

Notes on the samphires (*Salicornioideae*, *Chenopodiaceae*–*Amaranthaceae*) in Madagascar and Europa Island, with further conclusions on their chorology in Africa

Заметки о солеросах (*Salicornioideae*, *Chenopodiaceae*–*Amaranthaceae*) Мадагаскара и острова Европа, с заключениями об их хорологии в Африке

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Abstract. The last treatment of *Chenopodiaceae* in Madagascar was published in 1954 and since then, the generic circumscription of *Chenopodiaceae* including *Salicornioideae* has changed drastically. The Madagascan *Salicornioideae* (samphires) are still insufficiently studied. *Salicornia pachystachya* described from Madagascar had a turbulent nomenclatural and morphological history, frequently considered as *Arthrocnemum pachystachyum* due to the alleged similarity of the seed characters with other *Arthrocnemum* species, or considered in a broader sense including the related *Salicornia perrieri*. However, the reproductive features of *S. pachystachya* confirm its placement within *Salicornia*, and the thick inflorescences and longer seeds distinguish it from *S. perrieri*, another native Madagascan species. Two other members of *Salicornioideae* in Madagascar are the subshrubby *Salicornia mossambicensis*, erroneously named *S. fruticosa* or *Arthrocnemum natalense*, and *Tecticornia indica*. Herein, a diagnostic key is provided for the delimitation of four samphire species in Madagascar, and the lectotypes of *Salicornia pachystachya* and *S. perrieri* are designated. Only two species, *S. pachystachya* and *Tecticornia indica*, are recorded for Europa Island, and their habitat preferences in this location are presented, as well as a discussion of the species composition and chorology of samphires in continental Africa.

Keywords: *Salicornia*, *Tecticornia*, *Arthrocnemum*, Madagascar, Europa Island, taxonomy.

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Аннотация. Последняя обработка маревых Мадагаскара опубликована в 1954 году. С тех пор родовой состав как *Chenopodiaceae* в целом, так и *Salicornioideae* претерпел существенные изменения. Мадагаскарские *Salicornioideae* все еще недостаточно изучены. Описанный с Мадагаскара вид *Salicornia pachystachya* имеет сложную номенклатурную и морфологическую историю. Его часто рассматривали как *Arthrocnemum pachystachyum* по причине поверхностного сходства признаков семян с другими видами *Arthrocnemum* или объединяли с другим аборигенным мадагаскарским видом — *Salicornia perrieri*. Репродуктивные признаки свидетельствуют о принадлежности *S. pachystachya* именно к роду *Salicornia*; при этом он отличается от *S. perrieri* мясистыми соцветиями и более крупными семенами. Остальные два вида солеросов на Мадагаскаре — полукустарнички *Salicornia mossambicensis* (ошибочно называемый *S. fruticosa* или *Arthrocnemum natalense*) и *Tecticornia indica*. В настоящей работе обозначены лектотипы *Salicornia pachystachya* и *S. perrieri*; приведен ключ для определения четырех солеросов, произрастающих на Мадагаскаре. На острове Европа обнаружены только два вида: *S. pachystachya* и *Tecticornia indica*, приводятся описания их предпочтительных местообитаний на этом атолле. Также обсуждаются видовой состав и хорология *Salicornioideae* в континентальной Африке.

Ключевые слова: *Salicornia*, *Tecticornia*, *Arthrocnemum*, Мадагаскар, остров Европа, таксономия.

The last treatment of *Chenopodiaceae* Vent. in Madagascar included eleven species belonging to seven genera (Cavaco, 1954). In this treatment, *Chenopodium* L. is the only species-rich genus (5 spp.), other genera (*Arthrocnemum* Moq., *Atriplex* L., *Beta* L., *Salicornia* L., *Salsola* L., and *Suaeda* Forssk. ex J. F. Gmel.) are monospecific. Out of eleven species, four members (*Arthrocnemum pachystachyum* (Bunge ex Ung.-Sternb.) A. Chev., *Atriplex perrieri* Leandri, *Salicornia perrieri* A. Chev. and *Salsola littoralis* Moq.) are considered endemic to Madagascar (Cavaco, 1954). *Suaeda monoica* Forssk. ex J. F. Gmel. is reported to be native, and the island is the southernmost part of its wide distribution in tropical East Africa and Western Asia (Brenan, 1954a; Hedge, 1997; Sukhorukov et al., 2016).

Recently, the taxonomic status of many *Chenopodiaceae* genera has changed after extended molecular studies. According to the latest phylogenetic revisions (Fuentes-Bazan et al., 2012; Sukhorukov et al., 2018b; Uotila et al., 2021), *Chenopodioideae* Burnett comprise several genera with different positions in the molecular trees. In Madagascar, *Chenopodium* in a previous broader sense is represented by *Chenopodium* s. str. (*C. album* L. and *C. amaranticolor* H. J. Coste et Reyn.), *Chenopodiastrum* S. Fuentes, Uotila et Borsch (*C. murale* (L.) S. Fuentes, Uotila et Borsch), and *Dysphania* R. Br. (*D. ambrosioides* (L.) Mosyakin et Clemants, incl. *Chenopodium integrifolium* Vorosch.). Furthermore, according to an extensive phylogenetic analysis of *Salsoloideae* Raf. by Akhani et al. (2007), a part of *Salsola* is currently considered within *Caroxylon* Thunb.. Madagascan *Salsola littoralis* was not included in the phylogeny, but it shares all the principal morphological characters with other species of *Caroxylon* and should be regarded as *C. littorale* (Moq.) Akhani et Roalson (Akhani et al., 2007; Mucina, 2017). Europa Island (French Southern and Atlantic Lands) located in the Mozambique Channel about 300 km west of Madagascar hosts several *Chenopodiaceae* species, namely *Caroxylon littorale*,

Salicornia pachystachya Bunge ex Ung.-Sternb., *Suaeda monoica*, and *Tecticornia indica* (Willd.) K. A. Sheph. et Paul G. Wilson (Boullet et al., 2018). Recently, *C. littorale* was also recorded in the coastal parts of Inhambane Province (Mozambique) as a native species (Friis, Holt, 2016). Based on these records, *C. littorale* and *Salicornia pachystachya* cannot be considered as Madagascan endemics.

The taxonomy of *Salicornioideae* Luerss., also known as samphires, has undergone drastic changes after molecular phylogenetic studies. All perennial *Sarcocornia* A. J. Scott were nested within *Salicornia* (Kadereit et al., 2006) and later transferred into the latter genus (Steffen et al., 2015; Piirainen et al., 2017). Members of the Australian *Halosarcia* Paul G. Wilson, *Pachycornia* Hook. f., *Sclerostegia* Paul G. Wilson, *Tegicornia* Paul G. Wilson and *Tecticornia* Hook. f. form a large clade (Shepherd et al., 2004, 2005b), and they were united into *Tecticornia*, the oldest generic name for this group of genera (Shepherd, Wilson, 2007). The diversity of *Arthrocnemum* in West Africa and further nomenclatural problems in this genus were discussed by Sukhorukov and Nilova (2016). Simultaneously, Piirainen et al. (2017) described two new genera, of which *Arthrocaulon* Piirainen et G. Kadereit was a replacement name for *Arthrocnemum*.

