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Source: Willdenowia, 47(2) : 145-153

Published By: Botanic Garden and Botanical Museum Berlin (BGBM)

URL: <https://doi.org/10.3372/wi.47.47206>

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Mangleticornia (Amaranthaceae: Salicornioideae) – a new sister for *Salicornia* from the Pacific coast of South America

Version of record first published online on 13 July 2017 ahead of inclusion in August 2017 issue.

Abstract: *Mangleticornia ecuadorensis* is a newly recognized monotypic genus from SW Ecuador and adjacent N Peru, where it had previously been identified as *Salicornia fruticosa* (*Arthrocnemum fruticosum*) or *S. peruviana*. It occurs on the coast adjacent to or in Equatorial-Pacific mangroves. Molecular phylogenetic evidence determines that this genus is distinct from and sister to *Salicornia* sensu lato, and is supported by morphological evidence. The genus is distinguished by a unique combination of characters that are otherwise rare in *Salicornioideae*: flowers without a visible perianth, anthers and stigmas exerted through pores in the fleshy cortical tissue of the segments, fruit included in the segments, which are dispersed by disarticulation of the infructescence, and large seeds.

Key words: *Amaranthaceae*, Ecuador, *Mangleticornia ecuadorensis*, mangroves, new genus, new species, Peru, *Salicornia*, *Salicornioideae*

Article history: Received 28 February 2017; peer-review completed 9 May 2017; received in revised form 19 June 2017; accepted for publication 23 June 2017.

Citation: Ball P. W., Cornejo X. & Kadereit G. 2017: *Mangleticornia* (Amaranthaceae: Salicornioideae) – a new sister for *Salicornia* from the Pacific coast of South America. – Willdenowia 47: 145–153. doi: <https://doi.org/10.3372/wi.47.47206>

Introduction

Salicornioideae (Amaranthaceae) is a well-defined subfamily that is distributed worldwide on coasts and in inland saline habitats. They generally occur in temperate and subtropical regions, extending only locally to subarctic regions in the N hemisphere and into tropical areas (e.g. some Australian species). Most can be recognized by the succulent articulated stems and by the condensed spike-like inflorescences. Kadereit & al. (2006) gave a detailed account of the morphological and anatomical features of the members of the *Salicornioideae* and pre-

sented a molecular-phylogenetic study of the subfamily in which they accepted 15 genera. More or less simultaneously, Shepherd & al. (2004) and Shepherd & Wilson (2007) gave a more detailed account of the Australian taxa of the subfamily recognizing only two genera, *Sarcocornia* A. J. Scott and *Tecticornia* Hook. f. (the latter including *Halosarcia* Paul G. Wilson, *Pachycornia* Hook. f., *Sclerostegia* Paul G. Wilson and *Tegicornia* Paul G. Wilson), thus reducing the genera in the subfamily to 11. Recently Piirainen & al. (2017) conducted a more extensive molecular survey and re-examined the morphology, anatomy and biogeography of the subfamily. One

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important conclusion they reached was that *Salicornia* L. and *Sarcocornia* could not be satisfactorily separated. They proposed that *Sarcocornia* should be included in *Salicornia*, treating the expanded genus as containing the following four subgenera: *Salicornia* subg. *Salicornia* (annual species), *S.* subg. *Amerocornia* Piirainen & G. Kadereit (American perennial species), *S.* subg. *Afrocornia* Piirainen & G. Kadereit (South African-Australasian perennial species) and *S.* subg. *Arthrocnemoides* Piirainen & G. Kadereit (Eurasian perennial species). While *S.* subg. *Salicornia* can be more or less defined by morphological characters (annuals and a subtle inflorescence feature), the other three subgenera, which are perennials, are primarily distinguished from each other by molecular characteristics and geographical distribution. Another important taxonomic conclusion of the molecular findings was the separation of the Eurasian *Arthrocnemum macrostachyum* (Moric.) K. Koch and the North American *A. subterminale* (Parish) Standl. as two different genera, now *Arthrocaulon macrostachyum* (Moric.) Piirainen & G. Kadereit and *Arthroceras subterminale* (Parish) Piirainen & G. Kadereit, respectively. In their biogeographical analysis, Piirainen & al. (2017) showed that *Salicornioideae* dispersed at least four times from Eurasia into the Americas representing four independent lineages: (1) *Salicornia* subg. *Salicornia*, (2) *Salicornia* subg. *Amerocornia*, (3) *Heterostachys* Ung.-Sternb. / *Allenrolfea* Kuntze and (4) *Arthroceras subterminale*. When examining South American specimens during the course of locating material suitable for inclusion in molecular studies (Steffen & al. 2015), a number of specimens from Ecuador and N Peru could not be identified as they were either entirely vegetative or all the current year's growth and reproductive material had disarticulated and subsequently placed in large packets containing loose segments. Surprisingly, labels of one collection indicated that plants were up to 3 m high, which is above the usual maximum height of most other *Salicornioideae*, but others give 2 m or less as the maximum height. The South American species of *Salicornia*, under the genus name *Sarcocornia*, were the subject of a revision by Alonso & Crespo (2008). They demonstrated that the perennial species that occur in South America are mostly endemic to that continent and that the widespread lowland species in South America is distinct from Eurasian *Salicornia fruticosa*, and should be recognized as *Salicornia neei* Lag. Although they show *S. neei* on their distribution map as being present in S Ecuador they do not cite any specimens from Ecuador or N Peru. The aim of this study therefore was to determine the identity of these morphologically divergent plants from Ecuador and Peru and ascertain their relationship relative to other *Salicornioideae*.

