

A new species of *Arthrocnemum* (Salicornioideae: Chenopodiaceae-Amaranthaceae) from West Africa, with a revised characterization of the genus

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ABSTRACT

A new species *Arthrocnemum franzii* Sukhor. is described from the Republic of Cape Verde (Sal, Maio and Boa Vista islands). The species is recognized as distinct from *Arthrocnemum macrostachyum* (Moric.) K.Koch based on differences in the perianth shape, length of the anthers and style, and seed-coat ornamentation. No seed heteromorphism is observed within individuals of either species, despite differences in the size of the central and lateral flowers within each cyme (heteroanthocarpy). The North American *Arthrocnemum subterminale* (Parish) Standl. (syn. *Salicornia subterminalis* Parish) is morphologically distant from Eurasian *Arthrocnemum* or *Salicornia/Sarcocornia* group and should be excluded from these genera. The genus *Arthrocnemum* now comprises only two species (*A. macrostachyum* and *A. franzii*), distributed in the Mediterranean area, Macaronesia, West Tropical Africa and the Saharo-Arabian region. A generic description is here elaborated, clearly delimiting *Arthrocnemum* from morphologically similar species of *Sarcocornia*. A list of current species previously considered as *Arthrocnemum* is provided. It is argued that the taxonomic status of *Salicornia mucronata* Lag. (1817), mentioned in some references as a synonym of *Salicornia macrostachya* Moric. (1820) [= *Arthrocnemum macrostachyum* (Moric.) K.Koch], is indeed a new synonym of *Anabasis articulata* (Forssk.) Moq. (subf. Salsoloideae). Both names merged with *Arthrocnemum macrostachyum* – *Salicornia virginica* Forssk. and *Arthrocnemum glaucum* (Delile) Ung.-Sternb. var. *fasciculatum* Sennen were lectotypified. The typification of the genus *Arthrocnemum* has so far been lacking and requires a special proposal with a conserved type.

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Introduction

The genus *Arthrocnemum* Moq. belongs to the taxonomically and diagnostically difficult subfamily Salicornioideae, which differs from many other Chenopodiaceae-Amaranthaceae groups by the presence of fleshy, opposite or alternate leaves usually reduced to scales and often looking like bracts, the absence of bracteoles, and the flowers arranged in cymes consisting of three (one central and two lateral) flowers of whitish or brownish colour. *Arthrocnemum* was described by Moquin-Tandon (1840) who included several shrubby species of similar habit and reproductive characters (e.g. crustaceous seed coat and mealy perisperm in the seed). Both carpological traits indicated in the protologue are indeed variable in *Arthrocnemum*. In its earlier circumscription (e.g. Ball 1964; Aellen, Cullen and Coode 1967) *Arthrocnemum* also includes shrubby species of *Salicornia* L. However, the latter genus is characterized as distinct from *Arthrocnemum* by the limited amount of nutritive tissue present in the seed and the hair-like or papillate outgrowths of the seed testa cells, which do

not contain tannin-like outgrowths (so-called ‘stalactites’) on the outer wall (Bunge 1856; Brenan 1954b; Castroviejo and Coello 1980; Shepherd, Macfarlane and Colmer 2005a; Sukhorukov 2014).

In the past *Arthrocnemum* was considered to be a genus of several (three to ten) species distributed in Africa, America and Australia (Moquin-Tandon 1840; Koch 1853; Ungern-Sternberg 1866, 1876; Volkens 1893; Standley 1914; Brenan 1954a; Scott 1977; Meikle 1985; Kühn 1993). The nomenclatural confusion in the naming of the ‘*Arthrocnemum* – shrubby *Salicornia* group’ remained in many past treatments (Moss 1954; Ball 1964; Toelken 1967), until Scott (1977) typified the genus *Arthrocnemum* with *Arthrocnemum fruticosum* (L.) Moq. var. *macrostachyum* (Moric.) Moq., the variety mentioned by Moquin-Tandon (1840), which most closely matched the diagnosis of the genus. It should be pointed out that the lectotypification undertaken by Scott (1977) is incorrect as it is based on a name of non-specific rank (cf. Hedge 1997; ICN 2012 [Art. 10.1]), and none of the species recognized by Moquin-Tandon (1840) is appropriate for the typification. This

Table 1. Differences between *Arthrocnemum* and *Salicornia/Sarcocornia*.

Character	<i>Arthrocnemum</i>	<i>Salicornia/Sarcocornia</i>	References
Tracheidioblasts in the stem	–	+ (except <i>Salicornia natalensis</i> : O'Callaghan 1992)	de Fraine (1913, as different <i>Salicornia</i> species, <i>Arthrocnemum macrostachyum</i> as <i>S. glauca</i>); Wilson 1980; O'Callaghan 1992; Milič et al. (2011); Grigore et al. (2014)
Perianth	directed upward, not immersed in the stem	laterally directed, more or less immersed in the stem	e.g. Scott (1977); Sukhorukov (2014)
Tracheidioblasts in the perianth	–	+	Ungern-Sternberg (1866); Sukhorukov (2014); Sukhorukov and Nilova (present paper)
Style	+	not present or very short (to 0.25 mm)	(Ferguson 1964); Sukhorukov and Nilova (present paper)
Seeds	black	pale brown	Steffen et al. (2009; 2010); Sukhorukov (2014)
Seed-coat testa	contains of papilla-like (hard) cells, 25 µm or more thick; stalactites present in the outer cell wall	often contains hair-like or papillate (soft) outgrowths, sometimes testal surface smooth; up to 10 µm thick; stalactites absent from the outer cell wall	Shepherd, Macfarlane and Colmer (2005a); Steffen et al. (2009; 2010); Guilló et al. (2013); Sukhorukov (2014)
Perisperm	+	– (or traces)	Shepherd et al. (2005a); Sukhorukov et al. (2015)
Embryo	comma-shaped	almost straight	Shepherd et al. (2005a); Sukhorukov (2014)

nomenclatural problem needs to be addressed separately, together with the proposed conservation of the name *Arthrocnemum* with the type *Arthrocnemum macrostachyum* (Moric.) K. Koch (\equiv *A. fruticosum* (L.) Moq. var. *macrostachyum* Moq.) as type.

All shrubby taxa from Southern Africa formerly assigned to *Arthrocnemum* (Hiern, Rendle and Welwitsch 1896; Moss 1954; Toelken 1967; Lebrun and Stork 1991) or even *Arthrocnemum macrostachyum* reported from Angola (Baker and Clarke 1913; Lebrun and Stork 2003) belong in fact to various *Sarcocornia* species (O'Callaghan and Oliver 1992; Kadereit, Mucina and Freitag 2006), and thus *Arthrocnemum* is not represented in Southern Africa (Steffen, Mucina and Kadereit 2009, 2010). The same applies to the European (*A. fruticosum*, *Arthrocnemum perenne*) and South American (*A. fruticosum* auct.) species previously included in *Arthrocnemum* and now included in *Sarcocornia* (Davy et al. 2006; Alonso and Crespo 2008). *Arthrocnemum fruticosum* (L.) Moq. and *Arthrocnemum ambiguum* (Michx.) Moq. are now considered as *Sarcocornia fruticosa* (L.) A.J. Scott and *Sarcocornia ambigua* (Michx.) M.A. Alonso & M.B. Crespo respectively (Scott 1977; Alonso and Crespo 2008); *Arthrocnemum belangerianum* Moq. is now *Halostachys belangeriana* (Moq.) Botsch. (Botschantzev 1954; Sukhorukov 2014), and both *Arthrocnemum arbuscula* (R.Br.) Moq. and *Arthrocnemum indicum* (Willd.) Moq. are currently included in *Tecticornia* Hook.f. (Shepherd and Wilson 2007).

