



Comprehensive review of morphological adaptations and conservation strategies of cactiform succulents: A case study of *Euphorbia* species in arid ecosystems

A. Taha*, A. Ettaqy*, M. El Mderssa*, M. Belaqqiz**, M. Fokar***, H. Boukcim****, A. Zine El Abidine*****, Y. Abbas*

*Sultan Moulay Slimane University, Beni Mellal, Morocco

**Cadi Ayyad University, Marrakech, Morocco

***Texas Tech University, Lubbock, USA

****Mohammed VI Polytechnic University, Ben Guerir, Morocco

*****National Forestry School of Engineering, Salé, Morocco

Article info

Received 17.07.2023

Received in revised form 19.08.2023

Accepted 30.08.2023

Sultan Moulay Slimane University, BP 23000, Beni Mellal, Morocco. Tel.: +212-523-480-218. E-mail: contact@usms.ma

Cadi Ayyad University, B.P. 511, Marrakech, Morocco. Tel.: +212-524-437-741. E-mail: vp-ri@uca.ma

Texas Tech University, Lubbock, TX 79409, USA. Tel.: +1-806-742-69-27. E-mail: chiquito.craso@ttu.edu

Mohammed VI Polytechnic University, 70000, Laayoune, Morocco. Tel.: +212-525-073-100. E-mail: contact@um6p.ma

National Forestry School of Engineering, BP 511, Salé, Morocco. Tel.: +212-537-861-149. E-mail: contact@enfi.ac.ma

Taha, A., Ettaqy, A., El Mderssa, M., Belaqqiz, M., Fokar, M., Boukcim, H., Zine El Abidine, A., & Abbas, Y. (2023). Comprehensive review of morphological adaptations and conservation strategies of cactiform succulents: A case study of *Euphorbia* species in arid ecosystems. *Biosystems Diversity*, 31(3), 358–367. doi:10.15421/012342

Cactiform succulents, belonging to the *Euphorbia* genus, are distinctive species found in the arid and semi-arid ecosystems of Macaronesia and the Arabian Peninsula. Resembling cacti in appearance, they exhibit unique morphological characteristics, such as succulent, green-stemmed structures with ribs, accompanied by a pair of stipular spines. These plants have evolved to thrive in well-draining substrates, including both surface and rocky soils, potentially as an adaptive strategy to combat edaphic drought conditions. Although initially associated solely with arid and desert environments, it is important to note that these cactiform succulents are not exclusively specialized for prolonged dry periods. Rather, they demonstrate morphological adaptations that help them endure arid conditions. The primary objective of this review is to provide an up-to-date synthesis of knowledge concerning cactiform succulents within the *Euphorbia* genus. It aims to underscore their capacity to flourish in both arid and semi-arid zones, while underscoring the pressing conservation challenges that threaten these plants with degradation and potential extinction. The prevailing climatic conditions, marked by extended and recurrent droughts exacerbated by escalating temperatures, climate fluctuations, and escalating human impact, collectively pose a formidable obstacle to conserving these cactiform succulents and their respective ecosystems. All these threats jeopardize these invaluable natural resources, which hold multifaceted significance spanning environmental, socio-economic, and medicinal domains.

Keywords: spiny and ribbed-stem cactiforms; arid habitat; tropical climate; Macaronesia; Arabian Peninsula.

Introduction

Euphorbia is one of the giant genera of angiosperms, with over 2,000 species of widely varying growth forms, including succulent and xerophytic species (Frodin, 2004; Dorsey et al., 2013). In this genus, three major photosynthetic systems are found: C₃, C₄ metabolism, and crassulacean acid metabolism (CAM) (Webster, 1975; Horn et al., 2014). Plants in this genus are differentiated by a partial inflorescence, called cyathia that is reduced in size and assembled in a caliciform involucre associated with two subcyathial bracts (Bruyans et al., 2006, 2011).

Cactiform *Euphorbia* with ribbed stems, resemble “columnar cacti”, and are often confused with the Cactaceae, but are identifiable by their twin spines carried on a spine shield and their ability to secrete a “milky sap” called latex in response to physical aggression (Chaudhary et al., 2023). Furthermore, these cactiforms adopt the CAM photosynthetic system (Edwards & Donoghue, 2006; Al-Turki et al., 2014; Niechayev et al., 2019). This photosynthetic regime specifically allows it to adapt to prolonged drought (Evans et al., 2014; Masrahi et al., 2015). All belong to the stem succulent biome, distributed between 10° and 30° in both the Northern and the Southern latitudes round the Equator (Ringelberg et al., 2020). They are also found primarily in endemic “hotspots” from Africa, Arabian Peninsula, and Southern Asia (Carter, 1994; Swamy & Prasad, 2022).

Nevertheless, these species form a veritable “green blanket”, particularly in areas that seem unlikely to be colonized by plants, such as karst and igneous rock cliffs, coral reefs, and sandbanks (Ettaqy et al., 2020; Al-

Qthanin & Al-Yasi, 2021; Chaudhary et al., 2023). This type of substrate with a low water retention capacity is in perfect compatibility with the stem-succulence, the stem being endowed with specialized tissues for water storage (Evans et al., 2014). Therefore, succulents manage to survive in environments marked by high temperatures (Eggl & Nyffeler, 2009). These factors explain the lower vulnerability of *Euphorbia* ecosystems to fire, thanks to their high richness in succulents and their poverty in dry grasses (Eiserhardt et al., 2017). Conversely, *Euphorbia* ecosystems commonly located in dry areas are now threatened with extinction (Hernández-Teixidor et al., 2020; Al-Qthanin & Al-Yasi, 2021). The threat situation for this type of plant that is adapted to hostile environments requires a quick and strategic response for their conservation (Pennington et al., 2018; Al-Namazi et al., 2021). To meet the challenges of climate changes, these cactiforms are likely to become one of the best choices for urban landscaping in arid regions (Grace, 2019). Therefore, it is critical to safeguard phytoresources with significant ecological and socio-economic interest, mainly in their native areas, thus, contributing to the sustainable development of these arid-prone territories (Hall et al., 2010; Ali Al-Hajj et al., 2018). Note that these species also have multiple uses as melliferous or medicinal plants (Ait Abderrahim et al., 2019; Benjamaa et al., 2020). Moreover, the latex extracted from these plants contains bioactive substances of various types of macrocyclic diterpenoids (Bin Muhsinah et al., 2020; Zhao et al., 2022). These substances were proved to have medicinal and therapeutic benefits for various types of diseases and illnesses (Rosen et al., 2012; Si et al., 2018; Wang et al., 2019).

The objectives of this review are to characterize succulent *Euphorbia* with polygonal stems, update the knowledge of their ecological habitat, and to evaluate particularly their adaptation and their conservation in arid environments from Macaronesia and the Arabian Peninsula.

Distribution of cactiforms *Euphorbia* with ribbed stems in Africa and Arabia

Cactiform *Euphorbia* with ribbed stems are native to the African continent (Zimmermann et al., 2010). Today, these plant species found only in the hot spots of Africa and the Arabian Peninsula, represent the living remains of the ancient flora common to the entire continent, known as the “Rand Flora” (Sanmartín et al., 2010; Linder, 2014; Pokomy et al., 2015). Indeed, the distribution of these species was generally near the borders of these two regions (Pokomy et al., 2015). The reason is that in the Miocene, they were driven by aridity to wet areas (Thiv et al., 2010; Bruyns et al., 2011; Bellstedt et al., 2012). As consequence, succulent *Euphorbia* from Macaronesia and East Africa, as well as the Southern Arabian Peninsula, share ecological, geographical and phylogenetic traits (Xie et al., 2014; Riina et al., 2021).

In Northwest Africa, the region comprising Macaronesia and the Central High Atlas, this genus of cactiform *Euphorbia* is considered part of the Macaronesia species group (Ogbum & Edwards, 2010; Males, 2017) while the Arabian Peninsula region is also part of the “Somali-Masaai Center of Endemism”. Likewise, the southern region of the Arabian Peninsula includes a mixture of flora from Arabia, Africa, and the Mediterranean region (Alfarhan, 1999; Males, 2017; Al-Qathanin & Al-Yasi,

2021). Thus, it appears that cactiforms in the southwestern Arabian Peninsula emerged following the opening of the Red Sea about 23 million years ago (Bosworth & Stockli, 2016). This provides the soil conditions of bedrock as well as wet influences favourable for the establishment of this type of plant. Therefore, cactiform species from these regions are frequently found in areas influenced by ocean fog, such as islands, coastal areas, and highlands or high mountains. This oceanic fog is a sustainable water resource that waters these regions (Valjarević et al., 2023).

