe s.n.
19 (BM); N. Lundqvist s.n. (UPS); P. Martínez n.d. (COA); J.
20 Molero s.n. (BCN126720, BCN37836, BCN45959, BCN45961,
21 BCN45962, BCN45967, BCN45968, BCN45984, BCN45985,
22 BCN45986, BCN45991, BCN48883); J. Molero & G. de la Fuente
23 s.n. (BCN45983); J. Molero & A. Rovira s.n. (BCN37827,
24 BCN37828, BCN45970, BCN126719, BCN129354); C.J. Pitard 353
25 (L, P, WAG); C.J. Pitard 354 (L, P, WAG); C.J. Pitard 6570
26 (L); R. Riina et al., 2015 (MA); P. Rodrigo n.d. (COA-
27 26937-1); Rolf & Berg n.d. (O-2003110, O-2003111, O-
28 2003109); E.R. Sventenius s.n. (ORT14065, ORT14107,
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2
3 ORT14110); E. Valdés-Bermej 5025EV (MA-250333-1); J.H.
4
5 Vredébregt 324 (WAG-1800092). **WESTERN SAHARA:** Alferez
6
7 Feliu s.n. (RAB); J. Caujapé & A. Marrero s.n. (LPA, MA);
8
9 R. Maire 2461 (MPU); A. Marrero & J. Caujapé s.n. (LPA);
10
11 R. Maire 2536 (MPU); R. Riina & L. Pokorny 1966 (MA); R.
12
13 Riina & L. Pokorny 1967 (MA); R. Riina & L. Pokorny 1968
14
15 (MA).
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21 **5.4 *Euphorbia sepium* N.E. Br., Fl. Trop. Afr. 6(1): 551.**

22
23 **1911. (Fig. 6M-Q)**

24
25 *Euphorbia balsamifera* subsp. *sepium* (N.E.Br.) Maire in
26
27 Bull. Soc. Hist. Nat. Afr. Nord 29(26): 450. 1938.
28
29 Syntypes: Senegal, Sor Island, Brunner 21 (?); Togo, O.
30
31 Kersting 739 (B, destroyed); northern Nigeria: Katagum
32
33 District, J.M. Dalziel 320 (lectotype K000252777!,
34
35 designated here; isolectotype K000252778!). = *E. rogeri*
36
37 N.E.Br. Fl. Trop. Afr. [Oliver et al.] 6(1.3): 551.
38
39 1911. Syntypes: Senegal, Lampsar and Maka, May 1825,
40
41 Roger s.n. (lectotype K000252776!, designated here);
42
43 Senegal, 1906, L. Farmar 54 (K000252775!). - *E.*
44
45 *balsamifera* Ait. var. *rogeri* (N.E. Br.) Maire in Bull.
46
47 Soc. Hist. Nat. Afr. Nord 29(26): 450. 1938. - *E.*
48
49 *balsamifera* subsp. *rogeri* (N. E. Br.) Guinea in Anales
50
51 J. Bot. Madrid 8: 399. 1948.
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1
2
3 Open dendroid shrubs, (0.8)1.5-3(5) m tall, usually
4
5 dioecious, much branched, erect; upper branches 10-20 cm
6
7 long, semi-succulent. Rhytidome grayish white to pearly
8
9 white. Stem leaves (32.2)40.5-77.5(100) x 3.1-7.4 mm,
10
11 linear; apex obtuse or rounded, mucronate, mucron (0.1)1-
12
13 1.5(2) mm long; subcyathial leaves much shorter and wider
14
15 than cauline leaves, lanceolate, elliptic or obovate-
16
17 oblong. Cyathia solitary, terminal; involucre broadly
18
19 conical, 2.5-3.2 x 4.8-7.6 mm; glands 5, yellowish,
20
21 transversally oblong, 0.1-0.2 x 0.2-0.4 mm; ovary densely
22
23 pubescent-sericeous; styles 1.2-1.8 mm, fused 0.2-0.5 mm
24
25 from the base, tips bifid, stigmatic lobes 0.2-0.4 mm
26
27 long. Capsule (5.8)6.4-7.2(7.5) x (6.7)7.4-8.2(8.4) mm,
28
29 globose, smooth or rugulose, densely pubescent. Seeds
30
31 ecarunculate, 2.7-4.0 x 2.5-3.1 x 2.5-3.2 mm, ovoid-
32
33 subglobose, rarely ellipsoid or subglobose; hilar zone
34
35 with an angle of 30-40°.

36
37
38
39
40
41 **Distribution and habitat:** *Euphorbia sepium* is
42
43 distributed in wadis along a southern belt between the
44
45 Sahara desert and the Sahel region, at elevations between
46
47 sea level and 500 m (Table S1, Fig. 1). The species
48
49 geographic range has likely been expanded by the frequent
50
51 use of this species for live fencing (Fig. 6P) in the
52
53 Sahel, expanding its natural range further south into the
54
55 Sahelian savannas.
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2
3 **Common names:** "yaro" (Senegal, Nigeria, Brown 1911);
4
5 "waiyaro", "kagua", "kaguwa", "katagum" (Nigeria, Holland
6
7 1922).