Among these taxa, *Arthrocnemum macrostachyum* and *Sarcocornia fruticosa* are often found growing together in the Mediterranean area in the same ecological conditions associated with marshes and other saline supralittoral or inland habitats (Jalas and Suominen 1980; Kühn 1993; Guilló et al. 2014; Sukhorukov, pers. obs. in Cyprus and Israel), and they are often confused with each other. Indeed, many morphological or even anatomical characters of both articulated *Arthrocnemum*

and *Salicornia* including paraphyletic *Sarcocornia* (Shepherd, Macfarlane and Waycott 2005b; Steffen et al. 2015) are overlapping (Zare and Keshavarzi 2007). Despite many morphological homologies (shrubby life history; glabrous stem; opposite scale-like leaves and bracts; cymes consisting of three flowers; rupture of the lower part of both perianth and pericarp making the ripe seed free; vertical embryo position) and similar (saline) habitats, there are several important traits unambiguously distinguishing *Arthrocnemum* from the *Salicornia/Sarcocornia* group (Table 1; see also De Fraine 1913; Ferguson 1964; Sukhorukov 2014). In addition to the data presented in Table 1, it should be pointed out that the colour of many *Sarcocornia* varies from green to reddish, whereas both *A. macrostachyum* and *Arthrocnemum franzii* are always grey or (in some cases) yellowish (Sennen 1936; Sukhorukov, pers. obs. in Cape Verde). Additionally, some articulated Salsoloideae (e.g. *Anabasis*) habitually resemble *Arthrocnemum* or the *Salicornia/Sarcocornia* group and are often confused in herbaria (see also taxonomic comments below under *Salicornia mucronata* Lag.), but the representatives of both subfamilies are very dissimilar in stem anatomy (epidermal layers: Dangeard 1887; De Fraine 1913; O'Callaghan 1992; Milič et al. 2011; Grigore, Ivanescu and Toma 2014) or reproductive characters, especially fruit anatomy (Sukhorukov 2008, with further references herein; Sukhorukov et al. 2015).

Currently, a single North American species – *Arthrocnemum subterminale* (Parish) Standl. – is included in *Arthrocnemum* (Standley 1914; Ball 2003). This species appears to be unrelated to *A. macrostachyum* or *A. franzii* on account of differences in the perianth, pericarp and seed characters, and deserves further investigation concerning its taxonomic status (compare Parish 1898; Wilder, Felger and Romero-Morales 2008, both references as *Salicornia*; or Standley 1914; Ball 2003 as *Arthrocnemum*). We state here for the first time that this species possesses a unique perianth that

splits longitudinally into two parts in the fruiting stage (essentially making the fruit free), as well as having a thinner pericarp and brown (not black as in Eurasian *Arthrocnemum*) seeds with no papilla-like outgrowths. Steffen et al. (2015) suggest that *A. subterminale* is not related to *Arthrocnemum* s.str.

Another species, *Arthrocnemum indicum*, which is widely distributed in the coastal zones of the Indian Ocean (East and Southern Africa, Sub-Indian continent and Australia), has been transferred to *Halosarcia* Wilson (Wilson 1980) and then to *Tecticornia* Hook.f., a genus with the highest diversity in Australia (Shepherd, Waycott and Calladine 2004; Shepherd 2007; Shepherd and Wilson 2007). The differences between *Arthrocnemum* and *Tecticornia* (especially *Tecticornia indica* previously considered to be *Arthrocnemum indicum*) were clarified by Wilson (1980) based on the anther number (two anthers versus one abaxial anther, respectively). Other distinguished characters of *T. indica* are the rooting stem, flowers connate to each other (but details lacking where both flower types are located in the inflorescence: Jafri and Rateeb 1978, sub *Arthrocnemum indicum*), and pale brown seeds (Friis and Gilbert 1993, as *Halosarcia indica*).

Both molecular (e.g. Shepherd, Waycott and Calladine, 2004; Kadereit, Mucina and Freitag, 2006; Kadereit and Yaprak 2008) and carpological (Sukhorukov 2014) results show that *Arthrocnemum* is closely related to the monotypic genus *Microcnemum* found in the Mediterranean region. The genera are nested within one clade (Shepherd, Macfarlane and Waycott, 2005b; Kadereit, Mucina and Freitag, 2006; Kadereit and Yaprak 2008), which is clearly distant from both *Salicornia* and *Sarcocornia*, which together form a separate lineage. Carpologically both *Arthrocnemum* and *Microcnemum* possess black seeds with a thick, crustaceous coat often forming stout (papilla-like) outgrowths from the testa cells, and with “stalactites” on the outer cell walls of the testa (Sukhorukov 2014). Both genera are well-distinguished by the life history (shrubby habit in *Arthrocnemum* and annual habit in *Microcnemum*).

The genus *Arthrocnemum* has recently been considered to comprise only *A. macrostachyum* (Hedge 1997; Yaprak 2008), which is a widely distributed species in the Mediterranean basin with extensions into the Macaronesian, Saharo-Arabian and Irano-Turanian floristic regions, or to also include the North American *A. subterminale* (Standley 1914; Ball 2003). We recognize that the reproductive organs in *Arthrocnemum*, especially the perianth and pericarp, have not been sufficiently studied to date. In the present paper we devote particular attention to their taxonomic significance in the genus, and draw comparisons with similar-looking taxa. Besides, *A. macrostachyum* is morphologically heterogeneous and is re-circumscribed to exclude a new species from Macaronesia, which is recognized herein as *A. franzii* Sukhor.

Material and methods

The *Arthrocnemum* material was collected by A. Sukhorukov in Cyprus (November 2006) and in Cape Verde (August–September 2015, January 2016). Additionally, the first author has examined the *Arthrocnemum* material in the herbaria B, BM, BR, E, HUJ, K, LE, MHA and MW [herbarium abbreviations according to Thiers (2008+)], and has used some specimens for comparative study (see Appendix 1). The perianth sections were obtained using a microtome (embedding the perianth and pericarp in Technovit), with no staining of the sections. The images of the seed ultrasculpture were made using a scanning electron microscope (SEM) JSM-6380 (JEOL Ltd., Japan) at 15 kV. The seeds were cut by hand or with a microtome (no dye is needed for the seeds because all the seed-coat cells are impregnated with tannins). All the images were taken with the camera Carl Zeiss AxioCam MRc using light microscope Carl Zeiss Axioplan 2.