Phylogenetic, morphological and classification of cactiform plants with ribbed-stem within *Euphorbia*

Morphological characters of cactiform Euphorbia. Cactiform *Euphorbia*, native to Africa and Arabia, occur in three different types of plants, shrubs, trees and dwarfs. They are distinguished by the following morphological traits according to Hom et al. (2012): cyathial gland merosity, seed caruncle, inflorescence position, growth form and number of spines per shoot (Fig. 1).

Six morphological characters (Fig. 1) characterize cactiform *Euphorbia* species:

- character (1) cyathial gland merosity, as usually five glands (Fig. 1d);
- character (2) gland appendages, as absent;
- character (3) caruncle: caruncles are absent (Fig. 1c);
- character (4) growth form: cactiforms (Fig. 1e);
- character (5) phyllotaxy: alternate leaves including the backbone nodes (Fig. 1b);
- character (6) inflorescence position: lateral inflorescences (Fig. 1a).



Fig. 1. Morphological characters of cactiform xerophytic *Euphorbia*: a – lateral inflorescences of three cyathia, with a central male (desiccated) and two bisexual cyathia; b – two alternating spiny outgrowths present on each spine-shield; c – ecarunculate seeds of *E. resinifera*; d – involucre cup associated with two subcyathial bracts and bearing five glands (5-merous cyathia); e – cactiform growth-form (*E. echinus*)

In summary, cactiform *Euphorbia* from Macaronesia and the Arabian Peninsula share the following characteristics: glands are often five or six in number, gland appendages are absent, ecarunculate seeds, stems are ribbed like columnar cacti, spiny outgrowths of new shoots are paired and alternate, simple cyme inflorescence is placed laterally on green stems. The cyathia form sets of three, of which the central one is normally male, sessile, flowering first, and two lateral cyathia are bisexual (Fig. 1a).

Phylogenetic classification of ribbed-stem cactiforms within *Euphorbia*. The genus *Euphorbia* is divided into four monophyletic subgenera: *Athymalus*, *Chamaesyce*, *Esula*, and *Euphorbia* (Zimmermann et al., 2010; Wei et al., 2021). The subgenus *Euphorbia* is the largest in number of species (approximately 800 species), divided into 21 sections (Dorsey et al., 2013; Riina et al., 2013). The biggest division was the section *Euphorbia*, which includes all cactiform species of *Euphorbia* (Horn et al., 2014). Next, these spiny succulents of *Euphorbia* constitute a homogeneous group (Dorsey et al., 2013). Therefore, it is altogether appropriate to name them cactiform *Euphorbia* with ribbed stem.

Botany of cactiform *Euphorbia* with ribbed stem from Macaronesia and the Arabian Peninsula

Cactiform *Euphorbia* with ribbed stems from Macaronesia, covering southwest Morocco and the Canary Islands, are all succulents with leafless stems. They play a role in the creation of *Euphorbia* ecosystems (Fig. 2 and 3). These ecosystems are characterized by the coexistence of species of tropical, Saharan and Mediterranean origin (Médail & Quézel, 1999; Benabid, 2000; Ettaqy et al., 2023).



Fig. 2. Cactiform *Euphorbia* ecosystems in the Central High Atlas of Morocco: Tetraclino-Euphorbietum resiniferae (Photos by Mounir Mohamed)

Euphorbia officinarum subsp. *echinus* (Hook.f. & Coss.) Vindt. (1960), shrub with very tight stems of 5 to 8 ribs, bush type and can reach 1 m high (Fig. 3b). This species is the most widespread in space and density. The territory of this species is very extensive, covering the Moroccan Macaronesia enclave. It is found in southern Morocco, between Agadir and the city of Dakhla (Peltier & Msanda, 1995). This species grows on generally rocky substrates, at altitudes ranging from sea level to over 1900 m (Msanda et al., 2002; Carter, 2005). Cactiforms with ribbed stems from the Canary Islands are represented by two species, *E. canariensis* and *E. handiensis*. Also, the flora of the Canary Islands is closely related to that of North-West Africa and the Arabian Peninsula (Coello et al., 2023). Thus, the Canary Archipelago is made up of seven main islands of volcanic origin belonging to "Macaronesia" (Florenco et al., 2021).

Euphorbia handiensis Burchard (1912). A thorny cactiform, endemic to Fuerteventura, found between 50 and 300 m above sea level. It has leafless stems with 8 to 14 ribs (Marrero Gómez & Carqué Alamo, 2004).

Moroccan cactiforms with ribbed-stem are represented by two species, *Euphorbia officinarum* L. (1753) and *E. resinifera* O. Berg. (1863). The former is exclusively Macaronesian, located near the Atlantic coast, and comprises two subspecies, *Euphorbia officinarum* subsp. *beaumieriana* and *Euphorbia officinarum* subsp. *echinus*. The second species is continental, extending beyond the Macaronesian zone to the central High Atlas, where it covers the northern slopes of the Atlas Mountains exposed to the Atlantic Ocean.

Euphorbia resinifera O. Berg. (1863), endemic to Morocco. Vernacular names; Zeggoum in Arabic and Tikioute in Amazigh. This is a spiny succulent shrub usually with four ribs, leafless stems. That species is mostly distributed on calcareous karst substrates (Fig. 2). Currently, this plant is distributed in two regions distant from each other (Lawant & Winthagen, 2001). One very large population grows in central Morocco, on the northern slopes of the Central High Atlas, extending from Elksiba north of Beni Mellal to Demnat, from 640 to 1900 m in altitude (Ettaqy et al., 2020), while the other, extremely small, population is located in Tizi N'Taraktin village, near the town of Tafraout in Southwest Morocco (Carter, 2005).

Euphorbia officinarum subsp. *beaumieriana* (Hook. f. & Coss.) Vindt. (1960), named after the French explorer Auguste Beaumier. It is also called *E. officinarum* subsp. *officinarum*. This endemic of Morocco is a thorny cactiform, having leafless-stem of 8 to 13 ribs. This species frequents the Atlantic coast from sea level to 300 meters above sea level (Carter, 2005). It usually grows in association with *E. echinus* and *Argania spinosa* L. on limestone substrates near the Agadir region (Fig. 3a) (Msanda et al., 2002).

It grows on colluvial soils and covers an area of around 12 km² (del Arco Aguilar et al., 2010). It is closely related to *E. echinus* (Coello et al., 2023).

Euphorbia canariensis L. (1753), it is an endemic of the Canary Islands, distributed on all the islands in the archipelago except Lanzarote. They grow on rocky slopes, cliffs and lava flows, from sea level up to 900 m. This species usually has four-ribbed stems, 2 to 4 m high, with even, curved spines (Álvarez Escobar & Rodríguez Delgado, 2008; del Arco Aguilar & Rodríguez Delgado, 2018).

Cactiform *Euphorbia* with ribbed stem from Arabian Peninsula. The coastal and subcoastal area of the southern Arabian Peninsula, is part of the Somalia-Masai (formerly Eritrea-Arabia) regional center of endemism. This center has a high diversity of cactiform plants (Grace, 2019; Ringelberg et al., 2020), especially in mountainous areas with arid to sub humid climate (Al-Namazi et al., 2021). However, many species exhibit deciduous leaves. Therefore, we will briefly present the botany of some of these plants.