Two reported Madagascan members of *Salicornioideae* are still poorly investigated. The description of the first species, *Salicornia pachystachya*, was based on a fragment of the plant collected by L. H. Boivin in Madagascar. The species is considered as an annual plant related to other *Salicornia* species (Ungern-Sternberg, 1866). The name *S. pachystachya* had been widely accepted (e. g., Hemsley, 1919; Toelken, 1967; Scott, 1977; Piirainen et al., 2017). Chevalier (1922) changed the generic name into *Arthrocnemum pachystachyum* (Bunge ex Ung.-Sternb.) A. Chev. based on the presence of perisperm in the ripe seeds, a character lacking in other *Salicornia*. Simultaneously, he de-

scribed another *Salicornia* from Madagascar, *S. perrieri* A. Chev. Cavaco (1954), following Chevalier, accepted two *Salicornioideae* in Madagascar, *Salicornia perrieri* and *Arthrocnemum pachystachyum*, and corrected the life form of the latter species to be shrubby. Both names were also accepted by Moss (1954). Toelken (1967) synonymised *Salicornia perrieri* with *S. pachystachya*, while Bigot (1971) and O’Callaghan (1992) considered both species as independent taxa imitating “robust shrublets”. Two *Arthrocnemum* species, *A. indicum* (Willd.) Moq. and *A. natalense* (Bunge ex Ung.-Sternb.) Moss, were also reported in Madagascar only several decades ago (Bigot, 1971; Duranton, 1975; Thomasson, Théodore, 1993; Koechlin et al., 1997).

The analysis of the type material of *Salicornia pachystachya* and *S. perrieri*, as well as the revision of other herbarium material, led us to a distinct conclusion on the taxonomy of the Madagascan samphires, therefore this study aims to precise generic composition of the samphires in Madagascar and Europa atoll, with further notes on *Salicornioideae* in Africa.

Material and methods

The field observations in southwest Madagascar were made by V. Alyonkin in January 2020. The field observations in the Europa atoll were essentially made by Vincent Boulet and Jean Hivert between 2006 and 2016 with several expeditions organised by the Conservatoire Botanique National de Mascarin (CBNM) to study the flora and plant communities.

The Scattered Islands (Fr.: les îles Éparses) comprise five islands located in the southwest Indian Ocean, close to Madagascar, four in the Mozambique Channel (cited here from south to north): Europa, Bassas da India, Juan de Nova and the Îles Glorieuses, while the fifth, Tromelin, is located in the northern part of the Mascarene Archipelago. All these islands are relatively young, about 125,000 years old (Caceres, 2003) and administratively belong to the 5th district of the French Southern and Antarctic Lands (Terres Australes et Antarctiques Françaises, or TAAF), a French Oversea Territory since 2007 (TAAF, 2016, 2021). The native *Chenopodiaceae* are only present in the Europa atoll, not in the other Scattered Islands (Boulet et al., 2018). The ecology of samphire communities on the island has been specially studied and described by Boulet (2014). The Europa atoll is located at a low elevation (up to 12 m). Its tropical climate is semiarid with two prevailing seasons, a dry and relatively cool season (from May to November), and a warm humid season (from December to April) (Boulet et al., 2018). The island is located in the zone of formation and circulation of tropical depressions

and cyclones (Delépine et al., 1976; Caceres, 2003) and consists of a coral reef with a reduced terrestrial area (30 km²) built on an ancient volcanic cone. It is a remnant of old intra-plate volcanoes, nowadays morphologically present in the form of atolls (Goldberg, 2016).

The ecology of some samphires was studied by A. Sukhorukov (unpubl. data) in several parts of Africa (Cape Verde, South Africa, and Namibia) and the type material of the *Salicornia* species was investigated in the Herbarium of Natural History Museum, Paris, France (P). The analysis of other collections (BM, BR, K, LE) housing abundant material from other African countries was used for comparison.

The images of the seed ultrasculpture were taken using a scanning electron microscope (SEM) JSM-6380 (JEOL Ltd., Japan) at 15 kV. Before SEM observations, the seeds were soaked in a series of solvents and dried at the critical point (see for more Sukhorukov, 2014). The maps were prepared using the online tool SimpleMapp (Shorthouse, 2010).

Results

Diversity of samphires in Madagascar and the Europa Island

Our investigations show that the data on the diversity of the *Salicornioideae* in Madagascar should be corrected. Four samphire species present in Madagascar are three *Salicornia* members (*S. mossambicensis*, *S. pachystachya*, *S. perrieri*) and *Tecticornia indica*. Two species, *Salicornia pachystachya* and *S. perrieri*, are annuals, whereas *S. mossambicensis* and *T. indica* are prostrate or ascending subshrubs. *Salicornia pachystachya* and *S. perrieri* differ in seed length, with *S. pachystachya* having longer (1.2–1.4 mm) seeds than those of *S. perrieri* (0.7–0.9 mm) (Fig. 1: A, B). Besides, the dried inflorescences of *S. pachystachya* are thicker, reaching ca. 6 mm diam., compared to those of *S. perrieri* (less than 3 mm across). The third samphire species is a subshrubby *Salicornia mossambicensis* with papillate seeds (Fig. 1: C, D). The fourth species, previously confused with *S. pachystachya*, is *Tecticornia indica*, another subshrub with distinctly smooth or slightly rugose seeds (Fig. 1: E, F). Only *Salicornia pachystachya* and *Tecticornia indica* are present on Europa Island. A checklist of all *Salicornioideae* found in the territory under study is provided below.

Taxonomic account

Salicornia pachystachya Bunge ex Ung.-Sternb. 1866, Vers. Syst. Salicorn.: 51. ≡ *Arthrocnemum pachystachyum* (Bunge ex Ung.-Sternb.) A. Chev. 1922, Rev. Bot. Appl. Agric. Colon. 2 (16): 748. ≡ *Arthrocnemum*