Results

As a result of our studies, we consider that the populations in Cape Verde are distinguished from Mediterranean *A. macrostachyum* by several important reproductive characters and deserve recognition at species rank. This raised the need for a new generic delimitation of the genus *Arthrocnemum*, which is provided in the taxonomic treatment below. Additionally, a checklist of all the names assigned to *Arthrocnemum* is given.

Taxonomic treatment

Arthrocnemum Moq., *Chenop. Monogr. Enum.*: 111 (1840).

Type of the genus: not yet typified (the genus should be typified with a conserved name).

The genus *Arthrocnemum* can be morphologically characterized by the following distinct characters:

Shrubs to 1.5 m tall, very branched from the base often forming mats; annual shoots glaucous (sometimes yellowish), glabrous (or one-layered epidermis can be represented by mamillate cells). Phyllotaxis decussate; leaves reduced to opposite, basally concrescent and cuspidate scales up to 5 mm long, with fissures between the scales within one node. Inflorescence on lateral branches terminal, not branching or with short paraclasses; each cyme of three flowers subtended by a bract (each node contains two opposite bracts and hence six flowers). Flowers bisexual (sometimes the stamens in the lateral flowers are missing and so they may be pistillate only), protandric. Perianth always concrescent to the apex (sometimes with small terminal lobes), directed upwards, protruding by up to one-third to one-half the length of the bracts and consisting of parenchymatous, thin-walled cells arranged in several layers, with inclusion of scattered lignified cells as an inner layer, but never

completely indurated, and with no tracheoidioblasts; perianth of the central flower four-angled (probably consisting of four segments), and that of the two lateral (peripheral) flowers three-angled (heteroanthocarpy). Ovary conical, fruit wall (pericarp) of parenchymatous cells, thick and few-layered in upper part and thinning in lower portion. Stamen 1–2, anthers protruding from the perianth, 0.8–1.3 mm. Style present, with two stigmas. Seed black (reddish when unripe), testa crustaceous, mostly with papilla-like (conic) outgrowths located along one (embryo-bearing) side, 20–25 µm thick (in flattened cells) and up to 55 µm thick in conic cells, their outer wall bearing five to ten stalactites, cell content easily visible. Perisperm present. Embryo curved (comma-shaped), vertical, radicle in abaxial position, cotyledons located adaxially (close to the axis).

Morphological notes

We cannot confirm the statement that the lateral flowers in *Arthrocnemum* are staminate only (Kühn 1993) and so do not produce fruit. In fact all (central and both lateral) flowers in the cyme of *A. macrostachyum* and *A. franzii* sp. nov. (description of a new species is given below) possess a well-developed ovary, although they often remain sterile (for example, in the populations of *A. franzii* seen in Cape Verde in 2015). The causes of the sterility are still not known. The presence of an indurated pericarp in *Arthrocnemum*, mentioned by Ungern-Sternberg (1866), Scott (1977), Jafri and Rateeb (1978) or Friis and Gilbert (1993) has also been shown to be unfounded.

1. *Arthrocnemum macrostachyum* (Moris) K.Koch, *Hort Dendrol.* 96 (1853)

The same combinations of Moris and Delporte (1854) and Bunge in Ungern-Sternberg (1866) are superfluous.

Bas.: *Salicornia macrostachya* Moric., *Fl. Venet.* 1: 2 (1820).

Holotype: Des environs de Venise [surroundings of Venice], Malamocco, herb. Moricand (G – photo!).

≡ *Salicornia virginica* Forskål, *Fl. Aegypt.-Arab.* 2 (1775) nom. illegit. non L. (1753);

Described from Egypt. Lectotype (Sukhorukov, designated here): “Circa Alexandriam [leg.] Forskål 174” (C-10002990 – photo!).

≡ *S. glauca* Delile, *Fl. Egypt.* 69 (1813) nom. illegit. non Stokes (1812).

Described from Egypt without precise location (holo – LINN-HS20-13, photo!).

≡ *Arthrocnemum fruticosum* (L.) Moq. γ [var.] *macrostachyum* Moq., *Chenop. Monogr. Enum.*: 111 (1840).

≡ *A. glaucum* (Delile) Ung.-Sternb., *Atti Congr. Bot. Firenze*: 283 (1876);

≡ *A. glaucum* (Delile) Ung.-Sternb. var. *fasciculatum* Sennen, *Diagn. Nouv. Exs.*: 204 (1936).

Lectotype (Sukhorukov, designated here): Maroc, Melilla, a la Bocana, 24 November 1932, leg. Sennen & Mauricio 8917 (BM; iso-BC-141886, MPU-009401,

MPU-009401 – photo!). The plants of yellowish colour are collected in the late fruiting stage with condensed inflorescence (Sennen 1936). The seeds observed from collection in BM possess a small amount of the conic (papilla-like) cells.

≡ *A. indicum* (Willd.) Moq. subsp. *glaucum* (Delile) Maire & Weiller in Maire, *Fl. Afr. Nord.* 8: 99 (1962).

Taxonomic note

We argue that the still unresolved and forgotten *Salicornia mucronata* Lag. described from Spain (Lagasca 1817), cited in some references as a synonym of *Arthrocnemum macrostachyum* (Ungern-Sternberg 1876; Rouy 1910; Zohary 1966), is indeed a new synonym of *Anabasis articulata* (Forsk.) Moq. The holotype specimen of *Salicornia mucronata* kept at MA (photo!) is represented by a young branch with mucronate scale-like leaves (like in *Arthrocnemum*), but possesses the tufts of the simple hairs in the leaf axils (report of Charo Noya Santos) that is one of the most remarkable characters in the tribe Salsoleae, subf. Salsoloideae (Sukhorukov 2014).

2. *Arthrocnemum franzii* Sukhor. sp. nov. (Figure 1)

Shrub up to 1 m tall forming mats up to 3 m across, often with twisted perennial shoots; annual branches glaucous (sometimes yellowish) and glabrous. Leaves up to 5 mm long, cup-like, acuminate. Inflorescence cylindrical, to 10 cm, consisting maximum of 50 nodes, branched in lower parts or not, with short paraclades (if present). Bracts similar to leaves, not fused to the perianth. Flowers 3 in a cyme, free. Perianth of the central flowers four-angled, trapezoid, 1.5–1.7 mm long; perianth of lateral flowers three-angled, forming a cone, 1.3–1.5 mm long; one-third to one-half of all flowers protruding above the subtending bract. Stamen 1–2, anther 0.8–1.0 mm long. Ovary 1.3–1.6 mm long, gradually tapering to the style 1–1.5 mm long with two stigmas ~ 1 mm long. Fruit embedded in the perianth, with hyaline pericarp. Seeds developing in all central and lateral flowers, 1.0–1.3 mm long, 0.7–0.8 mm wide, 0.5–0.6 mm thick, black, generally with easily visible papilla-like outgrowths located along the embryo-bearing seed margin; testa cells (20)25 to 55 µm (the thickness depending on whether the cells have such outgrowths), their outer cell walls with five to ten stalactites. Perisperm copious. Embryo comma-shaped.