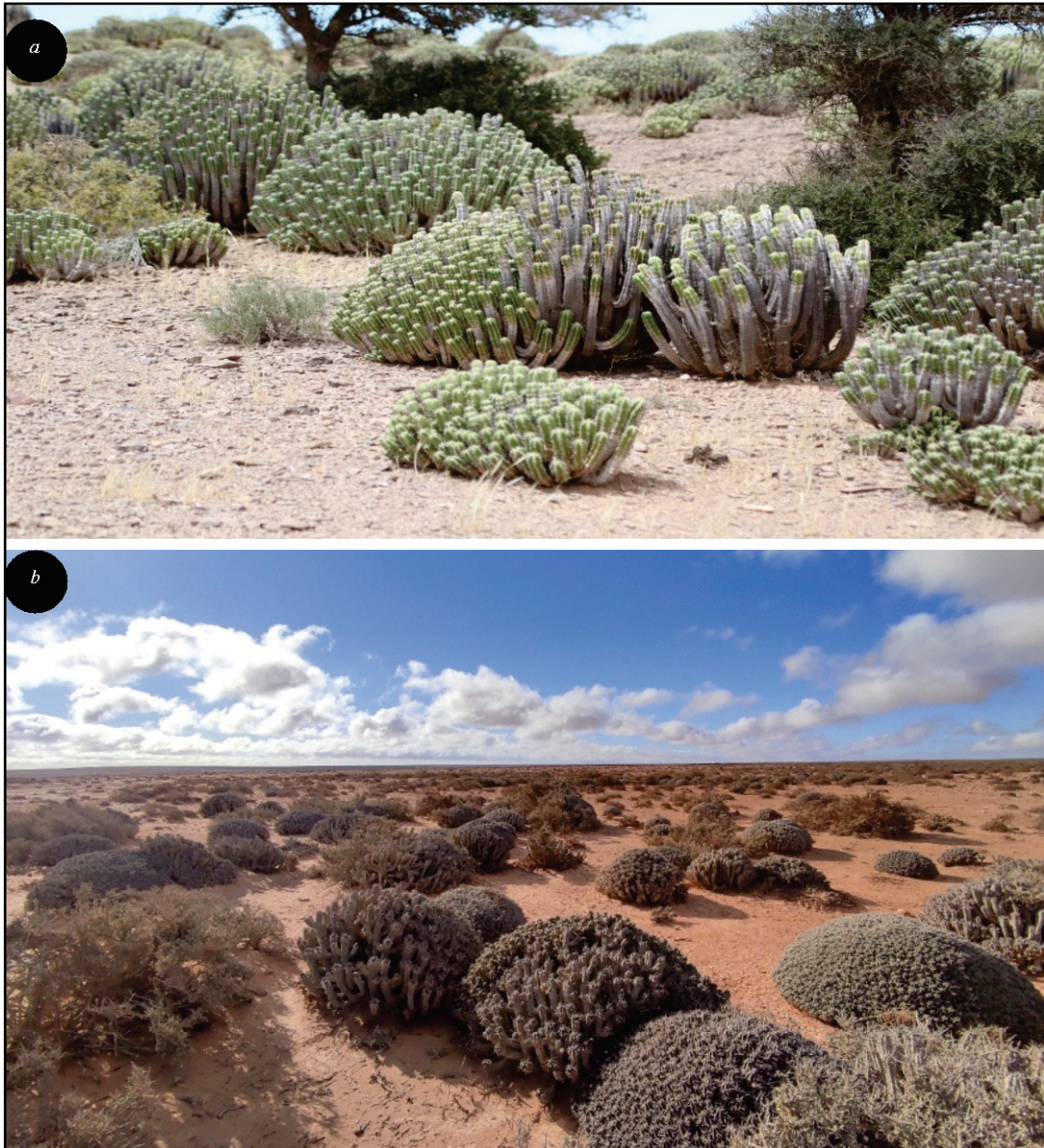


Fig. 3. Cactiform *Euphorbia* ecosystems in Southwest Morocco: *a* – phytosociation between *E. officinarum* L. with *Argania spinosa* (L.) Skeels, in Oued Massa near Agadir; *b* – *Traganopsis glomeratae* – *Euphorbietum echini* of Akhfennir-Laayounne (photos by Mounir Mohamed)

Euphorbia madinahensis Fayed & Al-Zahrani (2007). Spiny succulent shrubs up to 1.5 m high, with stems of 3 to 5 ribs. This species is present on granitic mountains with low rainfall, from 1050 to 2350 m altitude (Fayed & Al-Zahrani, 2007). It is considered a vulnerable species (VU) in accordance with IUCN Red List categories and criteria, according to Fayed & Al-Zahrani, (2007).

Euphorbia saudiarabica Fayed & Al-Zahrani (2007). Plant endemic to Southwestern Saudi Arabia in the Qunfudhah-Djizan Region. The two vernacular names are “Saab” and “Suoiab”. It is a cactiform whose main axis can reach 3 m high, having 3 to 5 ribs (Fig. 4b). The distribution of this species varies from sea level to 30 m, growing on sand and on cracks of basaltic rocks. This species is endangered (EN) (Fayed & Al-Zahrani, 2007).

Euphorbia parcircumulosa Schweinf. (1899). Species endemic to Yemen and Saudi Arabia. It is a spiny cactiform with 3 or 4 angles (Fig. 3g). This succulent is the sister of the two species of Macaronesia *Euphorbia*; *E. echinus* and *E. handiensis* (Bruyns et al., 2011). *E. parcircumulosa* grow on rocky and granitic sand soils at the foot of low altitude mountains between 400 and 2000 m (Fayed & Al-Zahrani, 2007).

Euphorbia taifensis Fayed & Al-Zahrani (2007), takes its name from the city of “Taif”, where this tree is endemic. The plant can reach 10 m,

succulent with a ribbed stem of 3 to 6 (7) angles (Fig. 4f). It is found on stony soils and rocky slopes of wadis (of river valleys), between 1,700 and 2,100 m altitude (Fayed & Al-Zahrani, 2007).

Euphorbia collenetteae Al-Zahrani & El-Karemy (2007). This species is a rudimentary deciduous cactus. This *Euphorbia* has stems with 3 to 8 ribs, branching from the base and reaching up to 3 to 4 m high (Fig. 4c and 4d). It grows on the islands and coasts of the Red Sea. The plant has been recorded on substrates of coral origin, as well as on basaltic outcrops, from sea level to 75 m above sea level. This species is proposed as Near Threatened according to IUCN criteria (Al-Zahrani & El-Karemy, 2007).

Euphorbia cactus Ehrenb. ex Boiss. (1862), is native to the endemic center of the Somalia-Masai region, which includes Eritrea, Ethiopia and the Arabian Peninsula. The species occurs in Saudi Arabia, especially in the Fayfa Mountains, Yemen, Oman and Dhofar. Its range extends from sea level to 2,000 m altitude, and it grows on rocky slopes, as well as on fluvial stone deposits. This shrub is 1 to 3 m tall, and consists of 3 to 4 dark green stems with three ribs (rarely 4 or 5) (Fig. 4e) (Carter & Wood, 1982; Al-Hamoud et al., 2022).

Euphorbia inarticulata Schweinf. (1899). Endemic plant of the Arabian Peninsula; Yemen and Saudi Arabia. *E. inarticulata* is a succulent plant up to 2 m high, with a short trunk, but often without trunk. The stems

have 3 to 5 angles, branched at the base. It grows on cliffs and stony grounds, from 300 to 2,000 m of altitude (Alasbahi et al., 2020).

Euphorbia fruticosa Forssk. (1775), endemic to Yemen, bearing two vernacular names, Shurur or Zaqum (Fleurentin & Pelt, 1982). It is a small spiny succulent bush of about 40 cm, with stems of 7–10 ribs, sometimes 12 ribs. The plant is found on cliffs and stony plains, at altitudes of 1094 to 2200 m (Alasbahi et al., 2020).

Euphorbia fractiflexa S. Carter & J. R. I. Wood (1982). This spiny spurge is endemic to Yemen and Saudi Arabia. This succulent has deciduous leaves, three-angled stems, branching at ground level and up to 2.5 m high. It grows generally on rocky gravel soils, stony soils from coastal plains with altitudes between 150 and 539 m (Carter & Wood, 1982; Al-Zahrani & El-Karemy, 2007).

Euphorbia ammak Schweinf. (1899), is a candelabra tree of 10 m high, endemic to Yemen and Saudi Arabia. It has generally 4-ribbed stems, with leaves sometimes appearing at the top of its branches. This tree is widespread on rocky areas at altitudes ranging from 1000 to 2500 m (Fayed & Al-Zahrani, 2007).