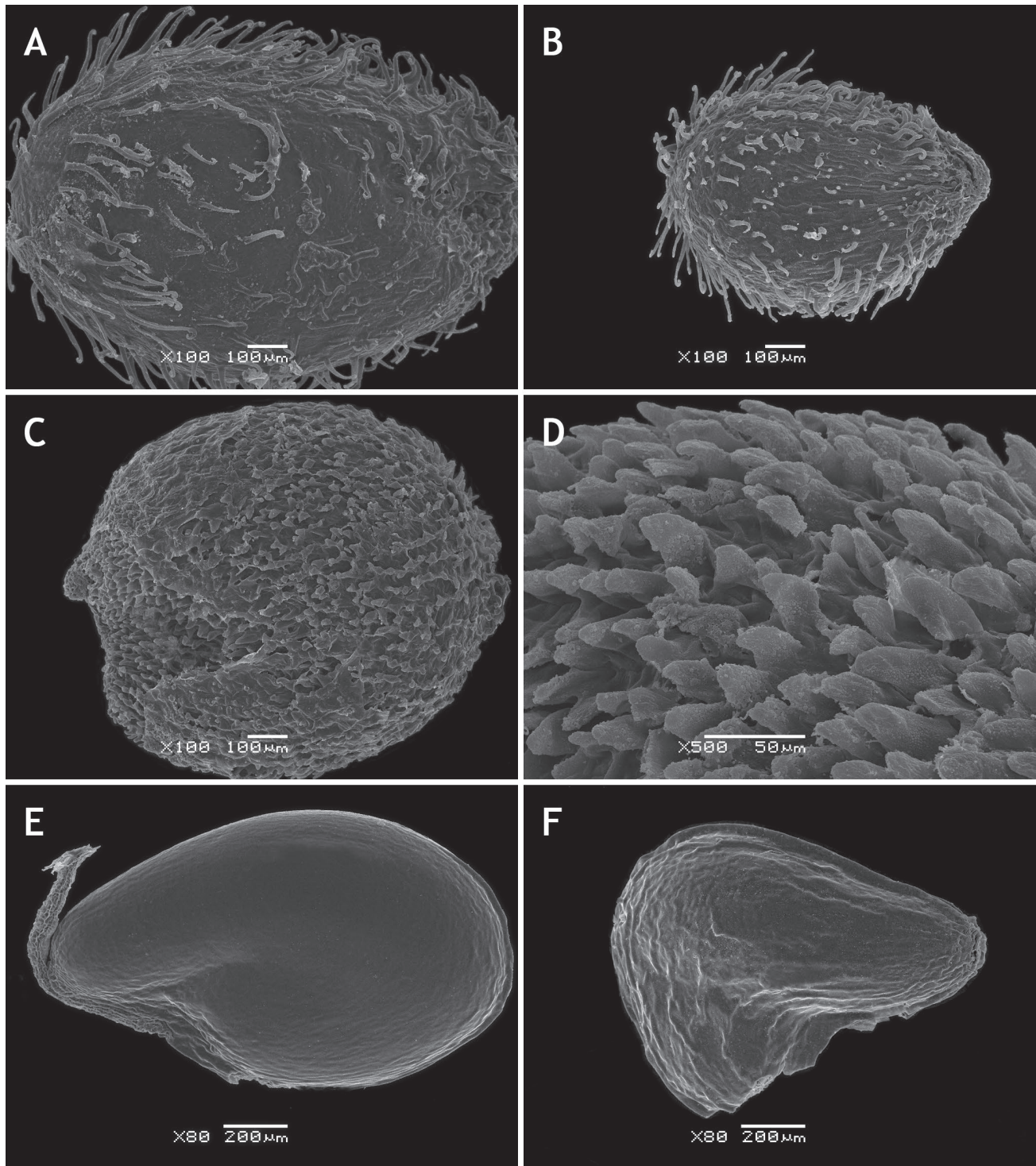


Fig. 1. SEM micrographs of samphire seeds.

A – *Salicornia pachystachya*; B – *S. perrieri*; C, D – *S. mossambicensis*; E, F – *Tecticornia indica*. Scale bars: A–C – 100 μ m, D – 50 μ m, E, F – 200 μ m.

Origin of the material: A: Madagascar, Baie de Diego-Suarez, II 1848, L. H. Boivin, № 2370 (P); B: Madagascar, Anony Lake, 26 II 1931, M. Decary, № 8569 (BM); C, D: Madagascar, delta of the Linta River, VIII 1928, H. Humbert, C. F. Swingle, № 5450 (K); E: Madagascar, near Toliara, IX 1924, H. Humbert, H. Perrier de la Bathie, № 2478 (P04618457); F: Angola, Mossamedes [Namibe], F. Teixeira, № 2059 (BM).

pachystachyum (Bunge ex Ung.-Sternb.) Moss, 1954, J. S. African Bot. 20: 16, isonym.

Lectotype (designated here): Nord de Madagascar, [Diana Region] baie de Diego-Suarez [Antsirana], II 1848, M. [L. H.] Boivin, № 2370 (P: without barcode). — Fig. 2.

Ungern-Sternberg (1866: 51) attributes the name *Salicornia pachystachya* to Bunge's "*Salicornia pachystachya* Bunge in herb." not validly published by Bunge. According to ICN (Turland et al., 2018: Art. 46.2), the authority of the name must be cited as *Salicornia pachystachya* Bunge ex Ung.-Sternb.

Ungern-Sternberg (1866) indicates that the specimens he examined are from the herbarium of Boivin (two sheets in total), and no collection numbers are cited in the protologue. Moss (1954) indicated that the type is in P, while Toelken (1967) reported the location of the type specimen in LE. In the latter Herbarium, no type collection of *Salicornia pachystachya* was traced. One of the two sheets (№ 2370) kept in P was labelled by an anonym as "type" (P00487041), and the other specimen labelled as "co-type" (also anonymously). The specimens correspond with each other in general morphological characters and belong to the same plant. However, the "type" contains a short fragment of the plant with several inflorescence branches and has been supplied with two labels: (1) "Madagascar. Coll. Boivin", and (2) "Zanzibar. Boivin" (Bunge's writing). The latter region is located in Tanzania and not mentioned in the protologue (Ungern-Sternberg, 1866). Due to the ambiguous location of the specimen (Madagascar versus Tanzania) and its incompleteness, we chose a lectotype that contains a fully developed twig collected in Madagascar.

The authentic material of *Salicornia pachystachya* was collected at the fruiting stage. The seeds with hair-like outgrowths of testa cells (Fig. 1: A) are very similar to those of other annual *Salicornia* investigated earlier (Shepherd et al., 2005a; Zare, Keshavarzi, 2007; Sukhorukov, 2014; Gasparri et al., 2016). This character has evolved in all annual and some perennial species of *Salicornia* (in its current circumscription), hence considered as a unique generic trait among all *Salicornioideae*. Besides, almost none of *Salicornia* species in its current circumscription have nutritive tissue (perisperm) in the seeds. The complete fusion of perianth segments and hyaline pericarp also unite all *Salicornia* species in its recent circumscription (Shepherd et al., 2005a; Sukhorukov, 2014; Fuente et al., 2016). Consequently, *S. pachystachya* cannot be considered within *Arthrocnemum* (\equiv *Arthrocaulon*) based on the seed structure and should be left in *Salicornia*.

Description. See Ungern-Sternberg (1866) and Chevalier (1922).

The species is easily distinguished by thick (5–7 mm) inflorescences and relatively large (1.2–1.4 mm long) seeds.

Habitat. *Salicornia pachystachya* is reported to be one of the dominants of the halophytic vegetation near Tsimanampetsotse Lake (Rauh, 1995; Eve, Pers, 2014), but it seems that these records belong to *Tecticornia indica*, an abundant plant around the lake (V. Alyonkin, pers. obs.). On the Europa Island, *Salicornia pachystachya* inhabits salt marshes of low topographic level, located at the borders of the mediolittoral and supralittoral domains (Fig. 3: A), which leads to weak and brief tidal flooding (up to a few centimetres deep or sometimes just a moistening of the substrate). These salt marshes have developed on coral-derived muddy substrate surrounding the rugged karstic rocky surface or rarely they occur on karst reef clogged with muds (Boullet, 2014). The plant stature varies according to the ecological conditions (see also Toelken, 1967), in particular according to the duration of tides and the exposure to the tidal flow. The plants of the intertidal habitats of the lagoon have an erect stem and obliquely orientated lateral branches (usually at an angle less than 45°). In the mangroves, on the edge of the supratidal habitat complex experiencing irregular tidal conditions, the plants often become decumbent and more irregularly branched (Fig. 3: B).