Holotype (Figure 2): **Republic of Cabo Verde**, Sal Island, 2 km west from Santa Maria town, 16°59'02.46" N, 22°92'42.72" W, sandy depressions near the sea, 30 August 2015, Alexander P. Sukhorukov 56 (MW-0198220 ! iso – BR, L, LE).

Additional specimens seen: **Republic of Cabo Verde**: Sal Island, [Rifes da] Parda, June 1934, A. Chevalier s.n. (K); Sal Island, Santa Maria, 19 October 1934, M. Dinklage 3194 (BM); Maio Island, Terra Salgadas Salinas N of Morrinho [c. 15°16'40" N, 23°12'30" W],

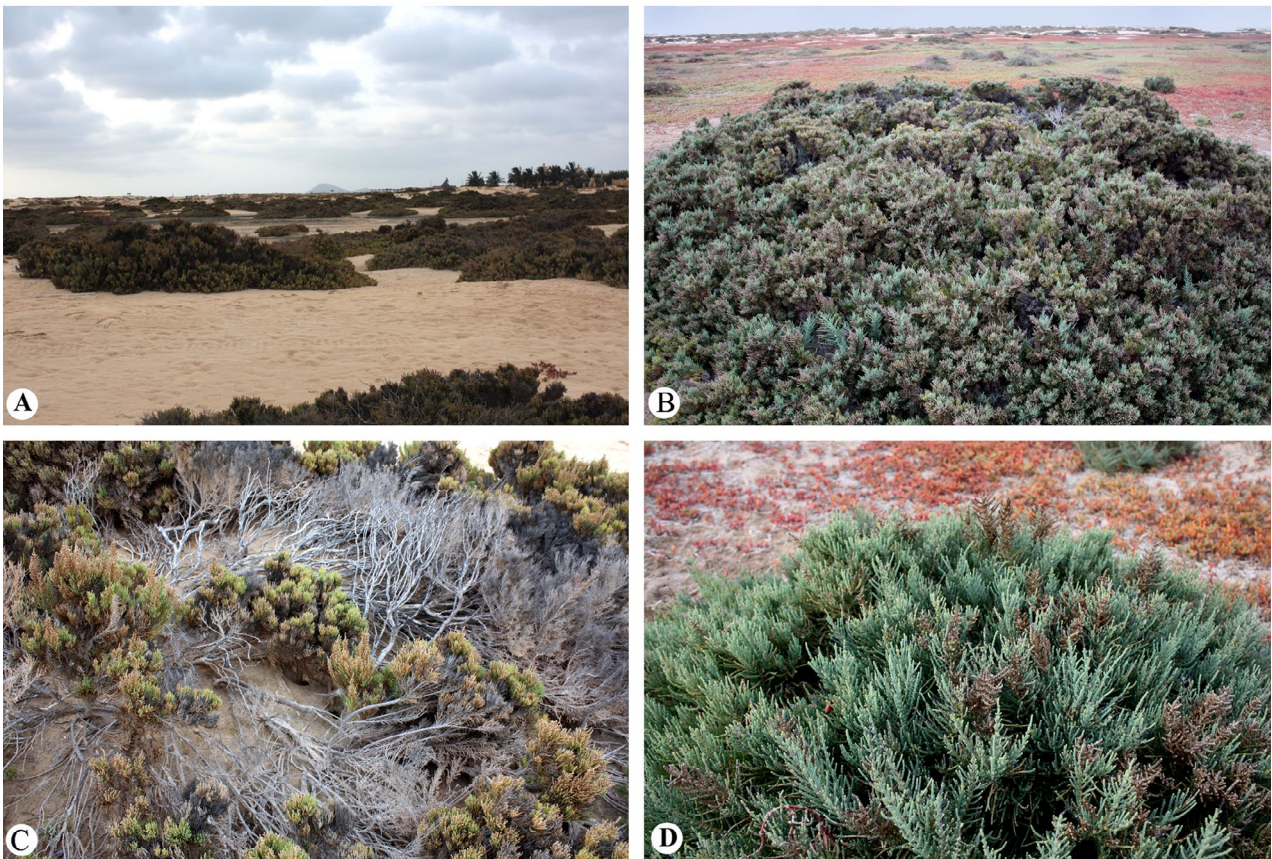


Figure 1. General view of *Arthrocnemum franzii* in Sal Island (August–September 2015). (A) Dominant in the sandy depressions (often together with *Sesuvium* sp., *Suaeda vermiculata* and *Zygophyllum waterlotii*). (B) Closer look at an individual. (C) Branching pattern of the new species. (D) Part of the plant with fruiting inflorescence. Photographer: A. Sukhorukov.

seasonally flooded plain on the landward side of the coastal dune belt, 4 January 1994, N. Kilian & T. Leyens NK3028 (B); Boa Vista Island, Sal Rei, 16°18'40.95" N, 22°91'66.38" W, salty plain on the landward side of the coastal dune belt, 10 January 2016, A.P. Sukhorukov & A. Konstantinova 683 (G, M, MW, W); Boa Vista, 8 km south of Sal Rei, 16°11'71.42" N, 22°90'29.04" W, sandy depressions near the sea, 10 January 2016, A.P. Sukhorukov & A. Konstantinova 693 (MW); Boa Vista, Santa Monica beach, 15°98'41.77" N, 22°84'24.79" W, seasonally flooded plain on the landward side of the coastal dune belt, 10 January 2016, A.P. Sukhorukov & A. Konstantinova 697 (MW).

On the Sal and Boa Vista Islands, this species was previously called *Arthrocnemum fruticosum* (Schmidt 1852) as well as *A. macrostachyum* (Martins 2002).

Distribution

The new species is distributed in Tropical West Africa – Cape Verde (Boa Vista, Maio, Sal as the most arid islands in the archipelago) (Figure 3). It is likely that the ranges of *A. macrostachyum* (Mediterranean area with extensions to the Saharo-Arabian floristic province) and *A. franzii* do not overlap.

Ecology and plant communities

Seasonally flooded, saline plain on the landward side of the coastal dune belt.

In Sal and Boa Vista Islands, the species is a dominant of the depressions in natural sandy landscapes near sea level, and grows together with *Suaeda vermiculata* Forssk. ex J.F. Gmel. (Amaranthaceae–Chenopodiaceae), *Sesuvium* sp. (Aizoaceae) incorrectly identified in the herbaria BM, K as *S. portulacastrum* L., and *Tetraena gaetula* (Emb. & Maire) Beier & Thulin subsp. *waterlotii* (Maire) Beier & Thulin (\equiv *Zygophyllum waterlotii* Maire) (*Zygophyllaceae*). In contrast to all the species mentioned, *Arthrocnemum franzii* do not appears as a constituent of disturbed plant communities.

Flowering and fruiting

Flowering: January–May; fruiting: May–July.

