Cytological and morphological differentiation in Caralluma burchardii (Asclepiadaceae)

U. Meve

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Caralluma burchardii is revised based on detailed investigations of vegetative and floral morphology, as well as chromosome numbers. The species is now divided into two taxa, the dodecaploid ssp. *burchardii*, an endemic of the Canary Islands, and ssp. *maura*, a hexaploid from the west coast of Morocco. The high ploidy levels involved, the highest known in the Asclepiadaceae, are discussed in conjunction with biogeographical aspects.

U. Meve, Institut für Botanik, Westf. Wilhelms-Universität Münster, Schlossgarten 3, D-48149 Münster, Germany.

Introduction

Oskar Burchard, an amateur botanist born in Hamburg, discovered *Caralluma burchardii* in 1911 (in schedis) in the neighbourhood of La Oliva in northern Fuerteventura. In 1912, Burchard provided N.E. Brown of Kew with material in the form of stems and pickled flowers, and Brown (1913) honoured Burchard's efforts by naming the species after him.

In subsequent years, more material of *C. burchardii* from the Canary Islands, but also from the African mainland became available, revealing considerable variability within the species. Consequently, the French botanist R. Maire and others were inspired to subdivide the species into many small entities, down to the level of forma. Small differences in colour and indumentum prompted the description of two additional infraspecific taxa, var. *purpurescens* Maire (1945) and var. *sventenii* H.& B. Lamb (1956), for specimens from Lanzarote and Fuerteventura, respectively.

In 1923, Maire described var. *maura* for Moroccan representatives of this species, and later recognized three further forms apart from the typical one in addition (Maire 1942, 1945).

Recently, a detailed survey of typical *C. burchardii* was given by Bruyns (1987), who did, however, not draw any taxonomic conclusions. In the latest account of *Ca*-

ralluma R. Br., Gilbert (1990) only accepted two infraspecific taxa for *C. burchardii*, namely var. *burchardii* and var. *maura*.

Material and methods

The living material originates from different sources (see Tab. 1), and was or is in cultivation in the Botanic Garden Münster.

For mitotic chromosome counts, root tips were treated with 0.002 mol 8-hydroxy-quinoline for 4 hours, fixed for 24 hours in ethanol: acetic acid (3:1) and treated for 24 hours in Snow's stain at 60° C.

For SEM investigations of epidermal features, parts of stems were dehydrated in acetone, critical point dried, gold-sputtered and scanned in a Hitachi S530 at 20 kV.

Results Morphology

Stems

Both taxa can be distinguished easily by using vegetative characters. Both possess a rhizomatous habit, but the stems are rather robust (usually 2–3 cm in diam.) in

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Fig. 1. A-D, *Caralluma burchardii* N.E. Br. ssp. *burchardii*. A, seedling, 3 weeks old; B, stem; C, flower in lateral view, corolla partly removed; D, pollinarium. – E-F, *C. burchardii* N.E.Br. ssp. *maura* (Maire) Meve & F. Albers. E, stem, F, flower in lateral view, G, pollinarium (A drawn from Bramwell s.n., B-D from Wiemers s.n.; E-G from Plowes 6619).



Fig. 2. Stem epidermal surfaces, SEM. A-B, Caralluma burchardii ssp. maura; C-D, ssp. burchardii.

Caralluma burchardii var. *burchardii*, while *C. burchardii* var. *maura* is of much more slender habit with stems not exceeding 2 cm in diameter (Fig. 1 B, E). The rudimentary leaves are relatively large in var. *burchardii* and are supported by elongated, deflexed tubercles along the sharply angled stems (Fig. 1 B); in contrast, in var.



Fig. 3. Caralluma burchardii N. E. Br. A- B, ssp. burchardii (A, Gran Canaria Mang s.n.; B, Fuerteventura: Betancuria, Wiemers s.n., c. 2×); C, ssp. maura (Plowes 6619, c. 2×).