For Madagascar and the East Coast of Africa, detailed ecological data are lacking, and a possibility of confusion between *Salicornia pachystachya* and *S. perrieri* is higher. Besides, *S. pachystachya* is also morphologically similar to *S. brachiata* Roxb. known from the southern coast of the Indian subcontinent. Bigot (1971) described the surroundings of Tulear (Madagascar) as "*Salicornia pachystachya* zone", referring to abundant dry and highly saline muddy coastal depressions.

Rarity status. The rarity status of *Salicornia pachystachya* in Madagascar has not been evaluated so far. On the Europa Island, *S. pachystachya* is present in seven cells of 100 × 100 m, in three geographically distinct stations. This local rarity renders its rarity status as "Exceptional". Its population on the island is estimated at around 1000 individuals and this population covers a total area of about 5800 m² (Hivert, 2021; Boullet, Hivert, pers. obs.). According to the criteria as proposed by the Conservatoire Botanique National de Mascarin (CBNM), and inspired by the IUCN Regional Red List (UICN France, 2011), but adapted to the case of small territories, *S. pachystachya* is considered "Vulnerable" on the Europa Island and the Scattered Islands (Hivert et al., 2018; Boullet, Hivert, pers. obs.). There are seemingly no direct threats to the Europa Island population, except for putative sea-level changes.

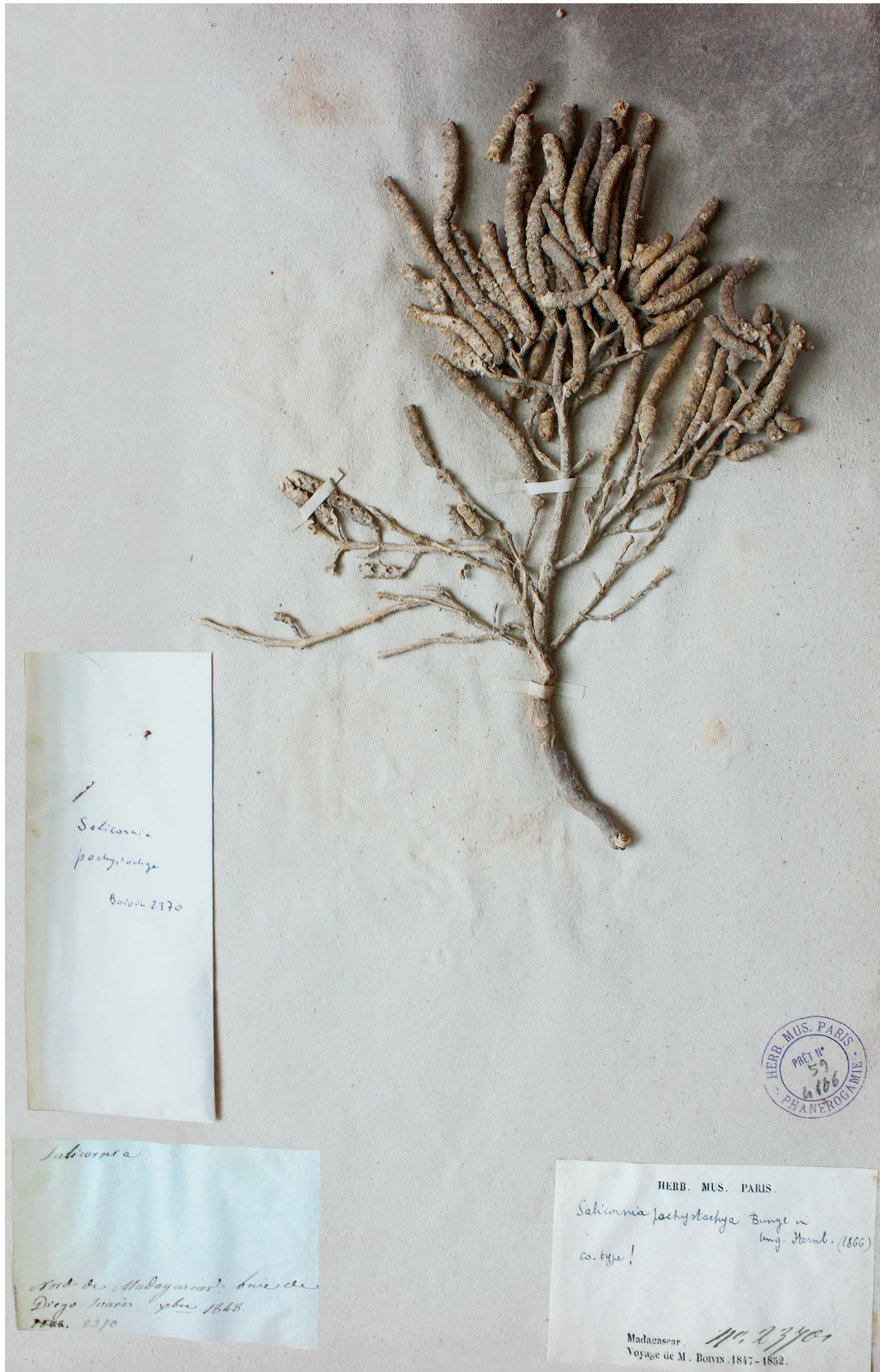


Fig. 2. Lectotype of *Salicornia pachystachya* (P).