IUCN Red List Category

Although appropriate data on abundance and/or distribution of the taxon are lacking for Maio Island, we recorded *A. franzii* as common on sandy inland plains on Sal and Boa Vista. However, the construction of new



Figure 2. Holotype of *Arthrocnemum franzii* kept at MW.

buildings elsewhere in Cape Verde (especially hotels on Sal as one of the most visited islands in the archipelago) drastically damages the natural landscapes (Romeiras et al. 2016; A. Sukhorukov, pers. obs.), and additionally the plants investigated produce few fruits (not more than 5% of flowers are fertile). We accordingly recommend inclusion of the new species in one of the Red List categories (IUCN 2014), but the exact categorization must be decided only after further detailed studies in other islands of Cape Verde. Till now, *Arthrocnemum* is not included in the list of threatened species in Cape Verde archipelago (Romeiras et al. 2016).

Etymology

The species is named after Baron Franz Ungern-Sternberg (1808–1885), botanist and physician, and expert on the Salicornioideae, Chenopodiaceae (see also Quattrocchi 2000).

Taxonomic notes

The new species is distinguished from *A. macrostachyum* by several reproductive characteristics, and these can be used for delimiting the species and refining the genus characterization. The species are compared with respect to each character.

Perianth

The perianth of the central and lateral flowers of both species consists of parenchymatous, often spongy and never indurated cells lacking tracheoidioblasts. Both *A. macrostachyum* and *A. franzii* are characterized by differences in perianth shape of three-flowered cyme (trapezoid perianth in the central flower and conus-like perianth in both lateral flowers), termed heteroanthocarp (Sukhorukov 2010) (Figure 4, 5). However, *A. macrostachyum* and *A. franzii* differ from each other in the outlines of the perianth shape of the central



Figure 3. Records of *Arthrocnemum franzii* (stars).

flowers (obconic in *A. macrostachyum* with small ear-like appendages (terminal lobes), and trapezoid perianth with no appendages in the latter species).

Anthers

Field-based collections by the first author confirm that the anthers of *A. franzii* are shorter (0.8–1 mm long) than those observed in *A. macrostachyum* s.str. (1–1.3 mm) growing in the Mediterranean area, which is in agreement with previous data for *A. macrostachyum* (Maire 1962; Castroviejo 1990).

Style

Arthrocnemum franzii is characterized by the longer (1.0–1.5 mm), easily visible, thick style (Figure 6, A) that splits into 2(3) stigmas of the same length. In contrast, *A. macrostachyum* is distinguished by the clearly shorter (0.4–0.7 mm) style, that hardly protrudes beyond the perianth, and the 2(3) stigmas being 1.0–1.5 mm long (Figure 6, B); see Castroviejo 1990). At the final fruiting stage, the stigmas and upper part of the style break off, with the lower portion persisting. This protrusion is approximately 0.5–0.7 mm long in *A. franzii*, which is twice the length of that observed in *A. macrostachyum* (0.25–0.4 mm).

Seeds

The seeds of both *A. franzii* and *A. macrostachyum* are morphologically and anatomically monomorphic. The length of the seeds in *A. franzii* is 1.1–1.3 mm, and the length/width ratio is 2 : 1 (the seeds are clearly elongated; for comparison see also Guilló, Alonso and Juan 2013). The seeds of *A. macrostachyum* are 1.0–1.1 mm long and 0.7–0.9 mm wide (length/width ratio 1.2–1.5 : 1). Moreover, the number of papilla-like outgrowths of the testa cells (mostly arranged along the embryo-containing part of the seed) in *A. franzii* is usually much greater than in *A. macrostachyum* (Figures 7, 8).

Conclusion

To conclude the discussion of the taxonomic diversity of *Arthrocnemum*, we reiterate that the genus as defined by us comprises only two taxa – *A. macrostachyum* (Mor.) K.Koch, mostly widespread in the Mediterranean area and the northern Sahara (White 1983; Greuter, Burdet and Long 1984), and a new species *A. franzii* Sukhor. in West Africa. However, the populations in the coastal regions of the Arabian Sea with an unusual habit, especially on Socotra archipelago (Yemen, see Brown and Mies 2012), as well as in Sudan, Somalia and Ethiopia

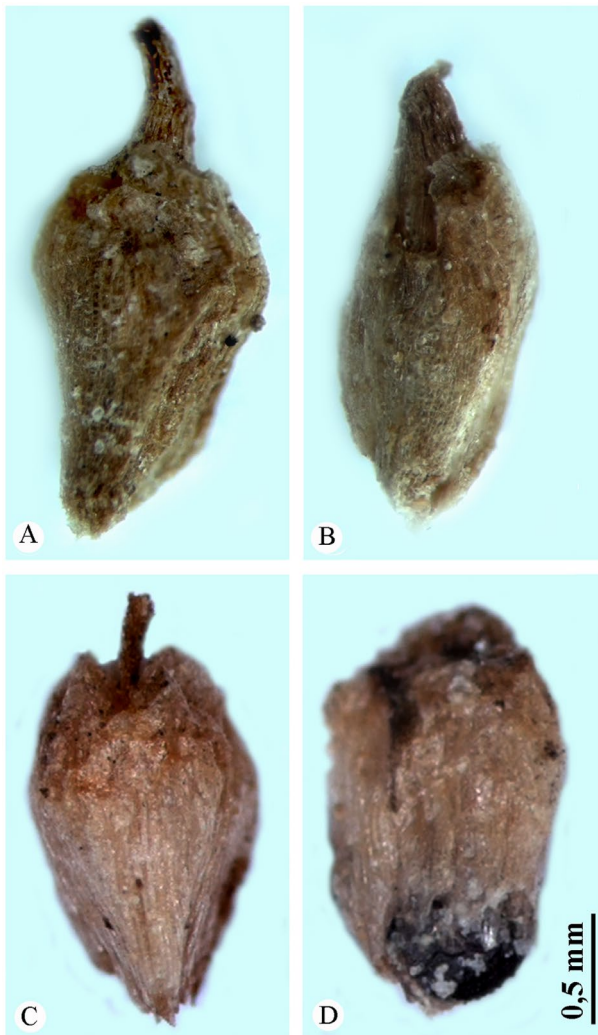


Figure 4. Flowers (front view). (A) Central flower in the cyme of *Arthrocnemum franzii*. (B) Lateral flower in the cyme of *A. franzii*. (C) Central flower in the cyme of *Arthrocnemum macrostachyum*. (D) Lateral flower in the cyme of *A. macrostachyum*. Origin of the material: (A, B) Alexander P. Sukhorukov 56 (holotype) and (C, D) H. Freitag, Egypt, 1987 (LE).

deserve a closer look, since the existing material is inadequate, and did not allow us to assess its taxonomic status or assign it to *A. macrostachyum*. We surmise that *A. subterminale* should be transferred to a new genus (based on the reproductive characters), and this suggestion will be supported by the preliminary molecular data (Steffen et al. 2015).