Euphorbia momccoyae Lavranos (2011), is a cactiform endemic to the Sultanate of Oman, Dhofar province, with tiny, rapidly deciduous deltoid leaves. This plant is 125 cm high, with 10 to 30 basal branches from a main stem, with 5 or 6 ribs. It is distributed on the limestone rocky cliffs along the shores of the Arabian Gulf bordering Yemen, up to an altitude of 1,000 m, governed by the influences of the southwest monsoon of the Indian Ocean (Lavranos, 2011).

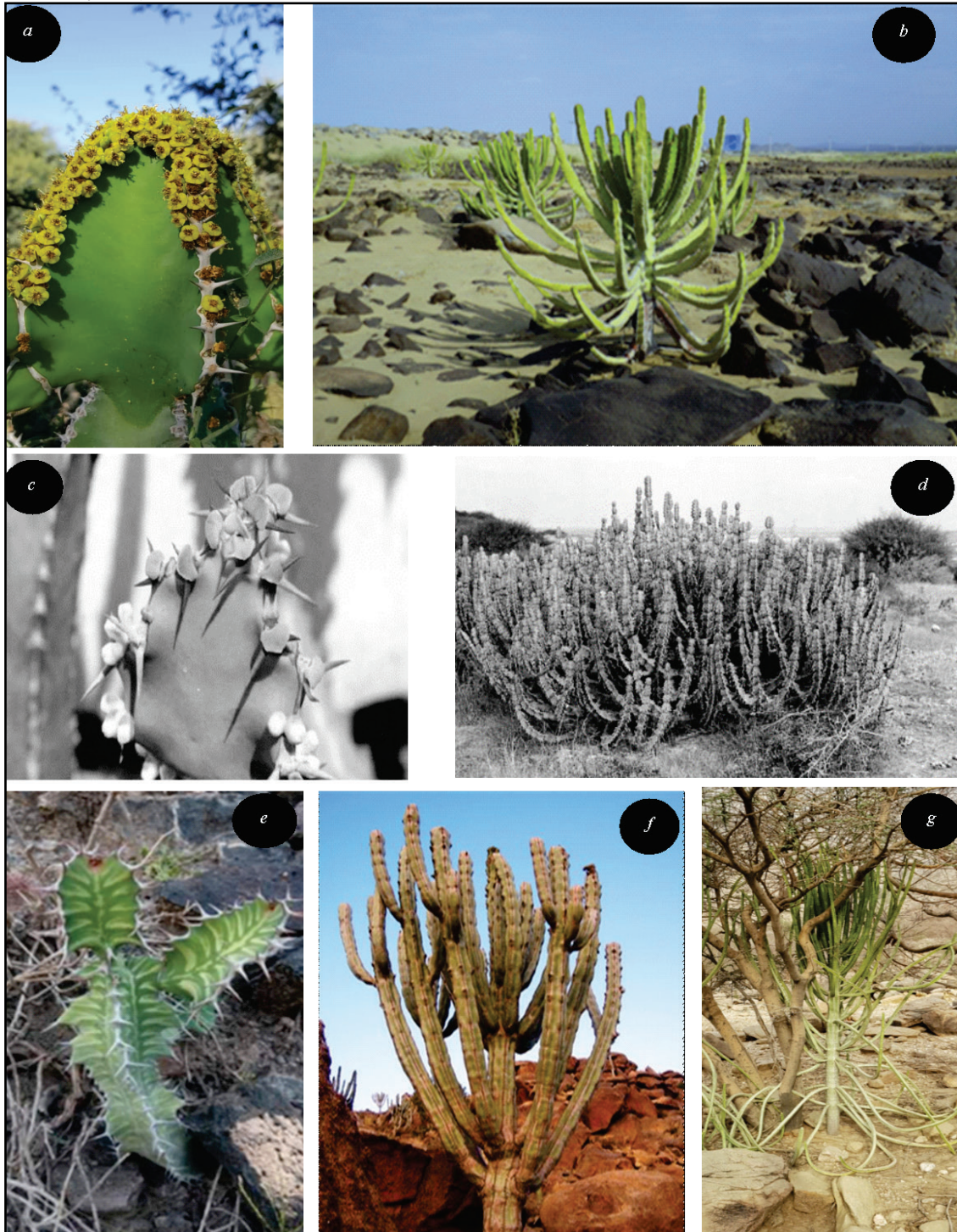


Fig. 4. Cactiform *Euphorbia* from Arabian Peninsula: *a* – *E. inarticulata* (photo of Fuad Alhood); *b* – *E. saudiarabica* (photo of @SaudiZoologist); *c* and *d* – *E. collenetteae* (photo of Al-Zahrani and El Karemy); *e* – *E. cactus* (photo of Fuad Alhood); *f* – *E. taifensis* (photo of Ammar Bader); *g* – *E. parcimulosa* (photo of @SaudiZoologist)

Adaptive features of cactiform *Euphorbia* with ribbed stems in arid and semi-arid environments

Evolution of cactiform architecture according to the environmental driver. The architectural model of a plant depends on its ecological performance and its capacity to draw the resources it needs (water, light and nutrients). Therefore, it evolves in parallel with the disturbances that affect its environment (water availability, temperature, humidity, fires, pests, etc.) (Bernays et al., 2004). However, the cactiform *Euphorbia* of Macaronesia and those of the southern Arabian Peninsula have three different architectural types (Fig. 5) associated with three climatic groups, arid, temperate and tropical according to Anest et al. (2021):

– architectural type 1 (Fig. 5a): this model includes giant *Euphorbia*, commonly known as candelabra trees. In a tropical climate, such a tree can reach 15 meters. This type of plant is distinguished by the presence of an orthotropic monopodial stem, presenting a rhythmic branching, an indeterminate growth in the three categories of axes (C1–C2 and C3), and a subapical reiteration position);

– architectural type 2 (Fig. 5b): these are shrubs or trees, which are adapted to arid or even hyper-arid climates, and which present an indeterminate growth in the two categories of axes (C1 and C2). The main stem gives rise to a delayed reiteration, distal or basal, giving this type a chamaephyte and phanerophyte character;

– architectural type 3 (Fig. 5c): this group is essentially made up of bushy to dwarf plants, with unbranched orthotropic monopodial branches, sometimes multi-stemmed at ground level. They are adapted to temperate and semi-arid climates. Their primary axis generates branches by reiteration at its lower parts; moreover, their growth is indeterminate in a single axis C1.

The majority of these cactiforms from the Arabian Peninsula are phanerophytes, but they tend towards the architectural type (2) and (3) that characterizes the chamaephytes (Table 1). However, these plants have smaller and early deciduous leaves, for example in the following species: *E. ammak*, *E. collenteteae*, *E. fractiflexa*, *E. taifensis*, and *E. momccoyae* Lavranos. Then, these species look like some cactiforms from tropical climates, either in East and South Africa (Bruyns & Berry, 2019), as well as some other non-spiny cactiforms endemic to Brazil (Riina et al., 2015).

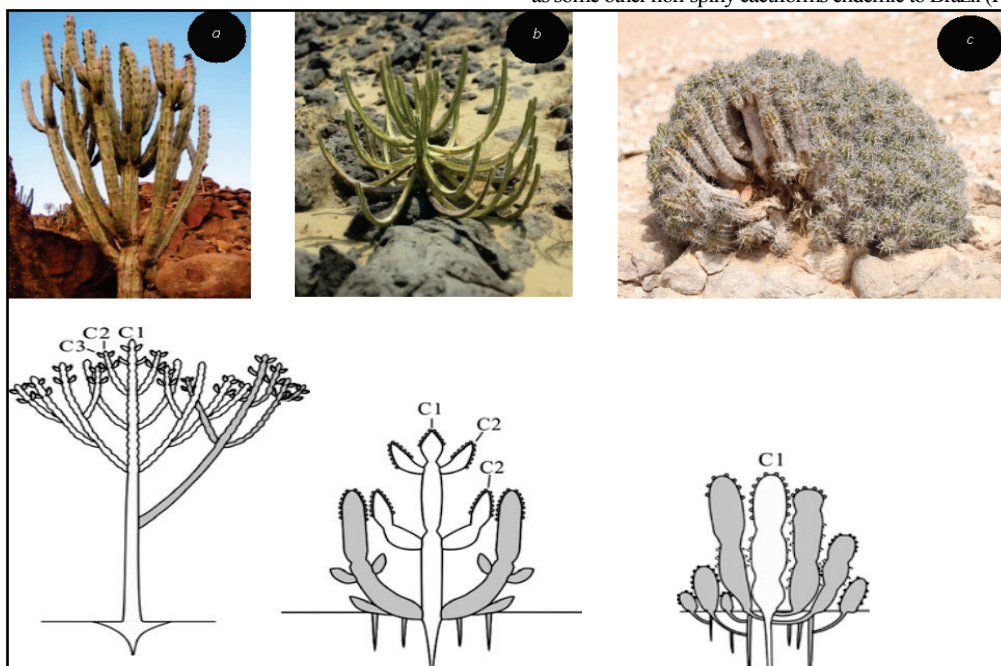


Fig. 5. Modified schema of the architectural types of cactiform *Euphorbia*, based on Anest et al. (2021), with examples of their respective plants: a – *E. taifensis* (type 1); b – *E. saudiarabica* (type 2); c – *E. echinus* (type 3)