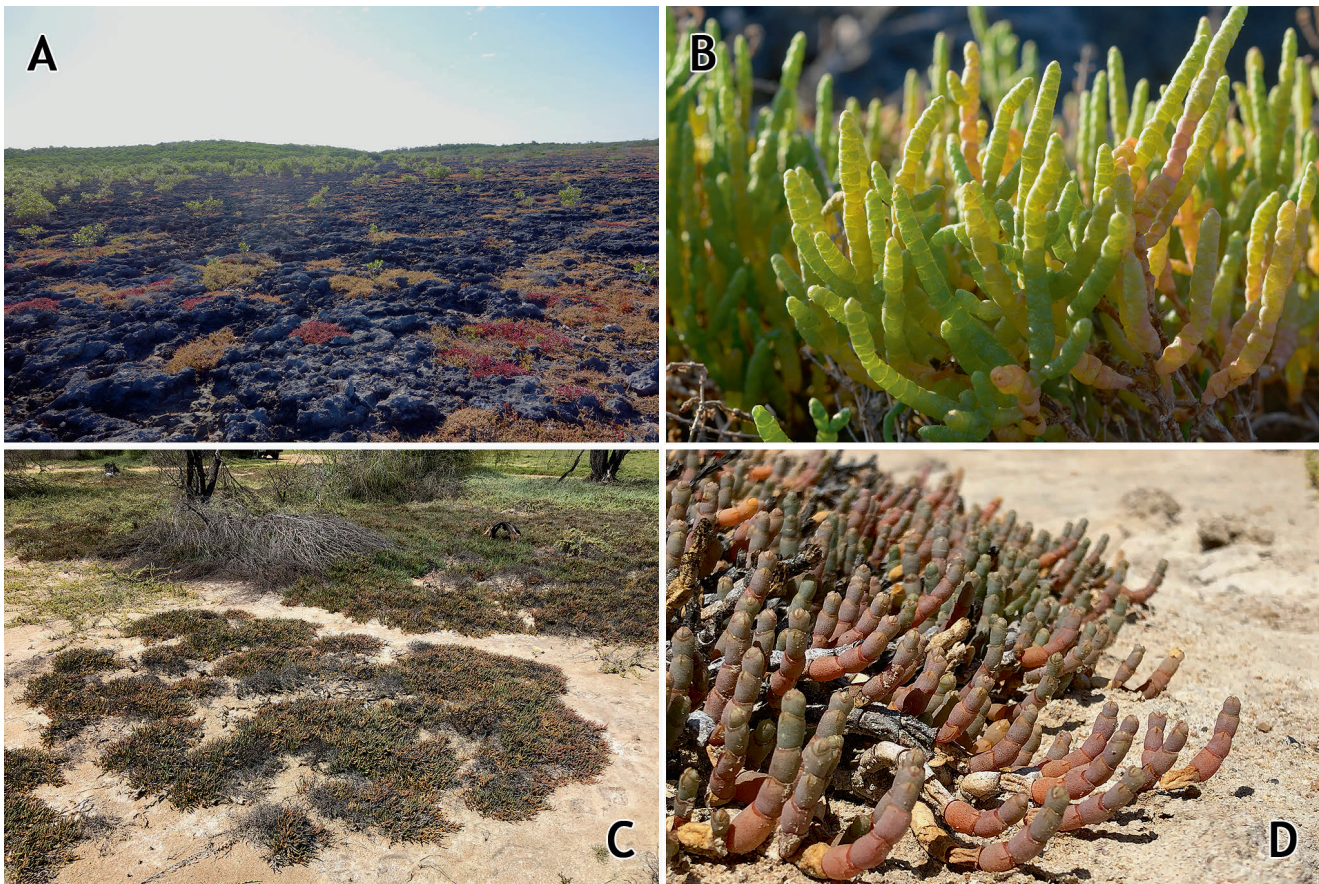


Fig. 3. Habitat and general view of the plants.

A, B – *Salicornia pachystachya*, Europa Island, 27 V 2016, photo by Vincent Boulet; C, D – *Tecticornia indica*, Madagascar, near Tsimanampetsotse Lake, I 2020, photo by Vitaly Alyonkin.

Distribution (Fig. 4: A). **Madagascar:** Diana Region (see lectotype); [Boeny Region] Antongomena Bevary, 23 VI 1965, R. Capuron, № 24275 (P04618438, K); [Mahajanga Region] Andranononby, XII 1928, H. Poisson, № 378 (P04618440). **Europa Island:** Petite Mangrove, 7 IV 2011, J. Hivert (CBNM-IE 92, CBNM, MO).

General distribution. Madagascar, French Southern and Atlantic Lands (Europa Island: Boulet et al., 2018) and the East Coast of tropical Africa (Kenya, Tanzania, and Mozambique). Also reported from the East Coast of KwaZulu-Natal, South Africa (Toelken, 1967; Germishuizen, Meyer, 2003).

Salicornia mossambicensis (Brenan) Piiirainen et G. Kadereit, 2017, *Taxon*, 66 (1): 125. ≡ *Sarcocornia mossambicensis* Brenan, 1988, *Fl. Zambes.* 9 (1): 153.

– *Salicornia fruticosa* auct., non (L.) L.

– *Arthrocnemum natalense* auct., non (Bunge ex Ung.-Sternb.) Moss.

Holotype: Mozambique, Inhambane Bay, Mocucuni Island, 26 IX 1958, Mogg, № 29306 (LISC – photol; isotype – SRGH).

Description. A detailed description is provided in the protologue (Brenan, 1988). It is distinguished from the related perennial *Salicornia* species by the seeds with papillate (not hairy) outgrowths. *S. mossambicensis* is mentioned by Leandri (1931) and later by Cavaco (1954) under *S. fruticosa* (L.) L., or as *Arthrocnemum natalense* (Bunge ex Ung.-Sternb.) Moss by Toelken (1967). The examined specimens from Madagascar correspond in their characters, especially papillate seed surface (Fig. 1: C, D), to *S. mossambicensis* described from Mozambique (Brenan, 1988, as *Sarcocornia mossambicensis* Brenan).

Habitat. According to the herbarium labels, the species occupies intertidal coastal salt marshes and depressions.

Distribution (Fig. 4: B). **Madagascar:** [Boeny Region] Majunga [Mahajanga], 24 VI 1912,

K. Afzelius (P051594880); [Atsimo-Andrefana Region] delta of the Linta River, VIII 1928, H. Humbert, C. F. Swingle, № 5450 and 5451 (P04618441, P04618442, P04618496, P04618497, K); [Atsimo-Andrefana Region] Tsimanampetsotsa, 17 III 1962, J. Bosser, № 15431 (P04618443); Atsimo-Andrefana Region, Toliara, Morombe Distr., Befandriana Sud commune, Andrianala, 8 VI 2015, C. Rakotovo et al., № 6640 (P00956436).

Note. The data on the presence of “*Salicornia fruticosa*” at Manampetsa Lake, Toliara Province of Madagascar (Leandri, 1931; Cavaco, 1954) may apply to *S. mossambicensis* (the herbarium sheets might not exist).

General distribution. Madagascar and Mozambique. Collections from the Scattered Islands are still lacking.

Salicornia perrieri A. Chev. 1922, Rev. Bot. Appl. Agric. Colon. 2: 749.

Lectotype (designated here): Madagascar, [Boeny Region] Soalala (Ambongo = Mahajanga II District), marais salants des environs du Soalala, VIII 1905, H. Perrier de la Bathie, № 1580 (P: P00157180!; isolectotype: P04618498!).

Description. See Chevalier (1922). The most indicative characters of this species are annual life history, inflorescences up to 3(4–5) mm thick, and seeds up to 1 mm long.

Habitat. Saline habitats, but a true nature of the habitats still remains elusive.

Distribution (Fig. 4: C). **Madagascar:** [Boeny Region] near Majunga [Mahajanga], 24 VI 1912, K. Afzelius, № 256 (P05158071); [Atsimo-Andrefana Region] near Toliara, IX 1924, H. Humbert, H. Perrier de la Bathie, № 2479 (P05267613); [Androy Region] Anony Lake, 26 II 1931, M. Decary, № 8569 (BM); [Bongolava Region] Bevato, s. d., B. Koechlin (P05047688); [Atsimo-Andrefana Region] Toliara, Morombe, 27 VIII 2014, M. L. Rabarivola et al., № 561 (K, P00910878); Atsimo-Andrefana Region, Toliara Prov., Tsimanampetsotsa National Park, 1 II 2018, U. Swenson et al., № 302 (P01182779).

General distribution. Madagascar. Reported from Mozambique (Brenan, 1988; Lebrun, Stork, 1991) and South Africa (O’Callaghan, 1992; Germishuizen, Meyer, 2003; Slenzka et al., 2013), but these records require confirmation.