8
9
10 **Specimens examined** (see Table S1 for additional
11
12 information): **BENIN:** A. Chevalier 23620 (P00570817,
13
14 P00570818); P. Houngnon s.n. (BENIN); J. Krohmer 1985
15
16 (FR0018633); Unknown (FR0022735). **BURKINA FASO:** O.
17
18 Bognounou 428 (P00570820); R. Martin 282 (FR); B. Toutain
19
20 776 (P00570821); B. Toutain 2735 (P00570822). **GHANA:** G.K.
21
22 Akpabla 541 (K). **MALI:** G. Boudet 6643 (P00570823); A.
23
24 Chevalier 1315 (P00570825, P00570826); A. Chevalier 1316
25
26 (P00570827); A. Chevalier 43094 (P00570829); A. Chevalier
27
28 43167 (P00570830); A. Chevalier 43180 (P00570824); A.
29
30 Chevalier 43181 (P00570831); A. Chevalier 43182
31
32 (P00570832); J.T. Davey 468 (K); S. de Ganay 148
33
34 (P00570834); C. Geerling 2671 (BR16386815, WAG1800090,
35
36 WAG1800091); F.N. Hepper 3733 (K, P00570828); A. Leclercq
37
38 42422 (P00570835); T. Monod 563 (P00570836); M. Wailly
39
40 4673 (K, P00570840); M. Wailly 4786 (P00570841); M. Wailly
41
42 5148 (P00570842); J. Molero & al. (BCN43587, BCN43588,
43
44 BCN45977); J. Raynal & A. Raynal 5506 (P00570838).
45
46
47
48
49
50 **MAURITANIA:** I. Arvidsson 30 (K); Biologie des Acridiens
51
52 23A (P00570814); C. Chatelain CC5259 (G); C. Chatelain
53
54 CC5260 (G); C. Chatelain CC5261 (G); M. Chudeau s.n.
55
56 (P00570811, P00570812, P00570813); M. Cludeau (P00570810);
57
58 J. Coddington 4 (K); Schmitt 28554 (P00570816); A.
59
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2
3 Marrero s.n. (LPA6573, LPA6574, LPA6723, LPA6724); A.
4
5 Marrero & M. González Martín s.n. (LPA6526, LPA6527); T.
6
7 Monod 3969 (P00570815, P00570837). **NIGER:** G. Boudet 5335
8
9 (P00570843); A. Chevalier 43622 (P00570844); A. Chevalier
10
11 43693 (P00570845, WAG1800088); Coen Foundation 13 (K);
12
13 Coen Foundation 31 (K); P. de Fabrègues 4358 (P05482482);
14
15 Gaillard-Mission Tilho s.n. (P00570847, P00570848); D.P.M.
16
17 Guile s.n. (K); J. B. Hall 18083 (K); J. Koechlin 6554
18
19 (P00570849); J. Lowe 3700 (K); K. J. Virgo 12 (K).
20
21
22
23 **NIGERIA:** J.M. Dalziel 320 (K000252777, K000252778); J.M.
24
25 Dalziel 528 (K); N. Etkin 3 (MO139898); R.W.J. Keay s.n.
26
27 (K); Sampson 8 (K). **SENEGAL:** J. Audru 2304 (P00570850); J.
28
29 Audru 3136 (P00570851); E. Bassene s.n. (BCN45976);
30
31 Brunner 21 (?); O. Caille s.n. (P00570852); O. Caille
32
33 25279 (P00570854); A. Chevalier 14610 (P00570853); A.
34
35 Chevalier 25701 (P00570856); A. Chevalier 25707bis
36
37 (P00570857); A. Chevalier 34052 (P00570858); L. Farmar 54
38
39 (K000252775); F.R. Leprieur s.n. (G); G. Paroisse 43
40
41 (P00570859); G.S. Perrottet 128 (P00570860); G.S.
42
43 Perrottet 741 (G-DC); J. Pujades s.n. (BCN43590); J.
44
45 Pujades s.n. (BCN43589); J. Raynal & A. Raynal 5762
46
47 (P00570861); G. Roberty s.n. (G, 2 sheets); Roger s.n.
48
49 (K000252776); R. Schnell s.n. (P00570862); F. Stauffer 908
50
51 (DAKAR); F. Stauffer 911 (DAKAR); J. Trochain 1543
52
53 (P00570863); J. Trochain 4332 (P00570864); M. Wailly 4598
54
55 (P00570865). **TOGO:** O. Kersting 739 (B, destroyed). **WESTERN**
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3 **SAHARA:** A. Marrero & J. Caujapé s.n. (LPA32987); R. Riina.
4
5 & L. Pokorny 1969 (MA); R. Riina & L. Pokorny 1970 (MA);
6
7 Chatelain, C. CC5182 (G).
8
9

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For Review Only

Table 1 Values of niche overlap (Schöner's D) obtained for each species pair-wise comparison of the studied *Euphorbia* taxa. Schöner's D varies between 0 (no niche overlap) and 1 (complete niche overlap)

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

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

	Equivalency					
	Greater	Lower	Greater	Lower	Greater	Lower
	<i>E. adenensis</i>		<i>E. balsamifera</i>		<i>E. sepium</i>	
<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					
	Greater	Lower	Greater	Lower	Greater	Lower
	<i>E. adenensis</i>		<i>E. balsamifera</i>		<i>E. sepium</i>	
<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	–	–

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>	—	—	—	0.0 01	0.9 99	0.1 21	0.5 52	0.4 47	0.2 64
<i>E. balsamifera</i>	0.1 21	0.8 79	0.0 01	—	—	—	0.4 65	0.5 35	0.6 37
<i>E. sepium</i>	0.2 65	0.7 35	0.5 52	0.6 37	0.3 63	0.4 65	—	—	—

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 (E)	133.9	S

Letters A-D correspond to the box plots in Fig. 5; S = significant (p < 0.001); NS = not significant

Figure Legends

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).

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).

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3 **Fig. 3.** Comparison of climatic niches among the three
4 species of *Euphorbia* recognized here: *E. adenensis*, *E.*
5 *balsamifera*, and *E. sepium*. Cells along the diagonal from
6 upper left to bottom right show the niche occupied by each
7 species, the other cells represent composed niche overlap
8 of species pairs. Colors indicate niche expansion (green),
9 niche stability (blue), and niche unfilling (red). Solid
10 lines enclose all available environments for each range;
11 dashed lines represent 90th percentile of the background
12 environment for the paired species ranges.
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28 **Fig. 4.** PCA scatterplot, including within-group centroid,
29 of the first two principal components based on 19
30 bioclimatic variables associated to occurrence points of
31 the three proposed *Euphorbia* species: orange circle (*E.*
32 *adenensis*), blue triangle (*E. balsamifera*), green square
33 (*E. sepium*).
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44 **Fig. 5.** Box-whisker plots and Principal Component Analysis
45 (PCA) of leaf size measurements of *Euphorbia* specimens (n
46 = 80) from *E. adenensis* (yellow), *E. balsamifera* (blue),
47 and *E. sepium* (green). Each box represents the
48 interquartile range, which contains 50% of the values and
49 the median (horizontal line across the box); the whiskers
50 are the lines that extend from the box to the highest and
51 lowest values, excluding outliers (o). **A**, Leaf length,
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3 including a silhouette of the average leaf shape and size
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5 for each species. **B**, Leaf maximum width. **C**, Length from
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7 leaf base to the point of maximum width. **D**, Mucron length.
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10 **E**, Ratio between leaf length (A) and leaf maximum width
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12 (B). **F**, Scatter plot of the first two components of the
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14 PCA based on the five leaf measurements. Row data are
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16 provided in Supporting Information (Table S3).
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21 **Fig. 6.** Representative field images of the three species:

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23 *Euphorbia adenensis*: **A**, Plant growing in stony desert,
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25 Oman. **B**, Male cyathium. **C**, Female cyathium. **D**, Habitat,
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27 Oman. **E**, Young female cyathium. **F**, Mature capsule.

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30 *Euphorbia balsamifera*: **G**, Population on volcanic rocks, El
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32 Hierro Island (Canaries). **H**, Male cyathium. **I**, Female
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34 cyathium. **J**, Plant in sandy substrate, coast of NW Africa.

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37 **K**, Developing ovary. **L**, Mature capsule. *Euphorbia sepium*:

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40 **M**, Population in a desert wadi, Western Sahara. **N**, Male
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42 cyathium. **O**, Female cyathium. **P**, Live fence, NE Senegal.

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45 **Q**, Detail of the long narrow leaves. Photos: Flickr public
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47 domain (A, B, C.), C. Dolbeare (P), C. Lemmel (M, N, Q),
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49 D. Marquina Reyes (K), J. Mesa (L), J.J. Morawetz (D, E,
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51 F), J.P. Peltier, www.teline.fr (H, I, J), R. Riina (O,
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53 R), T. Villaverde (G).
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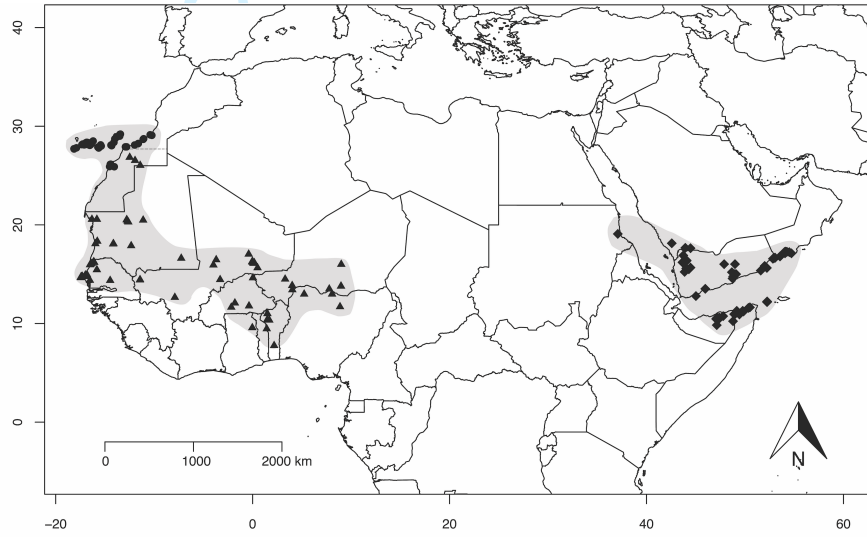
Supporting Information

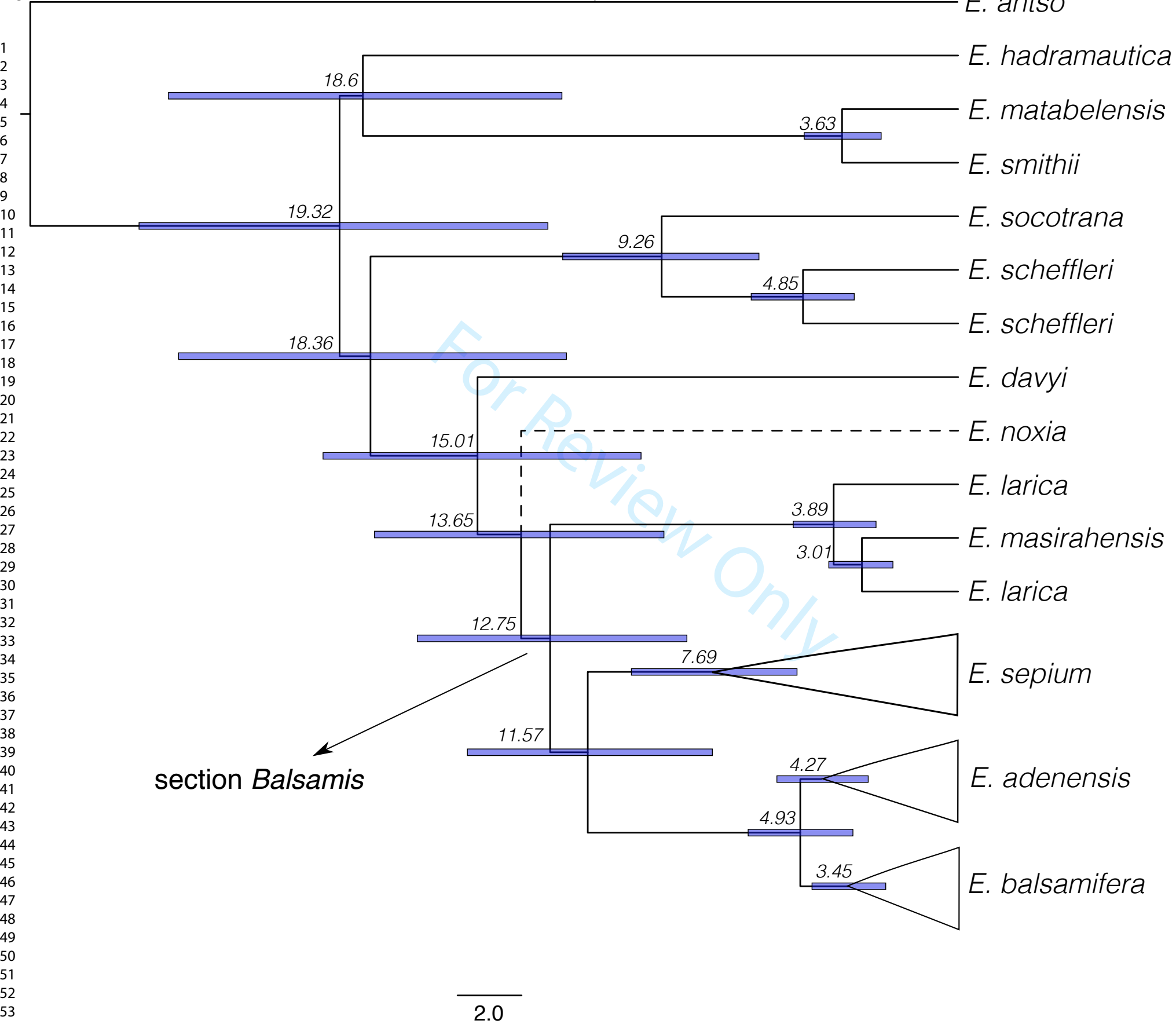
Table S1. List of plant specimens examined for the taxonomic treatment, climatic niche analysis, and distribution map (Fig. 1). Some records were filtered and curated from an original row-set of data downloaded from GBIF (<http://doi.org/10.15468/dl.0qiyuu>) others come from other sources (i.e., herbarium 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*.