Table 1
Main ecological traits of cactiforms from Macaronesia and the Arabian Peninsula

Species	Elevation	Number of ribs	Height, dm	Sub-region	Architectural type	Leaves	Plant life forms	Substrate	References
<i>E. resinifera</i>	600–2100	4 (3,5,6)	2–12	Mor, Mac	(3)	absent	Ch	Dol-lim and cong rock	Ettaqy et al. (2020)
<i>E. echinus</i>	0–1900	5–8	1–10	Mor, Mac	(3)	absent	Ch	Dol-lim, and granite rock	Carter (2005), Peltier & Msanda, (1995)
<i>E. beaumierana</i>	0–300	8–12	20	Mor, Mac	(3)	absent	Ch	Dol-lim rock	Carter (2005), Peltier & Msanda, (1995)
<i>E. canariensis</i>	1000	4(3)	+20	Mac	(2)	absent	Ch to Ph	Volcanic rocks	Coello et al. (2023)
<i>E. handiensis</i>	50–300	8–12	4–10	Mac	(2)	absent	Ch	Volcanic soil	Marrero Gómez, Carqué Alamo, (2004)
<i>E. ammak</i>	1766	4.5(3)	100	AP	(1)	present	Ph	Limestone block	Fayed & Al-Zahari, (2007)
<i>E. parcimulosa</i>	400–2000	3–4	10–60	AP	(2)	absent	Ph	Rocky slopes and granite sand	Fayed & Al-Zahari, (2007)
<i>E. fruticosa</i>	300–2000	7–13	5	AP	(3)	absent	Ch	Stony and cliff soils	Alasbahi et al. (2020)
<i>E. inarticulata</i>	2000	3–5	20	AP	(2)	absent	Ch	Stony and cliff soils	Alasbahi et al. (2020)
<i>E. cactus</i>	2350	3	10–30	AP	(2)	absent	Ph	Rocky slopes of the mountains	Fayed & Al-Zahari, (2007)
<i>E. madinahensis</i>	0–30	3–5	15	AP	(2)	absent	Ch	Granite stone	Fayed & Al-Zahari, (2007)
<i>E. saudiarabica</i>	1050–2350	3–5	30	AP	(2)	absent	Ph	Sand and fractured basaltic rock	Fayed & Al-Zahari, (2007)
<i>E. taifensis</i>	0–75	3.6(7)	100	AP	(1)	present	Ph	Stony soil	Fayed & Al-Zahari, (2007)
<i>E. collenteteae</i>	150–539	3–8	30	AP	(3)	present	Ph	Rocks of coral origin and cracked basalt	Al-Zahrani & El Karemy, (2007)
<i>E. fractiflexa</i>	150–550	3	25	AP	(3)	present	Ph	Rocky soil of gravels and clots	Carter & Wood, (1982)
<i>E. momccoyae</i> Lavranos	1000	5(6)	12.5	AP	(3)	present	Ch	Limestone rock	Lavranos (2011)

Note: AP – Arabian Peninsula; Ch – chamaephyte; Cong – conglomerate; Dol-Lim – dolomite-limestone; Lim – limestone; Mac – Macaronesia; Mor – Morocco; Ph – phanerophyte.

Many of these cactiforms have no leaves and even when they are present, they fall off quickly. These leaves are rarely persistent for species living in moist, foggy locations. In fact, the presence of leaf traces in the vascularization of collateral cortical bundles could be the result of ontogenetic alterations during the initial phase of meristem development (Mauseth, 2004; Arévalo-Rodríguez et al., 2022). This alteration interrupts

the expansion of the leaves, which would explain their acquisition, rudimentary size and early fall, since there is no fusion of the base of the leaf with the stem (Arévalo-Rodríguez et al., 2022). Consequently, the restriction of leaf growth through the redirection of their role to succulent stems, which have become the main photosynthetic organ in arid environments (Mauseth, 2006).



Fig. 6. Dehydrated and dying cactiforms in hyper-arid environments: *a* – *E. parcimulosa* in Saudi Arabia (photo of @SaudiZoologist); *b* – *E. echinus* in Southern Morocco

From this point of view, the adaptation of these plants to arid environments may be the result of either the induction of pre-existing genes, or the restriction or transfer of function of certain genes (Aloni, 2015; Ramanjulu & Bartels, 2002). This hypothesis is clearly represented in two very similar cactiform species, *E. makallensis* S. Carter (1981) from Ethiopia and *E. resinifera* from Morocco (Carter et al., 1981; Wilson & Munro, 2019). The former has deciduous leaves, and the latter has no leaves, but according to Lawant & Winthagen (2002), some young apical shoots of *E. resinifera* may occasionally have visible rudimentary leaves (1–2 mm), which are very rapidly deciduous. For comparison, the transition of these plants between tropical, arid and temperate climates could be responsible for these multiple morpho-physiological evolutions, as adaptive responses to aridity (Evans et al., 2014). All these adaptations have the essential role of

reducing water loss (Mauseth, 2004). For this, the architectural types (2) and (3) are the most represented in dry environments (Hom et al., 2012; Malpure et al., 2016).

Adaptation of cactiforms to arid and temperate climates. Spiny succulents with ribbed stems normally have three and four ribbed stems, but some also have 5–8 to 13 or more ribbed stems, including the following species: *E. fruticosa*, *E. handiensis*, *E. beaumierana* and *E. echinus* (Table 1). The multiplication of angles, could then be explained as an evolutionary innovation, aimed at acquiring an optimal stem conformation that allows water to be extracted from the wet sea fog (Bruyns & Berry, 2019). These conditions of high humidity and mild temperature enable the CAM photosynthesis system to function properly, especially at night, to ensure essential exchanges with its arid or semi-arid external environment (Nobel

& Hartsock, 1984). As in the Canary Islands, the cloud banks offer high humidity and mild temperatures (Beltrán-Tejera et al., 2013). Al-Turki (2014) confirmed the adaptive behaviours of these plants, on the diurnal and seasonal changes in the stomatal conductance of *E. fractiflexa*. This cactiform from the Arabian Peninsula adopts the obligatory CAM type, which switches to CAM-idling, when the environmental conditions become extreme. The CAM-idling is characterized by stomatal closure day and night, with no net CO₂ uptake (Masrahi et al., 2015). Therefore, these species can mitigate the effects of prolonged and severe drought during the summer (Borland et al., 2009; Horn et al., 2014; Winter, 2019).

Vulnerability of cactiforms to desert areas. African and Arabian cactiform *Euphorbia*, are native to tropical climates (Anest et al., 2021; del Arco Aguilar et al., 2010). Indeed, the humid tropical climate that prevailed until recently in North Africa is rapidly being transformed into an arid or semi-arid climate (Audissou, 2005). As a result, these species are restricted to the shores of seas or oceans, benefiting from the wet maritime trade winds, bringing fog and rain in the warm season (Valjarević et al., 2023). This climatic context presents a particularity of such coastal areas to be a refuge for these cactiform plants. As an example, the colonization of *E. echinus* in Southern Morocco took place even before the existence of the Sahara around 6 Ma (Sun et al., 2016). However, this interpretation is consistent with the hypothesis that proves that desert habitats and the Mediterranean climate are more recent than the tropical habitat, which was present during the Cenozoic (Edwards & Donoghue, 2006). That explains their vulnerability to the hyper-arid desert environment, where there are over four dry months in succession (Eiserhardt et al., 2017), and as a result, they have dried out (Fig. 6).