Tecticornia indica (Willd.) K. A. Sheph. et Paul G. Wilson, 2007, Austral. Syst. Bot. 20 (4): 327. ≡ *Salicornia indica* Willd. 1799, Neue Schriften Ges. Naturf. Freunde Berlin, 2: 111. ≡ *Arthrocnemum indicum* (Willd.) Moq. 1840, Chenop. Monogr. Enum. 111.

≡ *Halosarcia indica* (Willd.) Paul G. Wilson, 1980, Nuytsia, 3 (1): 63.

Holotype: India [Tamil Nadu State], Wepanscheri [Veppancheri], prope Trankenbar [Tharangambadi] [1797?], J. G. Klein, № 3601 (B-W 00054-01 0!).

Description. The morphological characters of Madagascan *Tecticornia indica* specimens agree with all previous descriptions of this species from other territories (e. g., Moquin-Tandon, 1840; Backer, 1948, both as *Arthrocnemum indicum*; Wilson, 1980). The most indicative characters of *T. indica* are: glabrous subshrubs forming sprawling mats (Fig. 3: C, D); stems prostrate or ascending, rooting at their base or not; annual shoots upright, up to 20 cm tall, fleshy, often reddish or reddish-green, producing 10–15 pairs of cuspidate leaves and terminating with dense cylindrical inflorescences; bracts similar to the leaves, each bract encloses three immersed flowers; fruit with indurated pericarp, contains yellowish-brown glabrous seed.

Habitat. Salt marches with *Tecticornia indica* are found in the western and southwestern regions of Madagascar. *T. indica* is found there on saline, sandy substrates, often in fringing mangroves and in temporary saline ponds (Bigot, 1971; Duranton, 1975; Thomasson, Théodore, 1993; Koechlin et al., 1997). The species is common around Tsimanampetsotsa Lake (Atsimo-Andrefana Region), where it grows with *Caroxylon littorale* (V. Alyonkin, pers. obs.). On the Europa Island, *Tecticornia indica* is a native species considered “relatively common” (i. e. present in 523 to 1062 (out of 3373) cells of 100 × 100 m; Boulet, Hivert, 2021). *Tecticornia indica* is a dominant species of the coastal paleotropical saltmarshes (Suaedo monoicae-Tecticornietea indicae Knapp ex Boulet 2014) in East Africa (from southern Somalia to southern Mozambique), in western and southwestern Madagascar, and in the Europa Island. The species grows in salt marshes at slightly elevated topography, corresponding to the upper part of the supratidal coastal border, that is flooded only at a very high tide (Salsolo littoralis-Tecticornion indicae (Boulet, 2014)). This succulent subshrub usually forms dense, low (not exceeding 15 cm) mats, showing spectacular purplish-red colour (Bigot, 1971; Koechlin et al., 1997; Boulet, 2014). On the Europa Island, the salt marshes with *T. indica* are formed on saline coral limestone muds around rugged stony karstic relief or surface karstic pavement, and on the median part of supratidal terraces, dry most of the year, except for the time of spring tides (Boulet, 2014). On the East Coast of Africa, the presence of the salt marshes with *T. indica* was recorded long time ago (Knapp, 1965, 1973) but their detailed ecological description is still lacking.

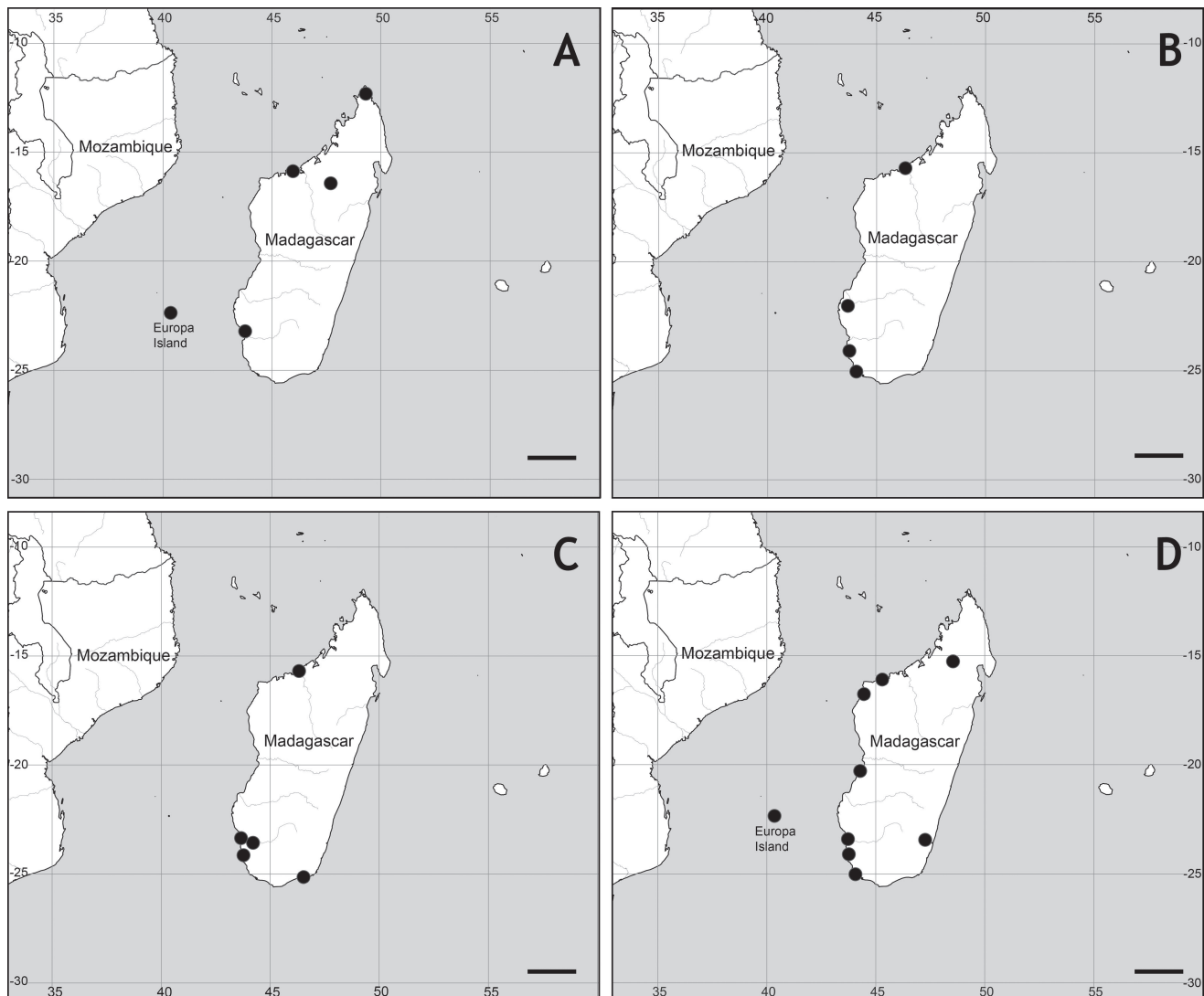


Fig. 4. Distribution maps of *Salicornia pachystachya* (A), *S. mossambicensis* (B), *S. perrieri* (C), and *Tecticornia indica* (D). Scale bars – 250 km.