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Fig. 4. Somatic metaphase plates from root tips. A. Caralluma burchardii ssp. burchardii, 2n=132; B-C. burchardii ssp. maura, 2n=66 (A drawn from Wiemers s.n.; B drawn from Jonkers 223).

maura, they are often rather inconspicuous on less prominent tubercles (Fig. 1 E). The young stem of var. *burchardii* appears fresh green and brilliant, but rather dull bluish green in var. *maura*. SEM investigations reveal structural differences to explain these different appearances. The dull surface of var. *maura* is caused by enlarged, papillate epidermal cells or cell complexes interspersed with a basal epidermal pattern of smaller, rather isodiametric cells with clearly convex periclinal outer walls (Fig. 2 A, B). Papillae are absent in var. *burchardii* and the outer periclinals of the equal sized, though in general larger cells are less convex (Fig. 2 C, D).

Flowers

Caralluma burchardii var. burchardii and var. maura can easily be distinguished by the much larger overall size of the flowers of var. burchardii. This is reflected in all floral parts except the pedicel, such as sepals, corolla, gynostegium with corona and pollinaria. Flowers of var. *maura* possess pedicels of 5–9 mm in length, which often point slightly downwards (Fig. 1 F); in contrast, flowers of the typical variety are more or less unstalked with pedicels at the most 3 mm long. The long pedicel of var. *maura* goes against the general floral trend of larger parts in var. *burchardii* and hence is of taxonomic significance.

Both taxa possess the characteristic deep corolla tube filled by a tubular gynostegium. The corolla is of greenish to brownish colour and completely covered with stiff, translucent trichomes (Figs 1 F; 3 A, C). Both var. *maura* and var. *burchardii* show this indumentum, though it is lacking in plants (whole population?) from the area of Betancuria (Fuerteventura, Fig. 3 B). Specimens with a rather sparse indumentum have also been found, predominantly in the north of Fuerteventura (Lamb & Lamb 1956, Bruyns 1987: 78).

Except for variation in size, the basic corona structure is fairly uniform.

Tab. 1. Chromosome numbers of specimens investigated.

Kuschel 91–1	2n=121
Kunkel 11772	2n=121 (Albers 1981)
Kuschel 91–2	2n=127
Wiemers s.n.	2n=130-132
Bramwell s.n.	2n=132 (Albers 1977)
Sventenius s.n.	2n=130-132
Mang s.n.	2n=141
Jürgens 28454	2n= 66
Jonkers 205	2n = 66
Jonkers 223	2n= 66
Jonkers 227	2n= 66
Plowes 6619	2n= 66
s.n.	2n= 66
	Kuschel 91–1 Kunkel 11772 Kuschel 91–2 Wiemers s.n. Bramwell s.n. Sventenius s.n. Mang s.n. Jürgens 28454 Jonkers 205 Jonkers 223 Jonkers 227 Plowes 6619 s.n.



Fig. 5. Distribution and chromosome numbers of Caralluma burchardii ssp. burchardii (A) and ssp. maura (I).

Follicles

In fruit, the two taxa can be distinguished by the tendency in *Caralluma burchardii* var. *burchardii* for the follicles to spread at a wider angle, resulting in a patent position (Bramwell & Bramwell 1974: photo 214); while in var. *maura* the follicles are less widely divergent (Jonkers & Walker 1993).

Karyology

Caralluma burchardii var. *burchardii* has been shown to be a dodecaploid species of 2n=132 chromosomes (Fig. 4; cf. Albers 1977, 1983). However, dodecaploidy does not seem to be stable throughout as counts for different clones vary considerably around 2n=132 (Tab. 1).

On Fuerteventura, which constitutes the centre of distribution and on Lanzarote, true dodecaploids (2n=132)dominate, apart from various aneuploids of 127, 130 or 131 chromosomes (Fig. 5). A decaploid (2n=110-112),

Tab. 2. Differential diagnostic features in Caralluma burchardii.

ssp. burchardii	ssp. maura
Canarian endemic	Moroccan endemic
2n=(110-)121-141	2n=66
pedicel 1-3 mm long	pedicel 5–9 mm long
flowers 13-16 mm in diam.	flowers 7–11(-13) mm in diam.
corolla glabrous to ciliate	corolla densely ciliate
stems robust, (1.5)2-3 cm diam.	stems slender, 1.5–2 cm diam.
stems dark green when young	stems bluish green when young
stem epidermis rather smooth	stem epidermis sculptured
leaf rudiments large and stout	leaf rudiments inconspicuous

however, is reported in the literature for Fuerteventura (Borgen 1974). Plants from the eastern islets of Lobos (Albers 1981) and Graciosa (north of Fuerteventura and Lanzarote respectively), however, possess only hende-caploid chromosome sets (2n=121, Fig. 5, Tab. 1).