Material and methods

A limited amount of herbarium material was available for examination, and this was supplemented by further loans

from herbaria, focusing on collections from Ecuador and Peru (see Acknowledgements). The material in packets was scrutinized to locate flowering and fruiting segments, selecting those that had not been distorted by pressing. These were rehydrated by soaking in water mixed with a small amount of ethyl alcohol and liquid detergent for 24 hours or more. The morphological examination focused on comparing the unknown specimens and *Salicornia neei*, which occurs further south in Peru, and other species that also occur elsewhere in South America (Alonso & Crespo 2008). Many attempts to extract DNA suitable for molecular analysis from herbarium specimens were unsuccessful and therefore the sequencing of molecular markers could not be undertaken until fresh material could be obtained. Fresh material was collected for molecular analysis and also for morphological examination from Reserva de Produccion Faunistica Manglares El Salado in SW Ecuador (Fig. 1). The molecular analysis followed the procedure described by Piirainen & al. (2017) using the same set of molecular markers and methods for phylogenetic inference with the addition of a single accession of this potential new taxon (GenBank accession numbers: ETS = KY928651; ITS = KY928650; *atpB-rbcL* spacer = KY928649; *matK-trnK* = KY928648).

Results and Discussion

The earliest collection we have seen dates from 1938 and was collected 5 km S of Guayaquil (MO1288108). From 1962 onwards a variety of collectors have obtained this plant, all from the Golfo de Guayaquil in SW Ecuador and extreme N Peru. According to field notes, the unknown plants range from low-growing, compact shrubs to tall, sprawling plants, 0.8–2(–3) m tall. Collections have generally been determined as *Salicornia fruticosa* (L.) L. or *Arthrocnemum fruticosum* (L.) Moq. or, less frequently, *S. peruviana* Kunth. The plants from Ecuador and Peru are superficially very similar to *Salicornia* with the young, succulent, stems appearing segmented due to the base of each of the opposite and decurrent leaves being fused to form a fleshy segment that completely encloses each internode. The leaf blades are highly reduced to form short, triangular tips at the distal end of the segment. The older stems are woody and the segmentation is no longer apparent. In this respect the plants are similar to several genera of *Salicornioideae* and so it is not surprising that non-flowering plants were determined as *Salicornia*.

Only one dried specimen has been seen in which there was at least part of an intact inflorescence present and a duplicate of that had disarticulated. Living material of inflorescences shows that these are much-branched, each consisting of several spike-like thyrses with more than 20 fertile segments per spike (Fig. 1C). Most of the branches are similar in length and arise at a wide angle (up to 90°). This contrasts with inflorescences of *Salicornia*,



Fig. 1. *Mangleticornia ecuadorensis* in Reserva de Produccion Faunistica Manglares El Salado. – A: Open ground with many young plants of *M. ecuadorensis* in rows (Sep 2016). The occurrence in rows might result from the deposition of the floating disarticulated segments on tidal drift lines. – B: *M. ecuadorensis* grows as compact, mostly 0.8–2 m high, sprawling shrubs (Sep 2016). – C: The inflorescence consists of branched spikes that are up to 10 cm long and composed of 5–20 fertile segments (27 Jan 2017). – D: One typical habitat of *M. ecuadorensis* is the understory in an *Avicennia germinans* stand (27 Jan 2017). – Photographs by Margarita Gallardo (A, B) and Xavier Cornejo (C, D).

which usually consist of a terminal, unbranched, spike-like thyrse, but shorter branches may arise from nodes beneath the base of the spike. In these instances, the side branches are at an acute angle (relevant to the main axis) and may curve upwards. In both the potentially new plant

and in most species of *Salicornia*, the fertile segments have two opposite, 3-flowered, axillary cymes.