Checklist of *Arthrocnemum* names

We set out the names previously known as *Arthrocnemum* and which have recently been assigned to other genera, especially to *Sarcocornia*. We mostly cite here the most recent references due to disambiguation of some names – e.g. *Arthrocnemum africanum* in Scott (1977) and Steffen, Mucina and Kadereit (2010). The accepted names are highlighted in bold although, in the light of the paraphyly of *Sarcocornia* (Shepherd, Macfarlane and Awayscott 2005b; Kadereit, Mucina and Freitag, 2006;

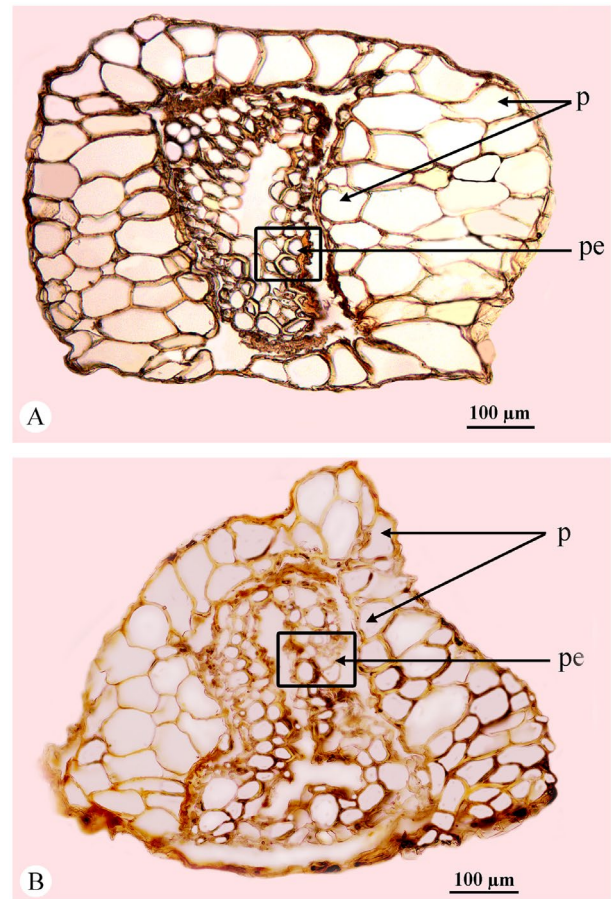


Figure 5. *Arthrocnemum franzii*, perianth shape in cross-section (taken from the holotype specimen). (A) Trapezoid perianth in the central flower. (B) Conic perianth in both lateral flowers. Abbreviations: p – perianth, pe – pericarp.

Steffen et al. 2015), all species now assigned to this genus should apparently be recognized as belonging to an extended *Salicornia*.

Arthrocnemum affine Moss \equiv ***Sarcocornia natalensis*** (Bunge ex Ung.-Sternb.) A.J. Scott **subsp. *affinis*** (Moss) S. Steffen, Mucina & G. Kadereit (Steffen et al. 2010);

A. africanum Moss \equiv ***Sarcocornia natalensis*** (Bunge ex Ung.-Sternb.) A.J. Scott (Steffen et al. 2010);

A. ambiguum (Michx.) Moq. \equiv ***Sarcocornia ambigua*** (Michx.) M.A. Alonso & M.B.Crespo (Alonso and Crespo 2008);

A. arbuscula (R.Br.) Moq. \equiv ***Tecticornia arbuscula*** (R.Br.) K.A. Sheph. & Paul G. Wilson (Shepherd and Wilson 2007);

A. australasicum (Moq.) Moss \equiv ***Tecticornia australasica*** (Moq.) (Paul G. Wilson) K.A. Sheph. & Paul G. Wilson (Shepherd and Wilson 2007);

A. belangerianum Moq. \equiv ***Halostachys belangeriana*** (Moq.) Botsch. (Botschantzev 1954; Sukhorukov 2014);

A. benthamii Paulsen \equiv ***Tecticornia indica*** (Willd.) K.A. Sheph. & Paul G. Wilson **subsp. *leiostachya*** (Benth.) K.A. Sheph. & Paul G. Wilson (K.A. Shepherd in herb. PERTH);



Figure 6. Fruiting inflorescence in *Arthrocnemum frantzii* (A) and *Arthrocnemum macrostachyum* (B). Abbreviations: sl–style (*A. frantzii*), stigmas fallen off; st – stigmas (*A. macrostachyum*); style not protruding. Origin of the material: *A. frantzii* from the holotype (Cape Verde), *A. macrostachyum*: Israel, Dead Sea, 1902, J.E. Dinsmore 9102 (HUJ).

A. bidens Nees \equiv *Tecticornia indica* (Willd.) K.A. Sheph. & Paul G. Wilson **subsp. bidens** (Nees) K.A. Sheph. & Paul G. Wilson (Shepherd and Wilson 2007);

A. brachystachyum Paulsen \equiv *Tecticornia indica* (Willd.) K.A. Sheph. & Paul G. Wilson **subsp. leiostachya** (Benth.) K.A. Sheph. & Paul G. Wilson (P.G. Wilson in herb. NSW);

A. capense Moss \equiv *Sarcocornia capensis* (Moss) A.J. Scott (Steffen et al. 2010);

A. caspicum (Pall.) Moq. nom. illegit. (invalid basonym: *Salicornia caspica* Pall. 1771 non L. 1753) \equiv *Halostachys belangeriana* (Moq.) Botsch. (Sukhorukov, in present article);

A. ciliolatum Bunge ex Ung.-Sternb. \equiv *Tecticornia indica* (Willd.) K.A. Sheph. & Paul G. Wilson **subsp. ciliolata** (Bunge ex Ung.-Sternb.) K.A. Sheph. & Paul G. Wilson (Shepherd and Wilson 2007);

A. coralloides Loscos & J. Pardo \equiv *Microcnemum coralloides* (Loscos & J. Pardo) Buen (Molero 1986);

A. decumbens Toelken \equiv *Sarcocornia decumbens* (Toelken) A.J. Scott (Steffen et al. 2010);

A. donaldsonii (Ewart & Jean White) C.A. Gardner \equiv *Tecticornia tenuis* (Benth.) K.A. Sheph. & Paul G. Wilson (P.G. Wilson in herb. MEL);

A. dunense Moss \equiv *Sarcocornia dunensis* (Moss) S. Steffen, Mucina & G. Kadereit (Steffen et al. 2010);

A. fruticosum (L.) Moq. \equiv *Sarcocornia fruticosa* (L.) A.J. Scott (Steffen et al. 2015);

A. fruticosum var. *californicum* Moq. \equiv see comments under *A. subterminale* (Sukhorukov, in present study);

A. glaucum (Delile) Ung.-Sternb. nom. illegit. (*Salicornia glauca* Delile 1813 non *S. glauca* Stokes 1812)

\equiv *A. macrostachyum* (Morici.) K.Koch (e.g. Castroviejo 1990);

A. halocnemoides Nees \equiv *Tecticornia halocnemoides* (Nees) K.A. Sheph. & Paul G. Wilson **subsp. halocnemoides** (Shepherd and Wilson 2007);