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section *Balsamis*

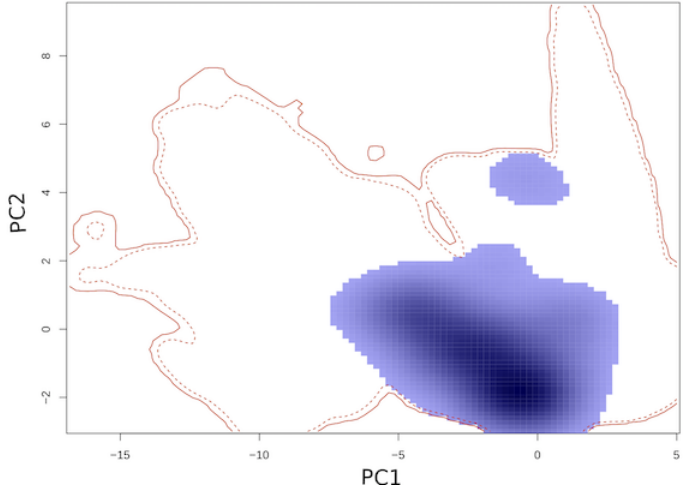
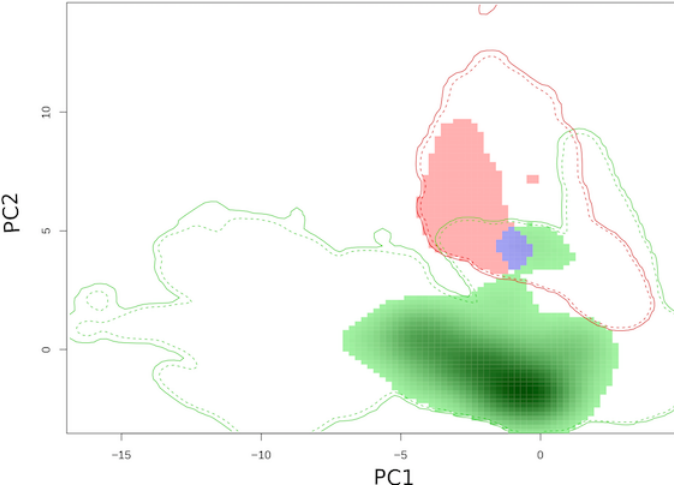
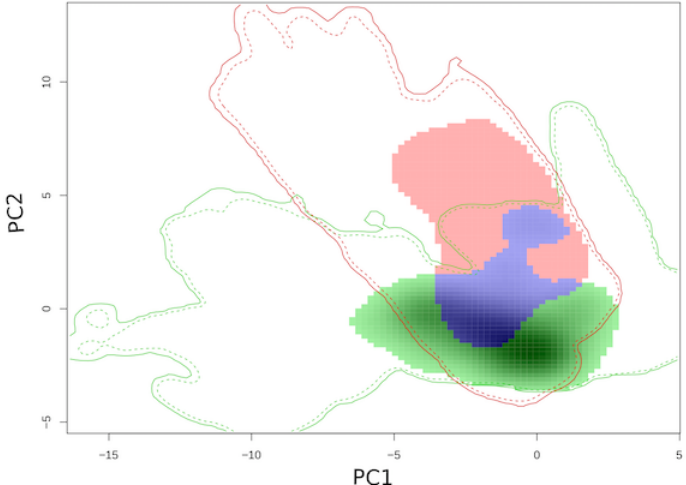
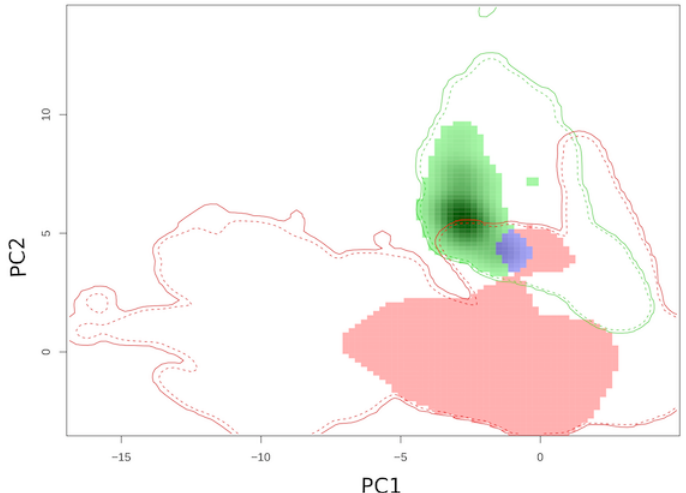
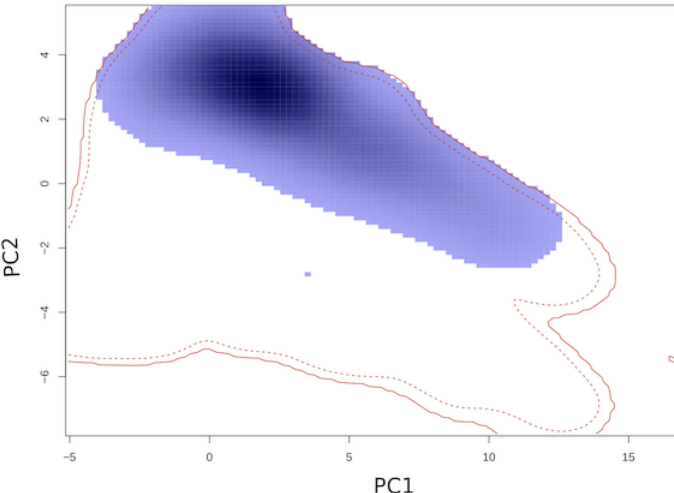
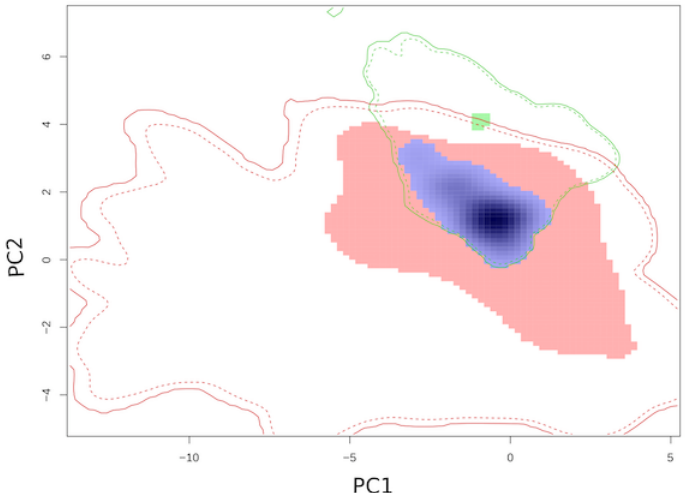