There is one important feature of this plant that clearly separates it from *Salicornia*: whereas the perianths typically are distinct from the fleshy internode tissue and

are either clearly visible or, if not, hidden behind the subtending bract in *Salicornia*, in the new plant no perianth is visible. Instead, the anthers and styles are exerted through very short, 3-lobed pores that are clearly visible in the fleshy tissue of the distal segment (Figs. 1C, 2C, D). It is not possible to determine the origin of the pore. Dissection of flowering segments determined that there is no differentiation between the fleshy cortical tissue of the segments and the tissue surrounding the flowers and the pore, so it seems likely that there are no perianth segments in these flowers, but a much more extensive anatomical-developmental study of the inflorescence is needed to confirm this. Based on limited material, the three flowers in each cyme have one or, uncommonly, two stamens each, but it seems that only the central, terminal flower is bisexual, the two styles being exerted after the stamens have opened and been shed. Only one specimen with mature fruit has been seen. In this plant there is only one seed developing in each fertile segment and the seed remains inside the fleshy cortical tissue (Fig. 2E). Presumably, as the inflorescence disarticulates, the individual segments containing one seed are the units of dispersal. The occurrence of the plants in rows (Fig. 1A) suggests that the disarticulated segments float and are deposited on tidal drift lines (but there are no other field observations to support this hypothesis). So far, no specimens or the recently obtained fresh material have fruiting inflorescences that appear to be more than a year old, but, as the young, non-flowering parts of the plant seem to disarticulate as they dry, it is difficult to determine to what extent this disarticulation is an artefact of drying as opposed to a natural dispersal mechanism.

The seed of the new plant is similar to the seeds of *Salicornia*, but is distinctly larger, without perisperm, and has a large U-shaped embryo enclosed in a flimsy, membranous testa, which in contrast to *Salicornia* is without ornamentation (Fig. 2E). With a length of c. 5 mm the seeds of the new plant are larger than in most other species of the *Salicornioideae* (Shepherd & al. 2005).

Our investigation integrated morphology and molecular data in order to determine the similarities and differences between the potentially new South American taxon and other genera in the *Salicornioideae* and to resolve its phylogenetic relationships within the subfamily. The molecular analysis by Piirainen & al. (2017) was extended to include the accession of this taxon from SW Ecuador (Fig. 3). This expanded molecular phylogeny shows that the South American plant is clearly distinct from, but also sister to, *Salicornia* without showing a close relationship to any of the subgenera of *Salicornia*. The separate analyses of the two gene trees (cp data and ITS/ETS data) showed identical results (not shown), which allowed the combination of the data sets. According to its position in the molecular tree, the new taxon is as old as *Salicornia* s.l. and probably originated during the middle Miocene (compare dated tree in Piirainen & al. 2017: fig. 2). We are recognizing this clearly distinct lineage as the new

genus *Mangleticornia* P. W. Ball, G. Kadereit & Cornejo, gen. nov. In contrast to *Salicornia* s.l., which has diversified and comprises c. 50 spp., *Mangleticornia* is monospecific and might be a relict of an old lineage.

Morphologically *Mangleticornia* is generally very similar to *Arthrocaulon*, *Arthroceras*, *Microcnemum* Ung.-Sternb., *Salicornia* and *Tecticornia* in vegetative features and the inflorescence is a compact, spike-like thyrses with opposite, usually 3-flowered cymes at each node in all these genera. The fruits of *Mangleticornia* are most similar to those of *Salicornia*, both being without perisperm and with a flimsy seed coat, but the seed coat of *Mangleticornia* is without ornamentation, whereas the seed coat of *Salicornia* is ornamented by straight to hooked hairs or papillae, which may be very sparse and restricted to particular areas of the coat. *Arthrocaulon*, *Arthroceras*, *Microcnemum* and *Tecticornia* have seeds with ample perisperm and a firmer seed coat, which is variously ornamented (Shepherd & al. 2005). The apparent absence of perianth distinguishes the flowers of *Mangleticornia* from other genera, although *Microcnemum* has flowers with a reduced perianth and the annual *S. heterantha* Beer & Demina, from Russia, has the terminal flower in each cyme lacking a visible perianth, with the anthers and styles emerging through a pore in the cortical tissue of the distal segment (Beer & Demina 2005). *Mangleticornia* is also unusual in not releasing the fruit from the infructescence segments and appears to produce only one fruit in each segment, the whole infructescence disarticulating when the fruit is mature. There is one taxon of *Salicornia* (*S. europaea* subsp. *disarticulata* (Moss) Lambinon & Vanderpoorten) in which the cymes are 1-flowered and the infructescence disarticulates to disperse the 2-fruited segments, and a few species of *Tecticornia* (e.g. *T. disarticulata* (Paul G. Wilson) K. A. Sheph. & Paul G. Wilson, *T. papillata* K. A. Sheph. and *T. uniflora* (Paul G. Wilson) K. A. Sheph. & Paul G. Wilson) in which the infructescence also disarticulates to disperse the fruits (Shepherd 2007; Shepherd 2008). *Mangleticornia* is also unusual in being restricted to localities near the equator (0°–5°42'S), whereas almost all species in *Arthrocaulon*, *Arthroceras*, *Microcnemum*, *Salicornia* and *Tecticornia* are more than 10° N or S of the equator, except for two species in Africa and the Indian Ocean (*S. pachystachya* Bunge ex Ung.-Sternb. and *T. indica* (Willd.) K. A. Sheph. & Paul G. Wilson). Both the morphological and molecular evidence support the view that this plant from the mangroves of SW Ecuador and N Peru is a distinct species, which is also distinct from *Salicornia* and other closely related genera and should therefore be treated at generic rank.