From the western Canaries, just one population on Gran Canaria is known, localized in the southwestern part of this large island (Fig. 5). Surprisingly, this collection is a (aneuploid) tridecaploid (2n=141).

In general, there are no morphological differences between the different cytotypes of the Canary Islands. The most striking variation observed, the absence of the typical corolla indumentum, occurs in plants from Fuerteventura (Betancuria) which possess exactly the same genome size as plants with hairy flowers from other localities on Fuerteventura (Tab. 1).

C. burchardii var. maura has been found to be hexaploid with 2n=66 chromosomes (Figs 4 B, 5; Tab. 1). Only one deviation from this genome was ever noted (2n=64, Reese & Kressel 1967). The 2n=22 published by Albers (1976) is due to a confusion with C. europaea (Guss.) N.E. Br. in the same paper.

Summarizing, a number of constant features differentiates both infraspecific entities of *C. burchardii*. Their allopatric distribution, in combination with considerable differences in karyology and vegetative and floral morphology (Tab. 2), shows that they have lost the capacity for interbreeding. Therefore, the two taxa might be considered as distinct species. However, the still far-reaching morphological similarity suggests that the division of this species into two subspecies provides the most satisfactory solution.

Within ssp. *burchardii*, variation is too small and irregularly distributed to deserve further formal recognition. The two varieties published by Maire (1945) and Lamb & Lamb (1956) are therefore regarded as superfluous.

Taxonomy

Caralluma burchardii N.E. Br.

Bull. Misc. Inform. Kew, 1913, 3: 121 (1913); Burchard, Bibl. Bot. 98: 163 (1929); A. White & B. Sloane, The Stapelieae, 1, ed.2: 220 (1937); Kunkel, Cuad. Bot. Canar. 8: 35 et 10: 32 (1970); Bruyns, Bradleya 5: 80 (1987); M. Gilbert, Bradleya 8: 17 (1990); Jonkers & C. Walker, Asklepios 59: 16 (1993). – Type: Canary Islands, Fuerteventura, "In rupestribus prope La Oliva", 11.11.1912, Burchard 385 (K! holotype; HBG! isotype).

= C. burchardii var. purpurascens Maire, Bull. Soc. Hist. Nat. Afr. Nord 36: 100 (1945). – Type: Canary Islands, Lanzarote, Burchard sub Gattefossé (presumably no type material was preserved).

= C. burchardii var. sventenii H. & B. Lamb, Natl. Cact. Succ. J. 11: 77 (1956). – Iconotype: N Fuerteventura, coll. Sventenius s.n., illus. p. 76 of protologue [lectotype, design. Gilbert, Bradleya 8: 17 (1990)].

For keying out the subspecies see Tab. 2.

Subspecies burchardii

Plants tufted, succulent subshrubs, branching from the base or subterranean, rhizomatous; stems: orthotropic to slightly plagiotropic, 10–20(–50) cm long, 4–(5)angled, dark green and brilliant when young, dull (bluish) green when old, sometimes mottled with purple, glabrous; leaf rudiments on elongated, conical podaria (tubercles), slightly deflexed, blades broadly deltoid, 1.5 mm in diam., stout, rather persistent, stipular rudiments absent. Inflorescence subterminal, 3-12 flowered, 2-8 flowers opening at the same time, umbelliform. Pedicels 1-3 mm long, 1 mm wide, terete, glabrous. Sepals deltoid-lanceolate, acuminate, green, occasionally with reddish tips, 3-4 mm long, c. 2 mm wide at the base. Corolla rotatecampanulate, 13-16 mm in diam., honey-scented; tube 3-4 mm long, 4-5.5 mm in diam., glabrous, lobes ovate, acute, 4-6.5 mm long, 3-4 mm wide, margins slightly reflexed, abaxially reddish green, glabrous, adaxially olive, greenish-brown or reddish brown, glabrous to more or less densely covered with flexible, whitish translucent hairs, 0.3-0.8 mm long. Gynostegium tubular, pentagonal, grooved, c. 3.5 mm long, 3 mm wide in the middle, filament tube with deeply sunk nectarial cavities filled with nectar to capacity, yellow, tube deeply and firmly sunk into the corolla tube though presenting the coronas outside corolla tube; anther wings very short, guide rail c. 0.5 mm short or less. Corona c. 5 mm in diam., double, staminal parts (Cs) oblong to spatulate, obtuse, 1-1.5 mm long, as long as or shorter than the anthers, incumbent on back of anthers, dorsally adnate to the interstaminal corona parts, yellow, often with a greenish tinge, ring of fused staminal and interstaminal parts of the corona [C(is) sensu Liede & Kunze (1993)] bowl-shaped, (golden-) yellow, with interstaminal lobules bifid into two spreading teeth, free teeth subulate, c. 1.5 mm long. Pollinarium: pollinia subquadrangular, $500-550 \times 400-450 \mu m$, yellow, pellucid margin c. 300 µm long, caudicles c. 100 µm long, subterminally inserted, corpusculum obovate, 350-400 µm long, reddish-brown, basally accompanied by two lateral gibbosities; stylar head snowy white. Follicles paired, erect, divergent to usually 80°-180°, slender, fusiform, terete, 7-12(15) cm long, 6-8 mm wide, glabrous, pale bluish green to pale purple, occasionally mottled with purple. Seeds oblong-obovate, $5-6 \times 4.5$ mm, with c. 1 mm broad margin, light brown, coma c. 30 mm long. Seedlings stout, c. 1.5–2 cm long, cotyledons ovate, concave, c. 5 mm long, 3-4 mm in diam. - (Figs 1 A-D; 3 A, B).