Despite this adaptive plasticity in these succulents, their resistance to water stress and attenuation only allowed for delayed dehydration during difficult months (Eggl & Giorgetta, 2020). Therefore, it should also be noted that these species are adapted to highly draining substrates, and the succulence of the stem allows for better water storage above ground, so their adaptation to arid environments benefits from this water management strategy. This allows us to state that the presence of succulence of the stem is not limited to a type of climate (Horn et al., 2012; Anest et al., 2021).

Conclusion

The majority of cactiform xerophytes, from Macaronesia and the Arabian Peninsula, are in decline. They are located in areas marked by long periods of drought. This situation is likely to worsen due to climate change and increased human pressure. Therefore, their presence and persistence in these regions are the result of their morphological evolution, through adaptation to different climates. These changes are strongly characterized by two morphological traits, firstly the transition from an architectural type of tree to a shrub, a bush or a dwarf plant. Secondly, its leaves are changing from evergreen to deciduous or even absent. It can be concluded that this group of cactiform *Euphorbia* is endemic to a tropical environment and will survive in an arid habitat. Basically, spiny cacti with ribbed stems are mainly adapted to draining soils, not to soils with high water retention, in humid tropical climates, which can lead to root asphyxiation. On the other hand, they are resistant to lack of water in the draining soils of warm climates. Indeed, the plant can store and maintain water in its stems. Although these species are widely distributed in arid environments, they are not completely adapted to these environments. In fact, they are restricted to areas with marine influences to mitigate the effects of heat waves. In fact, the cactus biome is undergoing not only a northward migration, but also an oceanward migration.

References

Ait Abderrahim, L., Taïbi, K., Ait Abderrahim, N., Boussaid, M., Rios-Navarro, C., & Ruiz-Saurí, A. (2019). *Euphorbia* honey and garlic: Biological activity and burn wound recovery. *Bums*, 45(7), 1695–1706.

Alasbahi, R., Salama, M. M., Alasbahi, R. H., & Al-Hawshabi, O. S. (2020). A review on some endemic and near endemic plants of Toor Al-Baha District, Lahej Governorate, Yemen. *Journal of Medicinal Plants Studies*, 8(2), 95–106.

Alfarhan, A. H. (1999). A phytogeographical analysis of the floristic elements in Saudi Arabia. *Pakistan Journal of Biological Sciences*, 2(3), 702–711.

Al-Hamoud, G. A., Fantoukh, O. I., Amina, M., Nasr, F. A., Al Musayeb, N. M., Ahmed, M. Z., Noman, O. M., Al-Sharidah, R. E., Alasmari, F., & Alqahani, A. S. (2022). Unprecedented insights on chemical and biological significance of *Euphorbia* cactus growing in Saudi Arabia. *Plants*, 11(5), 681.

Ali Al-Hajji, M. M., Al-Shamahy, H. A., Alkhatib, B. Y., & Moharram, B. A. (2018). *In vitro* anti-leishmanial activity against cutaneous *Leishmania* parasites and preliminary phytochemical analysis of four Yemeni medicinal plants. *Universal Journal of Pharmaceutical Research*, 3(4), 44–50.

Al-Namazi, A. A., Al-Khulaidi, A. W. A., Algami, S., & Al-Sagheer, N. A. (2021). Natural plant species inventory of hotspot areas in Arabian Peninsula: Southwest Al-Baha region, Saudi Arabia. *Saudi Journal of Biological Sciences*, 28(6), 3309–3324.

Aloni, R. (2015). Ecophysiological implications of vascular differentiation and plant evolution. *Trees*, 29(1), 1–16.

Al-Qthanin, R., & Al-Yasi, H. (2021). Progress towards an updated checklist of the Farasan Archipelago flora. *Journal of Arid Environments*, 189, 104488.

Al-Turki, T. A., Masrahi, Y. S., & Sayed, O. H. (2014). Photosynthetic adaptation of *Euphorbia fractiflexa* (Euphorbiaceae) and survival in arid regions of the Arabian Peninsula. *Journal of Plant Interactions*, 9(1), 107–111.

Álvarez Escobar, A., & Rodríguez Delgado, O. (2008). Contribución al estudio etnobotánico de las especies vegetales del tabaibal-cardonal (*Kleinio nerifoliae-Euphorbietea canariensis*) de la isla de Tenerife [Contribution to the ethnobotanical study of the plant species *Kleinio nerifoliae-Euphorbietea canariensis* of the island of Tenerife]. *Anuario Del Instituto de Estudios Canarios*, 50–51(1), 181–218 (in Spanish).

Al-Zahrani, D. A., & El-Karemy, Z. A. R. (2007). A new succulent *Euphorbia* (Euphorbiaceae) species from the Red Sea coast and islands. *Edinburgh Journal of Botany*, 64(2), 131–136.

Anest, A., Charles-Dominique, T., Maurin, O., Millan, M., Edelin, C., & Tomlinson, K. W. (2021). Evolving the structure: climatic and developmental constraints on the evolution of plant architecture. A case study in *Euphorbia*. *New Phytologist*, 231(3), 1278–1295.

Arévalo-Rodríguez, G., Hurbath, F., Prado, E., Galvão, I., Cordeiro, I., & Demarco, D. (2022). Adnate leaf-base and the origin of ribs in succulent stems of *Euphorbia* L. *Plants*, 11(8), 1076.

Audissou, J. A. (2005). Moroccan stapeliads. *Asklepios*, 94, 18–27.

Bellstedt, D. U., Galley, C., Pirie, M. D., & Linder, H. P. (2012). The migration of the palaeotropical arid flora: Zygophylloideae as an example. *Systematic Botany*, 37(4), 951–959.

Beltrán-Tejera, E., Rodríguez-Armas, J. L., Tellería, M. T., Dueñas, M., Melo, I., Díaz-Armas, M. J., Salcedo, I., & Cardoso, J. (2013). Corticoid fungi from arid and semiarid zones of the Canary Islands (Spain). *Additional data 2*. *Mycotaxon*, 123, 1–27.

Benabid, A. (2000). Flore et écosystème du Maroc Évaluation et préservation [Flora and ecosystems of Morocco: Evaluation and preservation of biodiversity]. Ibis Press, Paris (in French).

Benjamaa, R., Moujanni, A., Terrab, A., Eddoha, R., Benbachir, M., Moujahid, A., Nasser, B., Darkaoui, S., Zyate, N., Talmi, A., & Essamadi, A. K. (2020). Relationship among antibiotic residues and antibacterial activity of the endemic spurge honey (*Euphorbia resinifera* O. Berg) from Morocco. *Emirates Journal of Food and Agriculture*, 32(11), 795–807.

Bernays, E. A., Singer, M. S., & Rodrigues, D. (2004). Trenching behavior by caterpillars of the *Euphorbia* specialist, *Pygarctia roseicapitis*: A field study. *Journal of Insect Behavior*, 17(1), 41–52.

Bin Muhsinah, A., Eko Nugroho, A., Li, H., Lazzaro, S., DaSilva, N. A., Li, D., Ma, H., Alsayari, A., Morita, H., Liu, Y., & Seeram, N. P. (2020). Saudiarabicains A-E, bioactive 19-acetoxyingol diterpenoids from *Euphorbia saudiarabica*. *Tetrahedron Letters*, 61(32), 152203.

Borland, A. M., Griffiths, H., Hartwell, J., & Smith, J. A. C. (2009). Exploiting the potential of plants with crassulacean acid metabolism for bioenergy production on marginal lands. *Journal of Experimental Botany*, 60(10), 2879–2896.

Bosworth, W., & Stockli, D. F. (2016). Early magmatism in the greater Red Sea rift: Timing and significance. *Canadian Journal of Earth Sciences*, 53(11), 1158–1176.