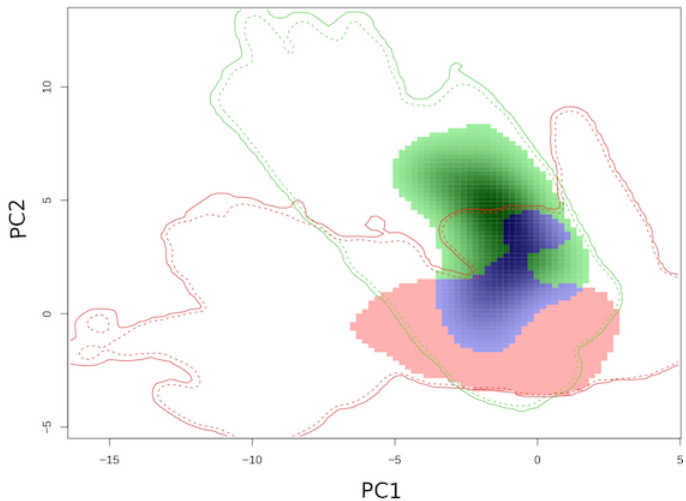
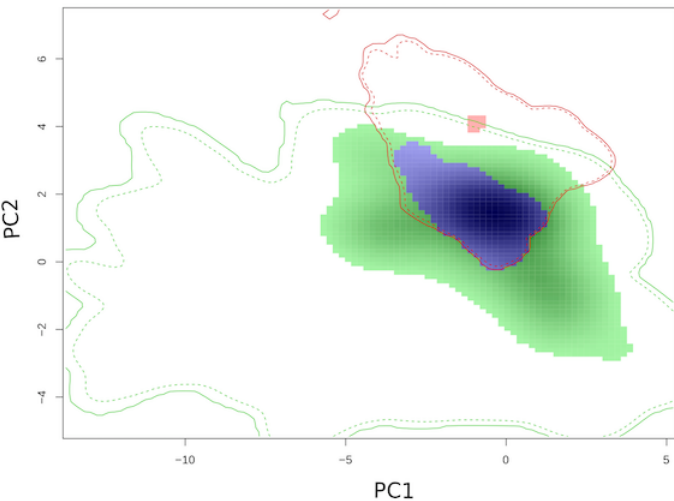
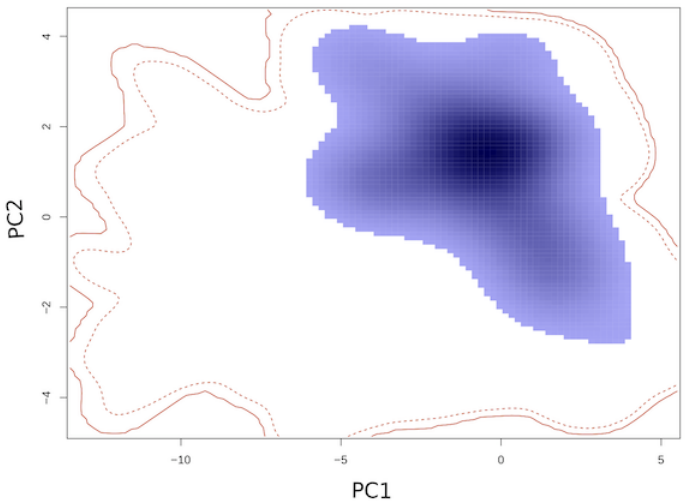
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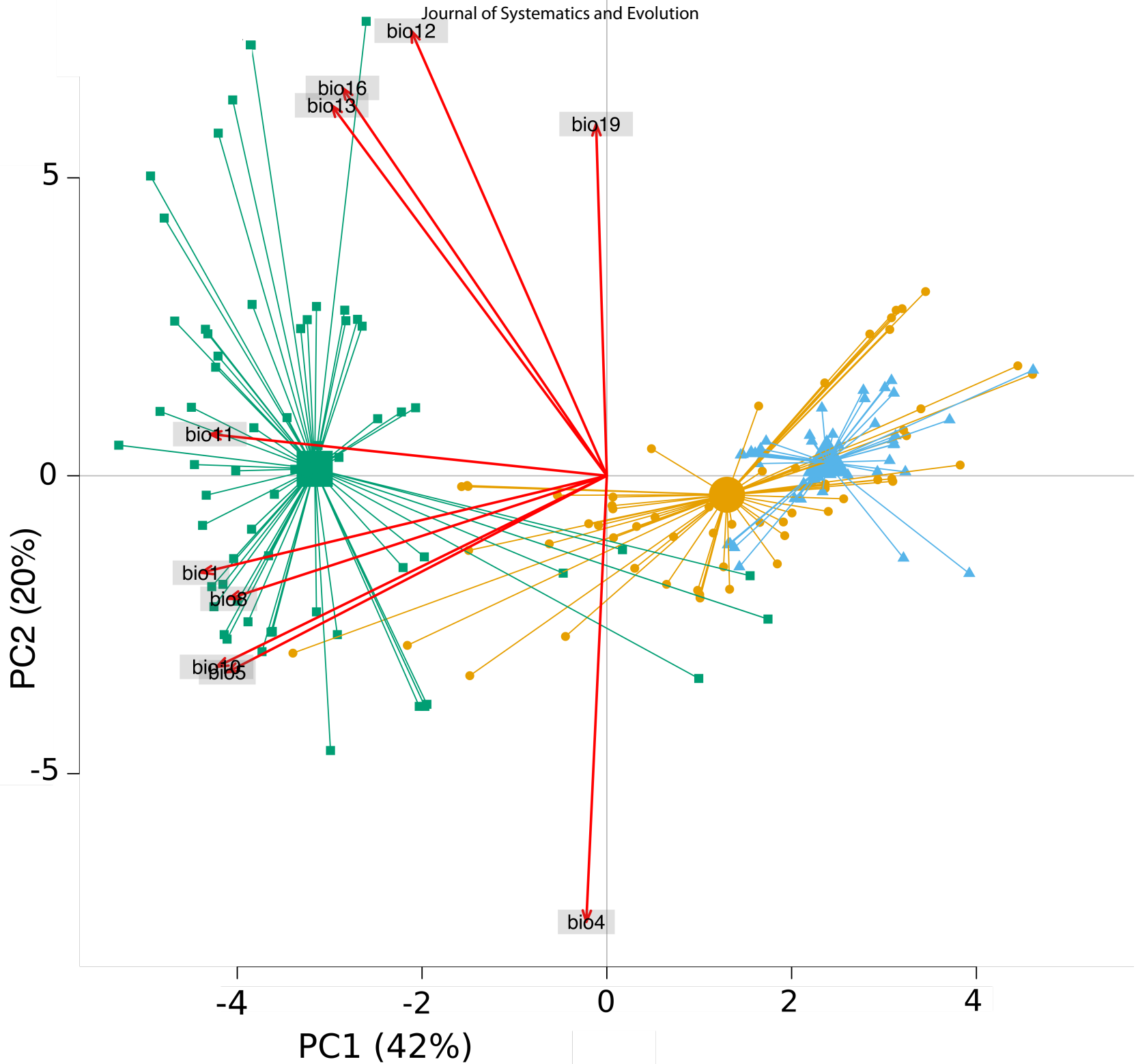
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E. adenensis