A. halocnemoides Nees var. *pergranulatum* J.M. Black \equiv *Tecticornia pergranulata* (Nees) K.A. Sheph. & Paul G. Wilson (Shepherd and Wilson 2007);

A. halocnemoides Nees var. *pterygospermum* J.M. Black \equiv *Tecticornia pterygosperma* (Nees) K.A. Sheph. & Paul G. Wilson (Shepherd and Wilson 2007);

A. heptiflorum Moss \equiv *Salicornia quinqueflora* Bunge ex Ung.-Sternb. (Toelken 1967) \equiv *Sarcocornia quinqueflora* (Bunge ex Ung.-Sternb.) A.J. Scott;

A. hottentoticum Moss \equiv *Sarcocornia pillansii* (Moss) A.J. Scott (Steffen et al. 2010);

A. indicum (Willd.) Moq. \equiv *Tecticornia indica* (Willd.) K.A. Sheph. & Paul G. Wilson **subsp. indica** (Shepherd and Wilson 2007);

A. leiostachyum (Benth.) Paulsen \equiv *Tecticornia indica* (Willd.) K.A. Sheph. & Paul G. Wilson **subsp. leiostachya** (Benth.) K.A. Sheph. & Paul G. Wilson (Shepherd and Wilson 2007);

A. littoreum Moss \equiv *Sarcocornia littorea* (Moss) A.J. Scott (Steffen et al. 2010);

A. lylei (Ewart & Jean White) J.M. Black \equiv *Tecticornia lylei* (Ewart & Jean White) K.A. Sheph. & Paul G. Wilson (Shepherd and Wilson 2007);

A. mossianum Toelken \equiv *Sarcocornia mossiana* (Toelken) A.J. Scott (Steffen et al. 2010);

A. namaquense Moss \equiv *Sarcocornia pillansii* (Moss) A.J. Scott (Steffen et al. 2010);

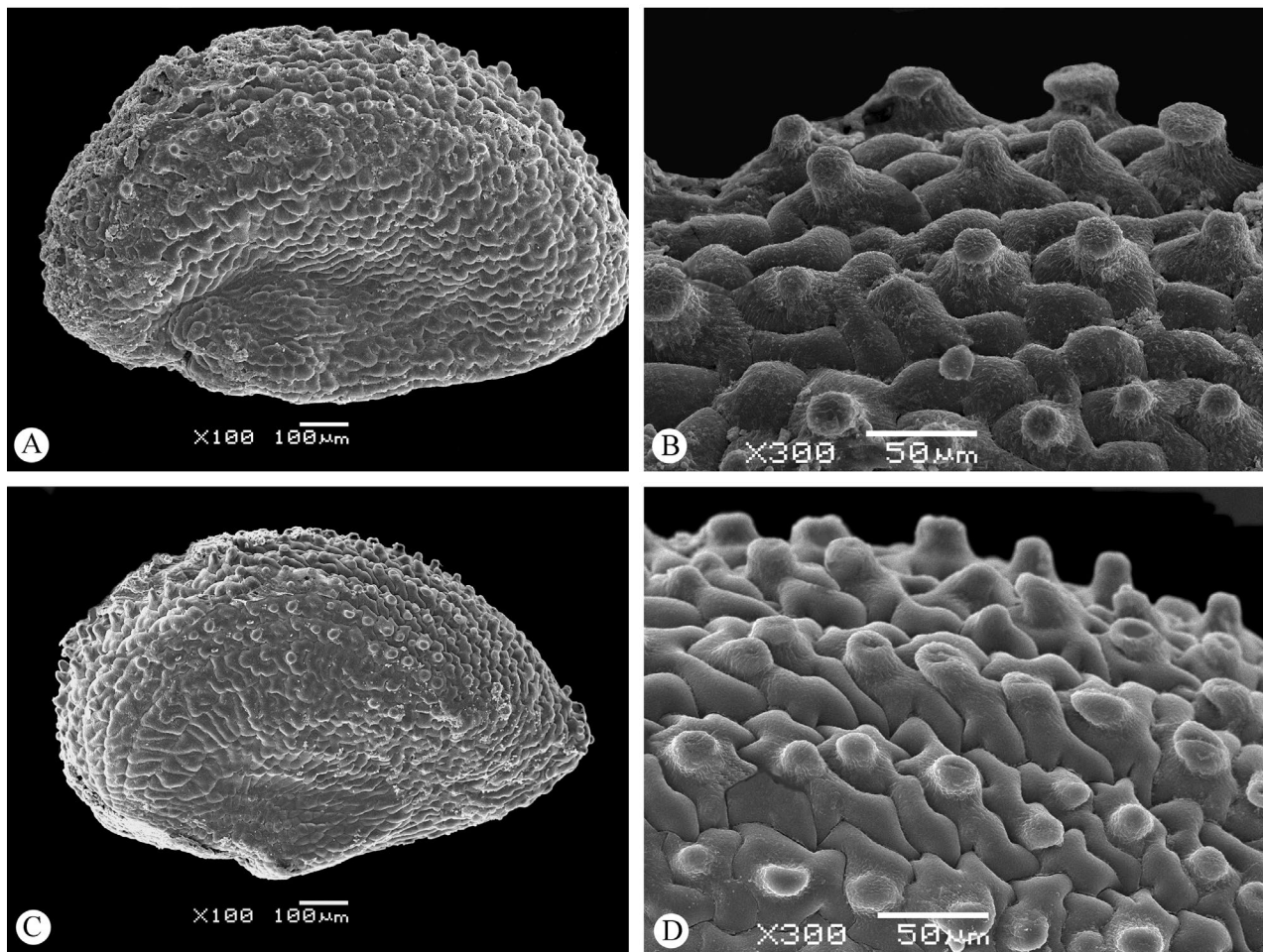


Figure 7. Seed micrographs of *Arthrocnemum franzii* (SEM) from the holotype. (A), (B) Seed of central flower (100× and 300×, respectively). (C), (D) Seed of lateral flower (100× and 300×, respectively).

A. natalense (Bunge ex Ung.-Sternb.) Moss ≡ ***Sarcocornia natalensis*** (Bunge ex Ung.-Sternb.) A.J. Scott ((Steffen et al. 2010);

A. natalense var. *affine* (Moss) Toelken ≡ ***Sarcocornia natalensis*** (Bunge ex Ung.-Sternb.) A.J. Scott **subsp. *affinis*** (Moss) S. Steffen, Mucina & G. Kadereit (Steffen et al. 2010);

A. pachystachyum (Bunge ex Ung.-Sternb.) A. Chev. ≡ ***Salicornia pachystachya*** Bunge ex Ung.-Sternb. (Brenan 1954b);

A. perenne (Mill.) Moss ≡ ***Sarcocornia perennis*** (Mill.) A.J. Scott (de la Fuente et al. 2013);

A. pillansii Moss ≡ ***Sarcocornia pillansii*** (Moss) A.J. Scott (Steffen et al. 2010);

A. pillansii var. *dunense* (Moss) Toelken ≡ ***Sarcocornia dunensis*** (Moss) S. Steffen, Mucina & G. Kadereit (Steffen et al. 2010);