Bruyns, P. V., & Berry, P. E. (2019). The nomenclature and application of the names *Euphorbia candelabrum* Welw. and *Euphorbia ingens* in tropical Africa. *Taxon*, 68(4), 828–838.

Bruyns, P. V., Klak, C., & Hanáček, P. (2011). Age and diversity in Old World succulent species of *Euphorbia* (Euphorbiaceae). *Taxon*, 60(6), 1717–1733.

Bruyns, P. V., Mapaya, R. J., & Hedderson, T. J. (2006). A new subgeneric classification for *Euphorbia* (Euphorbiaceae) in Southern Africa based on ITS and psbA-trnH sequence data. *Taxon*, 55(2), 397–420.

Carter, S. (1994). A preliminary classification of *Euphorbia* subgenus *Euphorbia*. *Annals of the Missouri Botanical Garden*, 81(2), 368–379.

Carter, S. (2005). *Euphorbias* of Southern Morocco. *Cactus and Succulent Journal*, 77(1), 34–37.

Carter, S., & Wood, J. R. I. (1982). Two new succulent *Euphorbia* species from Southwest Arabia. *Kew Bulletin*, 37(1), 73.

- Carter, S., Wilson, R. T., Lewis, J. G., Carter, S., Wilson, R. T., & Lewis, J. G. (1981). A new species of succulent *Euphorbia* from Ethiopia, with Ecological Notes. *Kew Bulletin*, 36(1), 31–38.
- Chaudhary, P., Singh, D., Swapnil, P., Meena, M., & Janmeda, P. (2023). *Euphorbia nerijolia* (Indian Spurge Tree): A plant of multiple biological and pharmacological activities. *Sustainability*, 15(2), 1225.
- Coello, A. J., Vargas, P., Cano, E., Riina, R., & Fernandez-Mazuecos, M. (2023). Phylogenetics and phylogeography of *Euphorbia canariensis* reveal an extreme Canarian-Asian disjunction and limited inter-island colonization. *bioRxiv*.
- del Arco Aguilar, M. J., & Rodríguez Delgado, O. (2018). Vegetation of the Canary Islands. Springer Nature.
- del Arco Aguilar, M.-J., González-González, R., Garzón-Machado, V., & Pizarro-Hernández, B. (2010). Actual and potential natural vegetation on the Canary Islands and its conservation status. *Biodiversity and Conservation*, 19(11), 3089–3140.
- Dorsey, B. L., Haevermans, T., Aubriot, X., Morawetz, J. J., Riina, R., Steinmann, V. W., & Berry, P. E. (2013). Phylogenetics, morphological evolution, and classification of *Euphorbia* subgenus *Euphorbia*. *Taxon*, 62(2), 291–315.
- Edwards, E. J., & Donoghue, M. J. (2006). *Pereskia* and the origin of the cactus life-form. *The American Naturalist*, 167(6), 777–793.
- Eggli, U., & Giorgetta, M. (2020). Dry season – wet season volume change of *Echinopsis atacamensis* ssp. *atacamensis* (Cactaceae) as proxy for the amount of utilizable water of a stem succulent plant. *Bradleya*, 38, 59.
- Eggli, U., & Nyffeler, R. (2009). Living under temporarily arid conditions – succulence as an adaptive strategy. *Bradleya*, 27, 13–36.
- Eisenhardt, W. L., Couvreur, T. L. P., & Baker, W. J. (2017). Plant phylogeny as a window on the evolution of hyperdiversity in the tropical rainforest biome. *New Phytologist*, 214(4), 1408–1422.
- Ettaqy, A., Kharchaf, Y., Benhssaine, K., Zine El Abidine, A., Bouderrah, M., Boukicim, H., Boulli, A., & Abbas, Y. (2023). Ecological insights and conservation imperatives for *Laurus azorica* in Morocco. *Biosystems Diversity*, 31(2), 229–237.
- Ettaqy, A., Taha, A., ElGhjouane, A., Elkhou, A., Boulli, A., & Abbas, Y. (2020). New data on the ecological distribution of *Euphorbia resinifera* O. Berg in the Beni Mellal-Khenifra region. *E3S Web of Conferences*, 183, 01001.
- Evans, M., Aubriot, X., Hearn, D., Lanciaux, M., Lavergne, S., Cruaud, C., Lowry, P. P., & Haevermans, T. (2014). Insights on the evolution of plant succulence from a remarkable radiation in Madagascar (*Euphorbia*). *Systematic Biology*, 63(5), 697–711.
- Fayed, A. A., & Al-Zahrani, D. A. (2007). Three new spiny *Euphorbia* (Euphorbiaceae) species from Western Saudi Arabia. *Edinburgh Journal of Botany*, 64(2), 117–129.
- Fleurentin, J., & Pelt, J.-M. (1982). Repertory of drugs and medicinal plants of Yemen. *Journal of Ethnopharmacology*, 6(1), 85–108.
- Florencio, M., Patiño, J., Nogué, S., Traveset, A., Borges, P. A. V., Schaefer, H., Amorim, I. R., Amedo, M., Ávila, S. P., Cardoso, P., de Nascimento, L., Fernández-Palacios, J. M., Gabriel, S. I., Gil, A., Gonçalves, V., Haroun, R., Illera, J. C., López-Darias, M., Martínez, A., ... Santos, A. M. C. (2021). Macaronesia as a fruitful arena for ecology, evolution, and conservation biology. *Frontiers in Ecology and Evolution*, 9, 718169.
- Frodin, D. G. (2004). History and concepts of big plant genera. *Taxon*, 53(3), 753–776.
- Grace, O. M. (2019). Succulent plant diversity as natural capital. *Plants, People, Planet*, 1(4), 336–345.
- Hall, M., Llewellyn, O. A., Miller, A. G., Al-Abbasi, T. M., Al-Wetaid, A. H., Al-Harbi, R. J., & Al-Shammari, K. F. (2010). Important plant areas in the Arabian Peninsula: Farasan Archipelago. *Edinburgh Journal of Botany*, 67(2), 189–208.
- Hernández-Teixidor, D., Santos, I., Suárez, D., & Oromí, P. (2020). The importance of threatened host plants for arthropod diversity: The fauna associated with dendroid *Euphorbia* plants endemic to the Canary and Madeira archipelagos. *Journal of Insect Conservation*, 24(5), 867–876.
- Hom, J. W., van Ee, B. W., Morawetz, J. J., Riina, R., Steinmann, V. W., Berry, P. E., & Wurdack, K. J. (2012). Phylogenetics and the evolution of major structural characters in the giant genus *Euphorbia* L. (Euphorbiaceae). *Molecular Phylogenetics and Evolution*, 63(2), 305–326.
- Hom, J. W., Xi, Z., Riina, R., Peirson, J. A., Yang, Y., Dorsey, B. L., Berry, P. E., Davis, C. C., & Wurdack, K. J. (2014). Evolutionary bursts in *Euphorbia* (Euphorbiaceae) are linked with photosynthetic pathway. *Evolution*, 68(12), 3485–3504.
- Lavrano, J. J. (2011). *Euphorbia momccoyae* Lavranos: A new and long misidentified species from the Sultanate of Oman. *Cactus and Succulent Journal*, 83(6), 256–263.
- Lawant, P., & Winthagen, D. (2001). *Euphorbia resinifera* portrayed in a manuscript herbal nearly fifteen hundred years ago. *Bradleya*, 19, 3–14.
- Linder, H. P. (2014). The evolution of African plant diversity. *Frontiers in Ecology and Evolution*, 2, 38.
- Males, J. (2017). Secrets of succulence. *Journal of Experimental Botany*, 68(9), 2121–2134.
- Malpure, N. V., Chandore, A. N., & Yadav, S. R. (2016). *Euphorbia gokakensis* sp. nov. (Euphorbiaceae) from sandstone formations in Karnataka, India. *Nordic Journal of Botany*, 34(3), 380–383.
- Marrero Gómez, M. V., & Carqué Alamo, E. (2004). *Euphorbia handiensis*. Atlas y Libro Rojo de la Flora Vascular Amenazada de España [*Euphorbia handiensis*. Atlas and Red Book of the threatened vascular flora of Spain]. Dirección General de la Conservación de la Naturaleza, Madrid (in Spanish).
- Masrahi, Y. S., Al-Turki, T. A., & Sayed, O. H. (2015). Photosynthetic adaptation and survival strategy of *Duvalia velutina* in an extremely arid environment. *Photosynthetica*, 53(4), 555–561.
- Mauseth, J. D. (2004). The structure of photosynthetic succulent stems in plants other than cacti. *International Journal of Plant Sciences*, 165(1), 380978.
- Mauseth, J. D. (2006). Structure-function relationships in highly modified shoots of Cactaceae. *Annals of Botany*, 98(5), 901–926.
- Médail, F., & Quézel, P. (1999). The phylogeographical significance of S.W. Morocco compared to the Canary Islands. *Plant Ecology*, 140(2), 221–244.
- Msanda, F., El Aboudi, A., & Peltier, J. P. (2002). Originalité de la flore et de la végétation de l'Anti-Atlas sud-occidental (Maroc) [Originality of the flora and vegetation of the south-western Anti-Atlas (Morocco)]. *Feddes Repertorium*, 113(7–8), 603–615 (in French).
- Niechayev, N. A., Pereira, P. N., & Cushman, J. C. (2019). Understanding trait diversity associated with crassulacean acid metabolism (CAM). *Current Opinion in Plant Biology*, 49, 74–85.
- Nobel, P. S., & Hartsock, T. L. (1984). Physiological responses of *Opuntia ficus-indica* to growth temperature. *Physiologia Plantarum*, 60(1), 98–105.
- Ogbum, R. M., & Edwards, E. J. (2010). The ecological water-use strategies of succulent plants. *Advances in Botanical Research*, 55, 179–225.
- Peltier, J. P., & Msanda, F. (1995). Diversité et originalité de la steppe à *Euphorbia officinarum* L. subsp. *echinus* (Hooker fil. et Cosson) VINDT du sud-ouest Marocain [Diversity and originality of the *Euphorbia officinarum* L. subsp. *echinus* (Hooker fil. et Cosson) VINDT steppe of Southwest Morocco]. *Feddes Repertorium*, 106(3–4), 15–229 (in French).
- Pennington, R. T., Lehmann, C. E. R., & Rowland, L. M. (2018). Tropical savannas and dry forests. *Current Biology*, 28(9), R541–R545.
- Pokomy, L., Riina, R., Mairal, M., Meseguer, A. S., Culshaw, V., Cendoya, J., Serrano, M., Carbajal, R., Ortiz, S., Heuert, J. M., & Sanmartín, I. (2015). Living on the edge: Timing of Rand Flora disjunctions congruent with ongoing aridification in Africa. *Frontiers in Genetics*, 6, 154.
- Ramanjulu, S., & Bartels, D. (2002). Drought- and desiccation-induced modulation of gene expression in plants. *Plant, Cell and Environment*, 25(2), 141–151.
- Riina, R., Marques, O., & Hurbath, F. (2015). *Euphorbia* from Brazil: The succulent section *Brasilenses*. *Euphorbia World*, 11(3), 5–11.
- Riina, R., Peirson, J. A., Geltman, D. V., Molero, J., Frajman, B., Pahlevani, A., Barres, L., Morawetz, J. J., Salmaki, Y., Zarre, S., Kryukov, A., Bruyns, P. V., & Berry, P. E. (2013). A worldwide molecular phylogeny and classification of the leafy spurge, *Euphorbia* subgenus *Esula* (Euphorbiaceae). *Taxon*, 62(2), 316–342.
- Riina, R., Villaverde, T., Rincón-Barrado, M., Molero, J., & Sanmartín, I. (2021). More than one sweet tabaiba: Disentangling the systematics of the succulent dendroid shrub *Euphorbia balsamifera*. *Journal of Systematics and Evolution*, 59(3), 490–503.
- Ringelberg, J. J., Zimmermann, N. E., Weeks, A., Lavin, M., & Hughes, C. E. (2020). Biomes as evolutionary arenas: Convergence and conservatism in the trans-continental succulent biome. *Global Ecology and Biogeography*, 29(7), 1100–1113.
- Rosen, R. H., Gupta, A. K., & Tyring, S. K. (2012). Dual mechanism of action of ingenol mebutate gel for topical treatment of actinic keratoses: Rapid lesion necrosis followed by lesion-specific immune response. *Journal of the American Academy of Dermatology*, 66(3), 486–493.
- Sanmartín, I., Anderson, C. L., Alarcon, M., Ronquist, F., & Aldasoro, J. J. (2010). Bayesian island biogeography in a continental setting: The Rand Flora case. *Biology Letters*, 6(5), 703–707.
- Si, L., Meng, K., Tian, Z., Sun, J., Li, H., Zhang, Z., Soloveva, V., Li, H., Fu, G., Xia, Q., Xiao, S., Zhang, L., & Zhou, D. (2018). Triterpenoids manipulate a broad range of virus-host fusion via wrapping the HR2 domain prevalent in viral envelopes. *Science Advances*, 4(11), eaau8408.
- Sun, Y., Li, Y., Vargas-Mendoza, C. F., Wang, F., & Xing, F. (2016). Colonization and diversification of the *Euphorbia* species (sect. *Aphyllis* subsect. *Macaronesicae*) on the Canary Islands. *Scientific Reports*, 6(1), 34454.
- Swamy, A. N., & Prasad, K. (2022). *Euphorbia ravii* (Euphorbiaceae: subg. *Euphorbia*), a new species from Andhra Pradesh, India. *Taiwania*, 67(2), 229–234.
- Thiv, M., Thulin, M., Hjertson, M., Kropf, M., & Linder, H. P. (2010). Evidence for a vicariant origin of Macaronesian–Eritreo/Arabian disjunctions in *Campylanthus* Roth (Plantaginaceae). *Molecular Phylogenetics and Evolution*, 54(2), 607–616.
- Valjarević, A., Algami, S., Morar, C., Grama, V., Stupariu, M., Tiba, A., & Lukić, T. (2023). The coastal fog and ecological balance for plants in the Jizan region, Saudi Arabia. *Saudi Journal of Biological Sciences*, 30(1), 103494.