Chromosome number. 2n=(110-)121-142 (for vouchers see Tab. 1, all were or are in cult., Bot. Garden Münster).

Reproductive system. Self-fertile.

Habitat. In succulent-rich plant communities, mainly on volcanic slopes.

Distribution. Canary Islands: Fuerteventura, Lanzarote, Graciosa, Lobos, Gran Canaria (Fig. 5).

Material examined. Fuerteventura: Taro, bei den Windmühlen, Kuschel 91–2 (MSUN); Montaña de la Oliva, Bramwell s.n. sub K 776 (MSUN); near Villaverde, in lava field, 31.3.1976, Kunkel 19004 (G); Jandia, Bco. del Malnombre, 6.9.1973, Kunkel 15885 (G); Betancuria, Bco. de Ajuy, Wiemers s.n. (MSUN); Lanzarote: Famara, Sventenius sub K 293; Gran Canaria: near Puerto Rico, Camera de Lobos, Mang s.n. (MSUN), Graciosa: N plains, on rocky slopes, 8.4.1970, Kunkel 13195 (G); Montaña Bermeja, Kuschel 91–1 (MSUN); Lobos: entre rocas al norte de la playa sur y al noroeste de la Montaña, 8 m, 21.12.1967, Kunkel 11772 (G); central part of the island, between rocks, 20 m, Kunkel 11636 (G).

Subspecies maura (Maire) Meve & F. Albers stat. nov.

Basionym: C. burchardii var. maura Maire, Bull. Soc. Hist. Nat. Afr. Nord 14: 156 (1923); A. White & B. Sloane, The Stapelieae, 1, ed.2: 220 (1937); Rauh, Cact. Succ. J. (US) 44: 195 (1972); M. Gilbert, Bradleya 8: 17 (1990); Jonkers & C. Walker, Asklepios 59: 16 (1993). -- Type: Morocco, Agadir-n-Ighir, broussailles et recailes calcaires ou dessous de la Karta vers Founti, Maire s.n. (MPU! holotype).

= C. burchardii var. maura f. grandiflora Maire, Bull. Soc. Hist. Nat. Afr. Nord 33: 89 (1942). – Type: Morocco, edge of Qued Massa, Maire s.n. (no type material traced).

= C. burchardii var. maura f. sordida Maire, Bull. Soc. Hist. Nat. Afr. Nord 33: 89 (1942). – Type: Morocco, Tiznit, Maire s.n. (no type material traced).

= C. burchardii var. maura f. viridis Maire, Bull. Soc. Hist. Nat. Afr. Nord 36: 99 (1945). – Type: Morocco, ravine of Qued Assaka, near Qued Noun, Gattefossé s.n. (no type material traced).