A. pruinatum Paulsen ≡ ***Tecticornia pruinosa*** (Paulsen) K.A. Sheph. & Paul G. Wilson (Shepherd and Wilson 2007);

A. radicans (Guss.) K. Koch nom. illegit. (bas.: *Salicornia radicans* Guss. (1832) non Smith (1807)) ≡ ***Sarcocornia ?perennis*** (Mill.) A.J. Scott;

A. subterminale (Parish) Standl. ≡ more related to *Salicornia/Sarcocornia* group, but has distinct characters in the reproductive sphere in reference to this group or *Arthrocnemum* (Sukhorukov, present study);

A. terminale Toelken ≡ ***Sarcocornia terminalis*** (Toelken) A.J. Scott (Steffen et al. 2010);

A. triandrum F.Muell. ≡ ***Tecticornia triandra*** (F.Muell.) K.A. Sheph. & Paul G. Wilson (Shepherd and Wilson 2007);

A. variiflorum Moss ≡ ***Sarcocornia sp.*** (putative hybrid of *Sarcocornia tegetaria* and another species: Steffen et al. 2010);

Arthrocnemum virginicum (Forskål) Fritsch nomen illegit. ≡ *Salicornia virginica* Forskål (1775) nom. illegit. non L. (1753);

A. xerophilum Toelken ≡ ***Sarcocornia xerophila*** (Toelken) A.J. Scott (Steffen et al. 2010).

Conclusion

The genus *Arthrocnemum* in its recent circumscription is a mostly Mediterranean and West African genus of two representatives, with no species occurring in Australia

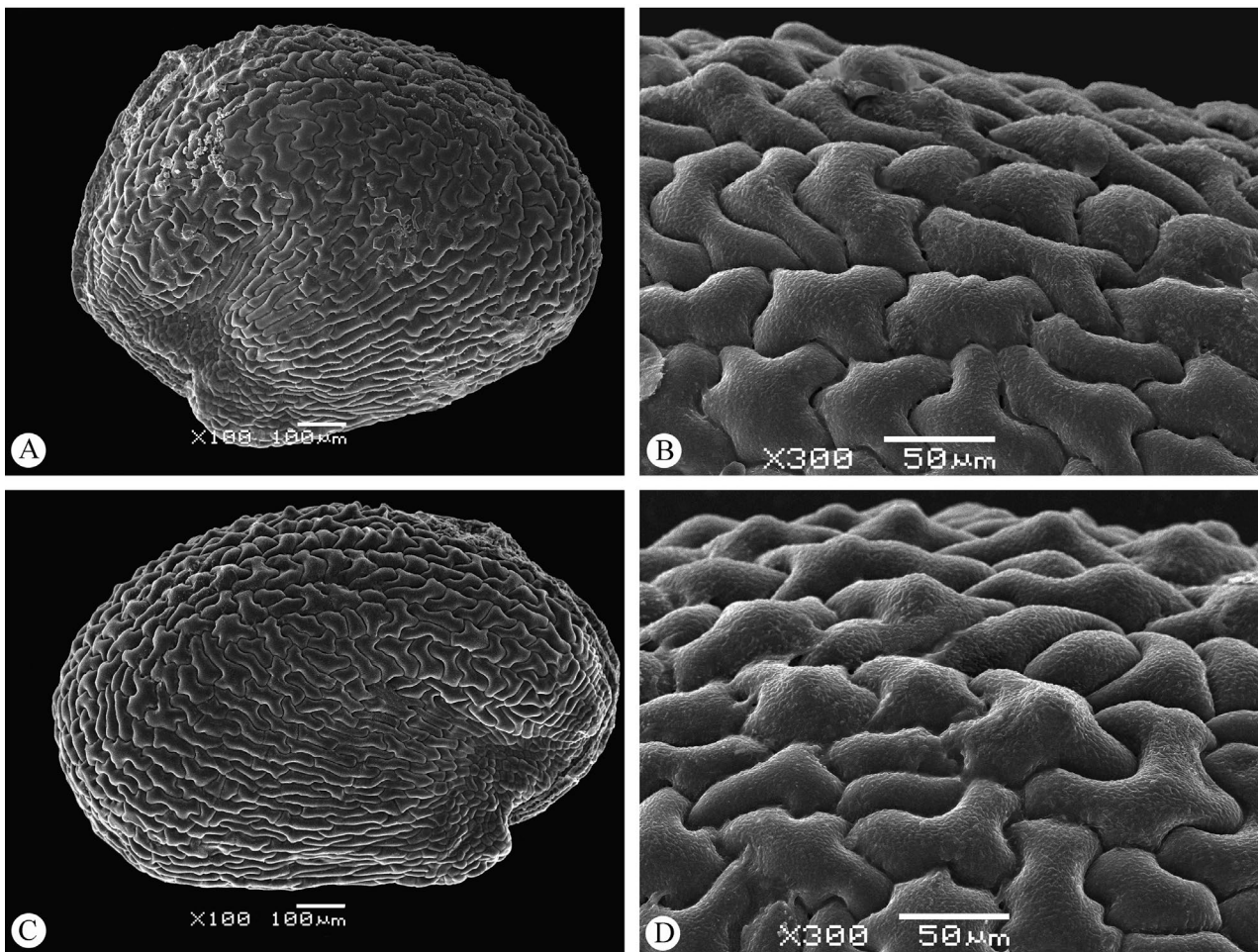


Figure 8. Scanning electron micrographs of *Arthrocnemum macrostachyum* seed. (A), (B) Seed of central flower (100× and 300×, respectively). (C), (D) Seed of lateral flower (100× and 300×, respectively). Origin of the material: Spain, Almeria, 1982, G. Kunkel 19855 (B).

or America. Despite the similarities in morphology and habitat of *Arthrocnemum* and the *Salicornia/Sarcocornia* group, the most important differences between them are found in anatomical characters, especially some involving the reproductive organs and which can be used in studies of other Salicornioideae.

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**Appendix 1. Specimens studied of
Arthrocnemum macrostachyum and
Arthrocnemum subterminale for purposes of
comparison**

Arthrocnemum macrostachyum: [Israel/Jordan] Mer Morte [Dead Sea] [without date] Tenore *s.n.* (LE); [Italy, Sicily] Trapani, September 1900, H. Ross 273 (LE); Israel, Dead Sea, 27 May 1902, J.E. Dinsmore 9102 (HUJ); [France] Rhone-Mündung, August 1951, Markgraf *s.n.* (B); [Spain] Almeria,

22 August 1982, G. Kunkel 19855 (B); Egypt, Burgh-el-Arab, 27 September 1987, H. Freitag 19688 (LE); Cyprus, Larnaca, November 2006, A. Sukhorukov *s.n.* (MW);

A. subterminale (a distinct taxon not referring to *Arthrocnemum* after present investigation): USA, California, Carpenteria, 11 August 1965, R.F. Thorne & P. Everett 35349 (BM); USA, California, San Diego co., city of San Diego, 9 July 2007, L. Morgan 0235 (K).