- Wang, S. Y., Huang, C., Sun, R. K., Lu, L. N., Liang, H. G., Gao, L., Huang, J., Wang, J. H., & Yang, B. F. (2019). New tirucallane triterpenoids from the dried latex of *Euphorbia resinifera*. *Phytochemistry Letters*, 29, 220–224.
- Webster, G. L. (1975). Conspectus of a new classification of the Euphorbiaceae. *Taxon*, 24(5–6), 593–601.
- Wei, N., Pérez-Escobar, O. A., Musili, P. M., Huang, W.-C., Yang, J.-B., Hu, A.-Q., Hu, G.-W., Grace, O. M., & Wang, Q.-F. (2021). Plastome evolution in the hyperdiverse genus *Euphorbia* (Euphorbiaceae) using phylogenomic and comparative analyses: Large-scale expansion and contraction of the inverted repeat region. *Frontiers in Plant Science*, 12, 712064.
- Wilson, T., & Munro, N. (2019). *Euphorbia makallensis* Carter, a Northern Ethiopian of very limited distribution. *British Cactus and Succulent Society*, 37(1), 43–46.
- Winter, K. (2019). Ecophysiology of constitutive and facultative CAM photosynthesis. *Journal of Experimental Botany*, 70(22), 6495–6508.
- Xie, L., Yang, Z. Y., Wen, J., Li, D. Z., & Yi, T. S. (2014). Biogeographic history of *Pistacia* (Anacardiaceae), emphasizing the evolution of the Madrean-Tethyan and the eastern Asian-Tethyan disjunctions. *Molecular Phylogenetics and Evolution*, 77(1), 136–146.
- Zhao, H., Sun, L., Kong, C., Mei, W., Dai, H., Xu, F., & Huang, S. (2022). Phytochemical and pharmacological review of diterpenoids from the genus *Euphorbia* Linn (2012–2021). *Journal of Ethnopharmacology*, 298, 115574.
- Zimmermann, N. F. A., Ritz, C. M., & Hellwig, F. H. (2010). Further support for the phylogenetic relationships within *Euphorbia* L. (Euphorbiaceae) from nrITS and trnL-trnF IGS sequence data. *Plant Systematics and Evolution*, 286(1–2), 39–58.