Plants similar to ssp. *burchardii* but differing in the following features (Figs 1 E-G; 3 C):

Stems slender, 15–50 cm long, 1.5–2 cm in diam., dull bluish green (already when young); leaf rudiments on stout and short podaria, horizontally spread to slightly reflexed, inconspicuous, obtusely deltoid to subquadrangular, not exceeding 1 mm in length and width, occasionally with a few glandular hairs along margin. Pedicels 5–9 mm long. Sepals 2–3 mm long. Flowers 7–11(13) mm in diam., corolla lobes densely covered with white, translucent hairs; pollinia 400–450 × 300–350 μ m, corpusculum 250 μ m long. Follicles erect to slightly divergent. Seeds and seedlings not seen.

Chromosome number. 2n=66 (for vouchers see Tab. 1, all in cult., Bot. Garden Münster).

Habitat. In succulent-rich plant communities under the influence of Atlantic Ocean humidity.

Distribution. Morocco, western areas from Cap Rhir to Qued Noun (Fig. 5).

Material examined. Morocco: Agadir, parmi les *Euphorbia beaumierana*, Gattefossé s.n., 25.11.1934 (G; K; MPU); Agadir, A.W. Tretteary 188, March 1935 (K); Agadir, 2.5.1993, Jahandieu 246 (MPU); Agadir, rochers en face le poste, March 1937,

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Weiller et Gattefossé 101.37 (MPU); Farhazoute, 20 m, Lewalie 9358 (WAG); s.loc., in Plowes 6619 (MSUN); Cap Rhir, Jonkers 205 (MSUN); Qued Massa, Jonkers 227 (MSUN); Sidni Ifni, Jonkers 223 (MSUN); Tafraoute, Jonkers 224 (MSUN); Barrage Joussef, Jonkers sub MC 616 (MSUN).

Discussion

Polyploidy is a rather rare event in the history of asclepiadaceous plants since euploid diploids (2n=22) are found in c. 90% of stapeliad species (Albers & Meve 1990). Of the over 300 stapeliad taxa investigated, 35 were found to be tetraploids, but only six were hexaploids. This polyploidy frequency of about 10% (at species level) is quite low compared to other angiosperm families, in which it reaches 30–47% (Lewis 1980).

The three other asclepiadaceous species of the Canaries are diploids – the stem-succulents *Ceropegia dichotoma* Haw. and *C. fusca* Bolle (Albers et al. 1990), and the woody shrub *Periploca laevigata* Ait. (Periplocoideae) (Gagnieu et al. 1973). Therefore, Borgen's (1979) calculation of polyploidy frequency of the Canarian vascular flora with just 28%, or 24% among endemics (compare Borgen 1969, 1974), fits astonishingly well with the 25% polyploidy frequency of the Canarian Asclepiadaceae.

The occurrence of polyploid Stapelieae Decne. in Morocco is considerably above stapeliad average; especially in the genus *Caralluma*, in which polyploids in general are rare (Albers 1983, Meve & Albers, unpubl.). Of the four Moroccan taxa, *C. joannis* Maire and *C. burchardii* ssp. *maura* were identified as hexaploids with somatic 2n=66 chromosomes (Reese & Kressel 1967, Reese 1971, and own counts). This pattern is quite interesting and still difficult to explain, because the only other four hexaploids known in the tribe – in the genera *Duvalia* Haw., *Huernia* R. Br. and *Tromotriche* Haw. – are all natives of southern Africa (Meve & Albers, unpubl.).

The concentration of highly polyploid taxa in northwest Africa culminates in the occurrence of the highest chromosome number known in the stapeliads. The dodecaploidy (tridecaploidy) of *C. burchardii* ssp. *burchardii* is the highest ploidy number ever reported for the Asclepiadaceae and even the whole Gentianales (maybe only surpassed by *Buddleya* L., Loganiaceae). The occurrence of different infraspecific cytotypes is a phenomenon reported for most angiosperm families. In the stapeliads, subspecific pairs or triplets of different ploidy levels are known from both main distribution areas of the Afro-Arabian *Duvalia sulcata* N.E Br. and the southeast African *Orbeopsis gerstneri* (Letty) L.C. Leach (Meve & Albers, unpubl.). Here, the different genomes also help in circumscribing the taxa.