Rarity status. The rarity status of *Tecticornia indica* is LC (Least Concern) at the scale of both the Europa Island and the Scattered Islands (Hivert et al., 2018; Boulet, Hivert, pers. obs.). No direct threats seem to impact the populations on the Europa Island; nevertheless it might be affected by the sea level fluctuations in future. The accompanying species are *Caroxylon littorale* (*Chenopodiaceae*) and *Sesuvium portulacastrum* (L.) L. subsp. *portulacastrum* (*Aizoaceae*).

Distribution (Fig. 4: D). **Madagascar:** [Atsimo-Antsiranana Region] Ambongo, 1841, N. O. Pervillé, № 661 (P04618444–P04618446, P04618448); [Sofia Region] way to Befandriana, s. d., herb. J. Decuaire, № 27485 (P04618447); [Atsimo-

Andrefana Region] South of Toliara, 30 VII 1909, F. Geay, № 6054 (P04618449); [Atsimo-Andrefana Region], Toliara, 9 X 1921, H. Poisson, № 347 (P04618465); [Atsimo-Andrefana Region], near Toliara, Befotaka, 12 V 1922, Petit, № 6 (P04618499); [Atsimo-Andrefana Region, near Toliara] Ihodo, 8 V 1924, R. Decary, № 2793 (P04618461); [Atsimo-Andrefana Region] near Toliara, IX 1924, H. Humbert, H. Perrier de la Bathie, № 2478 (P04618457, P04618460); [Atsimo-Andrefana Region], delta of the Linta River, VIII 1928, H. Humbert, C. F. Swingle, № 5452 (P04618452); [Boeny Region] Baie de Baly, 9 VI 1930, R. Decary, № 7838 (P04618458); [Melaky Region] Besalampy, 1932, H. Perrier de la Bathie, № 8639 (P04618450, P04618463); [Atsimo-Andrefana

Region], Tsimanampetsotsa, II 1947, H. Humbert, № 20244 (P04618462); [Menabe Region] Morondava, IX 1956, J. Bossier, № 10041 (P04618464); [Atsimo-Andrefana Region] near Toliara, 13 XI 1960, J. Leandri, R. J. de Dieu, № 3836 (P04618451); Toliara, 26 II 1966, M. Peltier, № 4925 (P04618453); [Atsimo-Andrefana Region] Tsimanampetsotsa Lake, 8 IX 1994, R. Ranaivojaona et al., № 29 (P06795100). **Europa Island:** Plaine centrale, 5 IV 2011, J. Hivert, V. Bouillet, L. D. B. Gigord (CBNM-IE 44, CBNM, MO, P).

General distribution. Madagascar, French Southern and Atlantic Lands (Europa atoll: Bouillet et al., 2018), tropical Africa (Kenya, Tanzania, Mozambique, Angola, and Senegal), Indian subcontinent, South-East Asia, North Australia. It has also been listed for the flora of South Africa (Germishuizen, Meyer, 2003, as *Halosarcia indica*).

A key to the samphire species of Madagascar

This key only includes the most remarkable characters of the plants. Anatomically, *Tecticornia indica* differs from other samphires by having only a single palisade layer of the stem chlorenchyma (see for more De Fraine, 1913; Wilson, 1980; Voznesenskaya et al., 2008). Some reproductive features are also different, the pericarp of *T. indica* is indurated and the seed has a slightly bent embryo and abundant perisperm, whereas all Madagascan *Salicornia* have a thin parenchymatous pericarp, seeds with horseshoe-shaped embryo and without nutritive tissue (perisperm). However, some Australian *Salicornia* have seeds with a perisperm (Shepherd et al., 2005a).

1. Erect or rarely decumbent annuals; seeds with hair-like hooked outgrowths 2.
- + Prostrate or ascending subshrubs; seeds smooth or with conical papillae 3.
2. Inflorescences thick, obtusely conical; seeds 1.2–1.4 mm long *Salicornia pachystachya*.
- + Inflorescences thin, narrowly cylindrical; seeds < 1 mm long *Salicornia perrieri*.
3. Perianth tip seen by the naked eye. Seeds papillate *Salicornia mossambicensis*.
- + Perianth completely hidden in bract. Seeds glabrous *Tecticornia indica*.

Discussion

The reproductive characters of the *Salicornioideae* genera in their recent circumscription were only precised recently (Shepherd et al., 2005a; Sukhorukov, 2014; Sukhorukov, Nilova, 2016), and they play a major role supporting the existing phylogenetic subdivision of this subfamily. Insufficiently known characters of each genus and taxonomic chaos often

led to misidentifications. The observations on the presence of perisperm in the seeds (Chevalier, 1922) and subshrubby life form (Cavaco, 1954) in *Salicornia pachystachya* (as *Arthrocnemum pachystachyum*) were erroneous and apply to *Tecticornia indica*, the only samphire in Madagascar with both traits. Figure II, images 6–8 of *Salicornia pachystachya* in Cavaco (1954, as *Arthrocnemum pachystachyum*) depict *Tecticornia indica*. Moreover, *Salicornia perrieri* cannot be synonymised with *S. pachystachya* as proposed by Toelken (1967) due to different seed lengths, hence they are treated here as separate species.

Distribution of *Tecticornia indica* in Africa

Tecticornia with approximately 33 species in its recent circumscription is predominantly distributed in Australia and adjacent parts of Malesia (Shepherd, Wilson, 2007). *T. indica* is the most widespread paleotropical species of the genus found in the mangroves, on tidal flats and other saline (mostly coastal) habitats of Australia, South Asia, and Africa including Madagascar. The distribution of *T. indica* in Africa was insufficiently known. According to the APD (2021), it is present in North Africa (Tunisia, Libya, Algeria), and West Africa (Senegal, Mauritania, Morocco, Western Sahara), East Africa (Somalia, Kenya, Tanzania, Mozambique), and South Africa. We agree with Jafri and Rateeb (1978, as *Arthrocnemum indicum*) that *T. indica* is absent in entire North Africa. All specimens from this region identified as “*Arthrocnemum indicum*” and cited in the literature (Maire, 1962) belong to *Arthrocaulon macrostachyum* and to other perennial samphires.

The presence of *Tecticornia indica* in West Africa used to be a matter of debate. It has been reported for Senegal (seashores of St. Louis town) by Hutchinson and Dalziel (1927, as *Salicornia indica*), but Brenan (1954b) and later Friis and Gilbert (1993) suggested that *T. indica* was confused with *Arthrocaulon macrostachyum* (cited as *Arthrocnemum glaucum* and *A. macrostachyum*, respectively). These doubts were also expressed by Lebrun and Stork (2003).

According to the herbarium specimens examined and partially revised by the first author (APS), *Tecticornia indica* is present in continental East Africa (Somalia, Kenya, Tanzania, and Mozambique: BM!, BR!, K!, P!), on the Europa Island (Bouillet et al., 2018) and Madagascar. We can also confirm the presence of *T. indica* on the western coast of tropical Africa, namely in Angola and Senegal (Hiern, 1900; Baker Clarke, 1913, as *Arthrocnemum indicum*; Figueiredo, Smith, 2008, as *Halosarcia indica*), but the herbarium collections from these areas are scarce. The seeds of the Angolan plants

are slightly smaller with a rugose (not smooth) surface (Fig. 3: F), but this may also be attributed to the infraspecific variability. The specimens from KwaZulu-Natal Province, South Africa (Germishuizen, Meyer, 2003, as *Halosarcia indica*) were not seen by us. *T. indica* is not known from other countries on the western coast of Africa, and this huge disjunction in the distribution of *T. indica* is highly intriguing.