E. balsamifera

E. sepium





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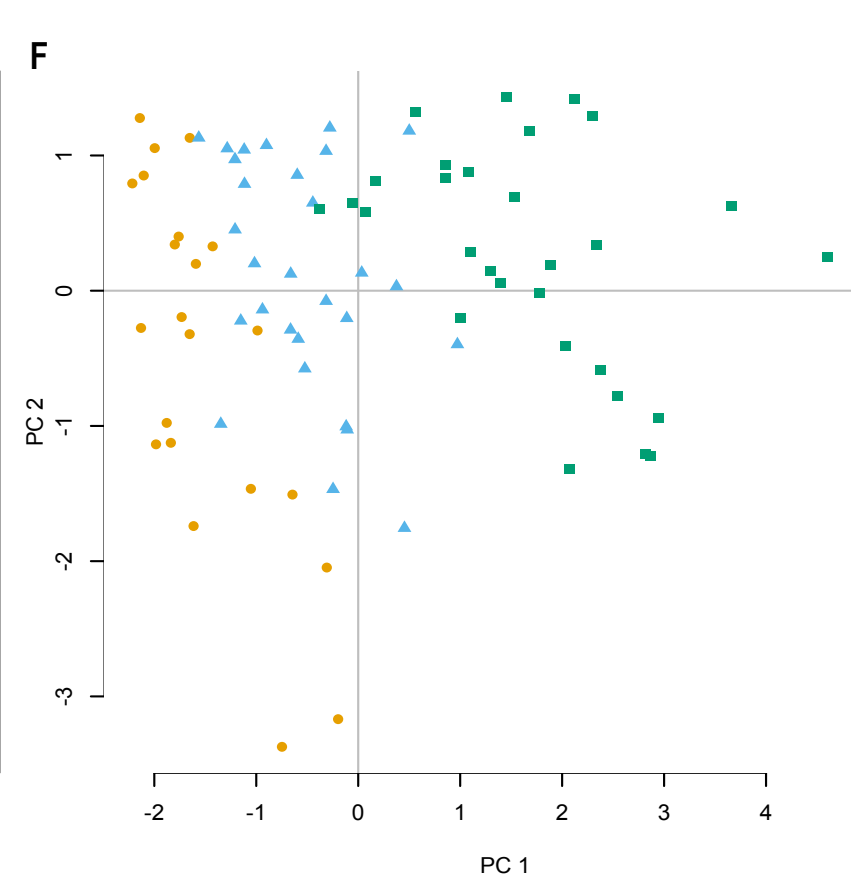
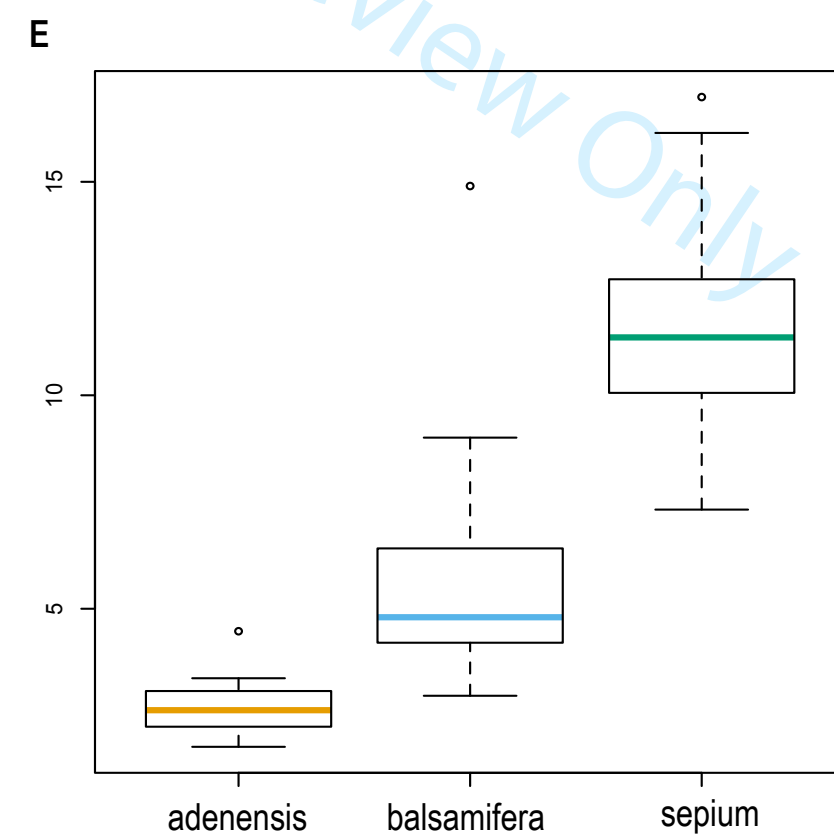
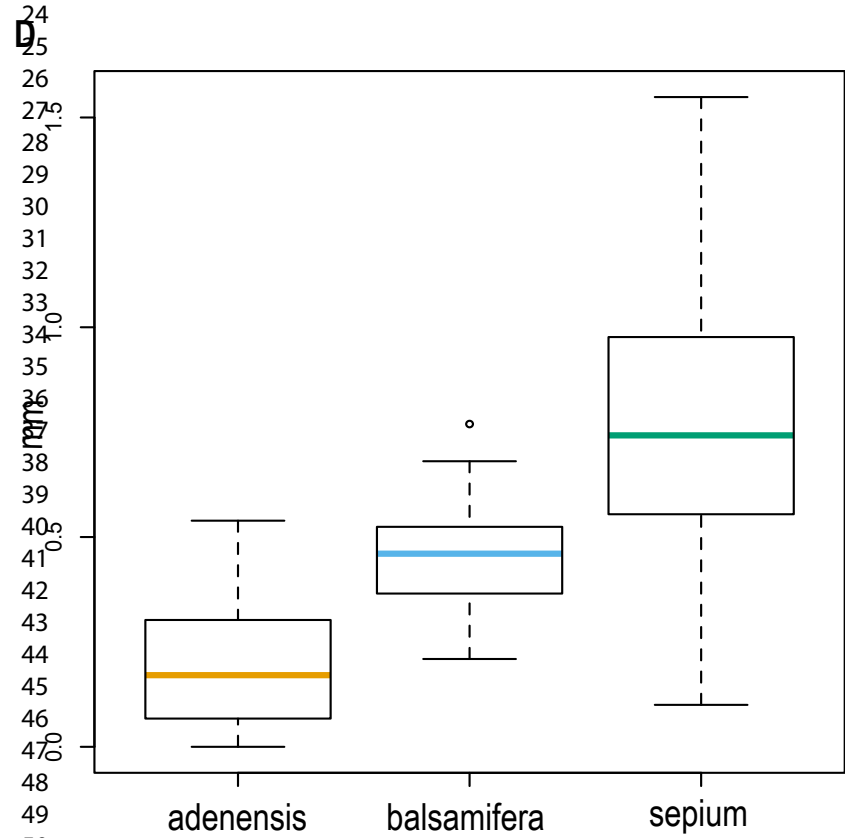
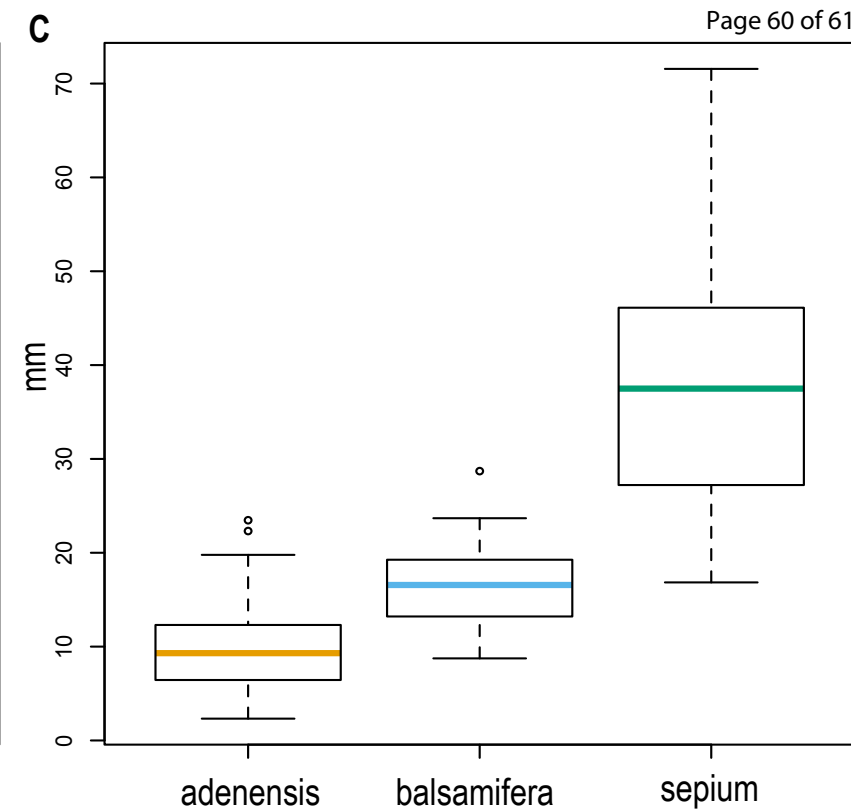