The different cytotypes of ssp. *burchardii* show a distinct distributional pattern with euploid-hendecaploid (2n=121) plants on the small Canary Islands of Lobos and Graciosa, and (sometimes aneuploid) dodecaploids (2n=132) on Fuerteventura and Lanzarote. Plants from the westernmost habitat, southwest Gran Canaria, possess an (aneuploid) tridecaploid genome (2n=141). The correlation between the size of the island from which the collection originates and the size of the genome is noteworthy. The small islets harbour plants with the smallest genome, while the large islands support plants with the largest genome ever found in the Asclepiadaceae. This pattern also indicates a topocline, from the smallest genomes in the northeast to the largest in the southwest.

The most likely explanation for this pattern is cytological rather than biogeographical. Obviously, the buffering effects of the large populations within the centres of distribution on Fuerteventura and Lanzarote help to stabilize the regular dodecaploidy here. In the small and rather isolated populations on Lobos, Graciosa and Gran Canaria, however, meiotic and mitotic irregularities, which can easily occur at this ploidy level, should have a much smaller chance for quick repair. Also, there is little chance for outbreeding in small and isolated populations. Therefore, karyological alterations, or even morphological ones like the corolla indumentum, for example, become fixed more easily in inbreeding than in outbreeding colonies. For that reason, inbreeding species tend to generate small intra- but relatively wide inter-populational variation (Stace 1989). C. burchardii was shown to be self-fertile, a feature typically distinguishing polyploid stapeliads (Jahnke 1989, Meve & Albers, unpubl.). Therefore, effects of breeding behaviour need to be taken into account while discussing the considerable inter-populational karyological and morphological variation within the typical subspecies.

Geological events probably may explain the distribution of C. burchardii: Parts of the eastern islands, Fuerteventura, Lanzarote, Graciosa and Lobos, have been shown to be part of North Africa (cf. Rothe 1968, Dietz & Sproll 1970). Their separation is dated at the time the continents Africa and South America split from Gondwanaland at least 100 m.y. ago (compare Axelrod & Raven 1974, Rothe 1968), or parallel to the initial rifting between North America and Africa about 200 m.y. ago (compare Dietz & Sproll 1970). Rothe (1968) showed that parts of Fuerteventuran sediments can be dated back to the late or even early Cretaceous, and may be of African origin. According to Dietz & Sproll (1970) parts of the eastern Canary Islands rest on the continental crust and once formed a single landmass, the Eastern Canaries Block. Before rifting, this block was situated at the rim of the African plate, todays Moroccan coast near Sidni Ifni ("Ifni Gap" sensu Dietz & Sproll 1970). The times given for the age of the Canary Islands vary tremendously and the entire hypothesis on the origin of the eastern Canaries is still a matter of debate (Schmincke 1976). However, the present shape of the eastern Canaries as well as the whole central and western Canaries (Gran Canaria, Tenerife, La Palma, La Gomera, El Hierro) is due to volcanism during the last 20 billion years (Schmincke 1976).

It can be noted that the tectonic events outlined above

coincide strikingly with the present-day distribution. Subspecies *burchardii* is almost restricted to the arid eastern Canaries, that is the Eastern Canaries Block, while the distribution area of ssp. *maura* exactly spans the "Ifni Gap" of Dietz & Sproll (Fig. 5). Additional support for this scenario comes from the fact that *C. burchardii* is without closely related species (see also Bruyns 1987), neither diploids nor polyploids, and therefore has to be regarded as a palaeopolyploid palaeoendemic (according to the classification of Favarger & Contandriopoulos 1961).

The scenario outlined above would require a very high age of about 100 m.y. for *C. burchardii*. This seems, with respect to the evidence for very high age (> 60 m.y.) in other Stapelieae complexes as well (cf. Meve & Porembşki 1993), not unlikely considering all evidence, but highly hypothetical.

One main argument against it is that asclepiad plants generally have left no fossil record. Also, nothing is known about later landbridges between the eastern Canaries and Africa or of possible drastic lowering of the sea level.

Strong Saharan winds have been named as plausible cause for the assumed distribution from Morocco to the Canaries during more recent times (Bruyns 1987). The heavy seeds of *C. burchardii* render this hypothesis rather unlikely, because the distances involved are substantial (c. 300 km at present, perhaps less in the past). Though, at least the single population on the rather young and truely volcanic island of Gran Canaria presumably arose from windborne seeds from Fuerteventura, if not, it was introduced by man. It therefore remains also possible that wind may have moved seed of *C. burchardii* from the Moroccan coast to the Canaries.

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