The chorology of samphires in Africa

There are five genera of samphires in Africa, *Arthrocaulon* (2–3 species), formerly known as *Arthrocnemum* (Piiirainen et al., 2017), *Salicornia* which today includes also *Sarcocornia* with ca. 20 species (Steffen et al., 2015; Piiirainen et al., 2017), *Tecticornia* (1 species) in its recent circumscription (Shepherd, Wilson, 2007), *Halocnemum* represented by subshrubby *H. cruciatum* (Forssk.) Tod. (Biondi et al., 2013; Sukhorukov, 2014) and two *Halopeplis* Bunge ex Ung.-Sternb., an annual *H. amplexicaulis* Ung.-Sternb. ex Ces., Pass. et Gibelli and subshrubby *H. perfoliata* Bunge ex Ung.-Sternb. (Maire, 1962; Boulos, 1999).

Salicornioideae are unevenly distributed in Africa. The recent records of *Arthrocaulon* south of the Equator (Figueiredo, Smith, 2008, as *Arthrocnemum macrostachyum*) belong to the perennial *Salicornia* species known from Namibia, South Africa and Mozambique (Scott, 1977; Brenan, 1988; O'Callaghan, Oliver, 1992; Craven, 1999; Steffen et al., 2010; all as *Sarcocornia*). In fact, Senegal and Cape Verde in the west and Horn of Africa in the east are the southernmost regions where *Arthrocaulon* is present, and the genus is mainly associated with the subtropical regions of North Africa and Western Asia. It is represented in Senegal by *A. franzi* (Sukhor.) Piiirainen et G. Kadereit (Sukhorukov et al., 2018a), the species described from Cape Verde Archipelago (Sukhorukov, Nilova, 2016) and previously identified as *Arthrocnemum macrostachyum* (Morici.) K. Koch or *A. glaucum* (Delile) Ung.-Sternb. (e. g., Brenan, 1954b; Berhaut, 1974; Martins, 2002). Both *Arthrocnemum franzi* and *A. macrostachyum* (incl. *A. glaucum*) now belong to the recently established genus *Arthrocaulon* Piiirainen et G. Kadereit (Piiirainen et al., 2017). *A. macrostachyum*, a species widely distributed on the seashores of North Africa and Western Asia (Friis, Gilbert, 1993; Sukhorukov, Nilova, 2016; Ramírez et al., 2019), has the southernmost records in Mauritania and Somalia. The ranges of both *Arthrocaulon* and *Tecticornia* overlap in Senegal in the west and Somalia in the east (Berhaut, 1974; Friis, Gilbert, 1993). *Arthrocaulon meridionalis* Est. Ramírez, Rufo, Sánchez Mata et Fuente is present in North Africa, at least in Morocco (Ramírez et al., 2019). In contrast to *Arthrocaulon*,

the range of *Tecticornia indica* is limited entirely to the tropical Africa (Brenan, 1954a; O'Callaghan, 1992).

Salicornia (incl. *Sarcocornia*) is sometimes considered to be cosmopolitan (O'Callaghan, 1992), but is absent in some regions of Africa, especially in the Gulf of Guinea and Horn of Africa (Cavaco, 1963; Friis, Gilbert, 1993; APD, 2021). The annual samphires are represented in North Africa by *S. perennans* Willd. and probably also by *S. procumbens* Sm. subsp. *procumbens* (Kadereit et al., 2012). Other annual species in Africa include *S. meyeriana* Moss (incl. *S. uniflora* Toelken) found in South Africa and Namibia (Slenzka et al., 2013), *S. senegalensis* A. Chev. in Senegal (Chevalier, 1922; Berhaut, 1974; APD, 2021) and probably also in Mauritania (Lebrun, 1998), *S. pachystachya* from Madagascar, Mozambique, Tanzania, and Kenya (Brenan, 1954a; Cavaco, 1954, as *Arthrocnemum pachystachyum*; Brenan, 1988), the Europa Island (Boulet, 2014) as well as South Africa (Lebrun, Stork, 2003), and *S. perrieri* from Madagascar and Mozambique (Brenan, 1988). *S. pachystachya* and *S. perrieri* are tropical elements that are absent in the subtropics of southern Africa (O'Callaghan, 1992).

Although *Salicornia pachystachya* was included in the molecular analysis (Steffen et al., 2015; Piiirainen et al., 2017; Ball et al., 2017), the samples originated from South Africa (KwaZulu-Natal) and belong in fact to a perennial *Salicornia* (MJG – images seen!), not a “true” *S. pachystachya*. Thus, the phylogenetic position of *S. pachystachya*, as well as that of *S. perrieri* and *S. senegalensis*, has not been evaluated yet.

The perennial *Salicornia* (formerly *Sarcocornia*) are found mainly in warm-temperate regions of Africa. At least two species were recorded for North Africa, *S. alpini* Lag. and *S. pruinosa* (Fuente, Rufo et Sánchez Mata) Piiirainen et G. Kadereit (Fuente et al., 2016, as *Sarcocornia*; Piiirainen et al., 2017), which comprise a Mediterranean clade of the genus. They may belong to the *Salicornia* subgen. *Arthrocnemoides* Ung.-Sternb., which incorporates the morphologically similar *S. fruticosa* and *S. perennis* Mill. (Piiirainen et al., 2017). Two further species were described by Chevalier (1934) from South Algeria, but they have not been properly studied yet. The first one, *S. deserticola* A. Chev., is not an annual (Chevalier, 1934) but rather a suffruticose perennial (Piiirainen, 2015); it was accepted by Maire (1962) but synonymised with *S. fruticosa* (Piiirainen, 2015, as *Sarcocornia fruticosa*). The other species, *S. longispicata* A. Chev., was also accepted by Maire (1962) but merged with *S. perennis* Mill. in APD (2021). The plants with the same small habit as in *S. longispicata* were collected by V. P. Bochantsev at the fruiting stage in the neighbouring regions of Algeria

(LEI, as *Salicornia arabica* L.) and found to belong to *Arthrocaulon*. Both *Salicornia deserticola* and *S. longispicata* need further investigation.

The samphires in southern Africa are represented by perennial species belonging to the *Salicornia* subgen. *Afrocornia* Piirainen et G. Kadereit and all are endemic to this region (Steffen et al., 2010, 2015; Piirainen et al., 2017). The Mediterranean *S. fruticosa* is not found in Madagascar and southern Africa, and all its records belong to different species, such as *S. natalensis* Bunge ex Ung.-Sternb., *S. mossiana* (Toelken) Piirainen et G. Kadereit and *S. mossambicensis*.

In total, *Salicornia* in Africa is represented by ca. 20 species, with at least four of them known in the North and 13 in the southern Africa.

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