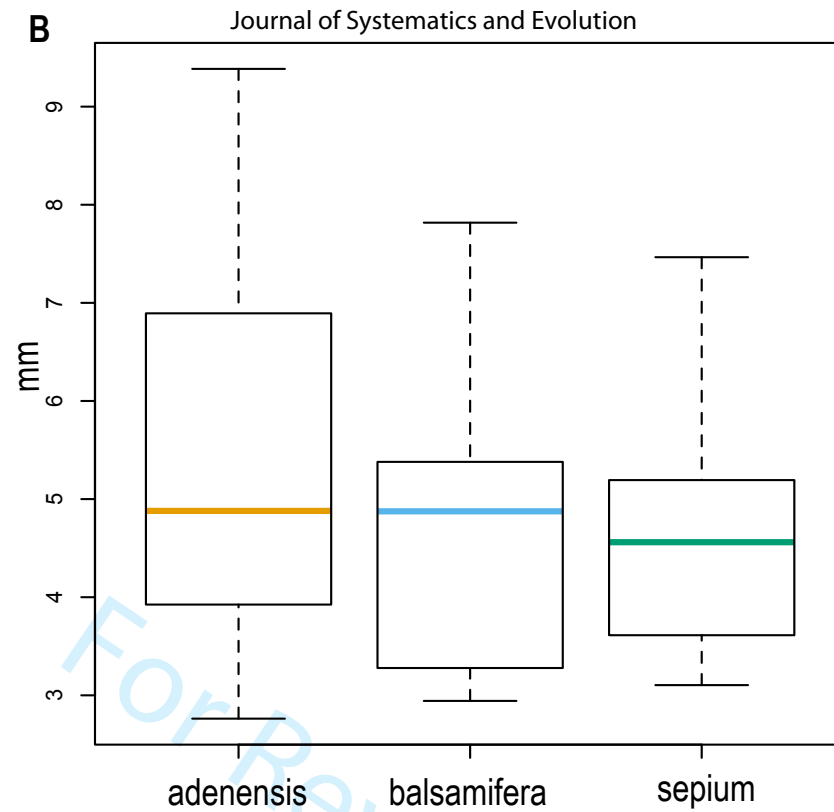
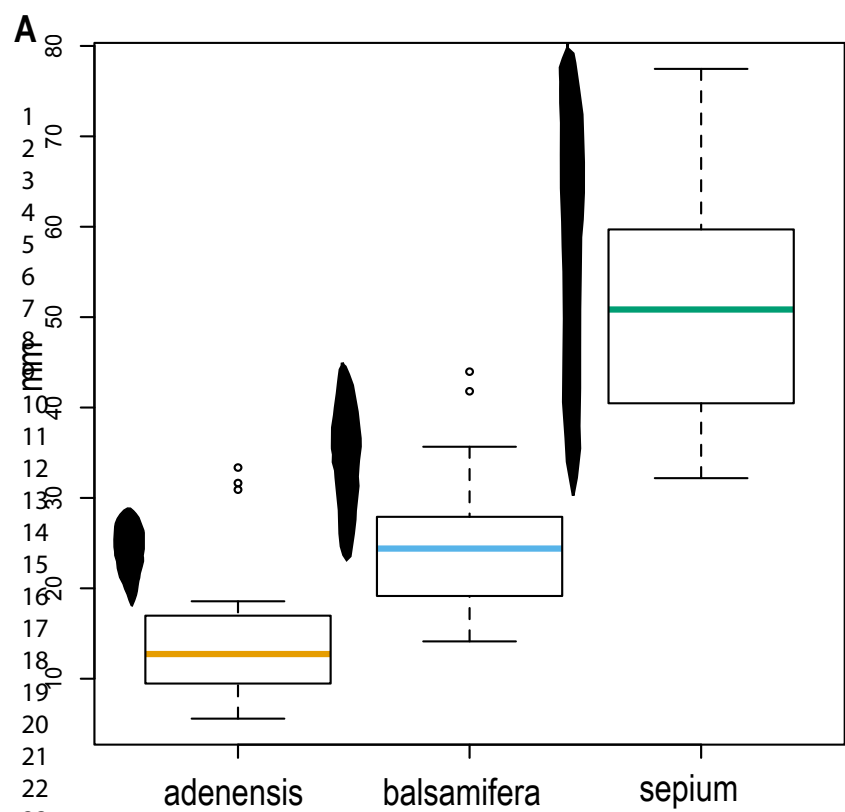




Fig. 6. Representative field images of the three species: *Euphorbia adenensis*: A, Plant growing in stony desert, Oman. B, Male cyathium. C, Female cyathium. D, Habitat, Oman. E, Young female cyathium. F, Mature capsule. *Euphorbia balsamifera*: G, Population on volcanic rocks, El Hierro Island (Canaries). 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. 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).

182x297mm (600 x 600 DPI)