Taxonomy

Mangleticornia P. W. Ball, G. Kadereit & Cornejo, **gen. nov.** – Type: *Mangleticornia ecuadorensis* P. W. Ball, G. Kadereit & Cornejo.

Diagnosis — Differing from *Salicornia* in the absent perianth with the flowers enclosed in the fleshy tissue of the distal internode, flowers exposed through shortly 3-lobed pores in the fleshy tissue; only one flower producing a fruit in each segment, which is dispersed by the disarticulation of the infructescence spikes; testa without ornamentation. Differing from *Arthrocaulon*, *Arthroceras*, *Microcnemum* and *Tecticornia* also by the absence of perisperm.

Description — Shrubs; *stems* opposite-branched, apparently jointed and fleshy when young, becoming woody and not jointed, not armed, some terminated by an inflorescence, others entirely vegetative. *Leaves* opposite, decussate, sessile, joined at base, decurrent, forming fleshy joints on each node (vegetative segments), eventually deciduous; *leaf blades* fleshy projections at distal end of each joint, edges with scarious margin. *Inflorescences* terminal, branched, each branch terminating in a spike-like thyse, jointed at nodes, each joint consisting of 2 opposite, axillary, 3-flowered cymes enclosed by proximal end of distal internode (fertile segments), each flower exerted through a shortly 3-lobed pore near base of fleshy tissue. *Flowers* bisexual (terminal) and unisexual (staminate) (lateral), probably protandrous; *perianth* absent; *stamens* 1 or occasionally 2, exerted through a pore in distal internode; *styles* 2, exerted through same pore as stamens. *Fruiting spikes* disarticulating, segments enlarged in fruit, with fruits included in fleshy tissue of fertile segments and not released, only 1 fruit developing in each fertile segment. *Fruits* with pericarp not clearly differentiated from fleshy tissue of segment. *Seeds* with testa membranous, without ornamentation; *perisperm* absent; *embryo* U-shaped.

Number of species — One.

Etymology — The name is derived from *mangletum*, mangrove swamp (inferred from *mangle*, mangrove) compounded with *cornu*, horn, referring to the occurrence of the plant adjacent to or in mangrove swamps as well as its horn-like appearance.

Mangleticornia ecuadorensis P. W. Ball, G. Kadereit & Cornejo, **sp. nov.** – Fig. 1, 2.

Holotype: Ecuador, Guayas Prov., Isla Puna, vicinity of Puna Nueva, 79°55'W, 02°44'S, 0 m, disturbed salt marshes, herbaceous, to 2 m tall, stem segments typically 4 mm thick, 1 Oct 1987, J. Madsen 63972 (AAU!; isotype: GUAY 7257).

Vernacular names — Parachique, Vidrillo and Vidrillo salado.

Description — Plants 0.8–2(–3) m tall, with single erect basal stem, diffusely branched above, some branches vegetative, others fertile, older woody stems up to 10 mm in diam.; *fleshy vegetative segments* ± cylindric, 10–20(–30) mm long, 3–5(–6) mm in diam. on main

branches, smaller on lateral branches, green becoming yellowish, stomata prominent; free tips of segments (leaf blades) 1–2 mm long. *Inflorescence* of branched spikes up to 10 cm or more long, composed of 5–20 or more fertile segments; *fertile segments* ± cylindric, 5–8 mm long, 4–5 mm in diam., green, becoming yellow-green in fruit; free leaf tip c. 1 mm long, broadly triangular with rounded apex; pores 0.5–0.7 mm in diam.; anthers 1.2–1.5 mm long. *Fruiting segments* 7–10 mm long, 5–6 mm in diam., somewhat barrel-shaped. *Seeds* c. 5 mm long.

Phenology — Flowering specimens observed from October to February; a fruiting specimen was collected in March.

Distribution — Ecuador: Guayas, El Oro, possibly Manabi. Peru: Tumbes, possibly Piura. *Mangleticornia ecuadorensis* occurs in SW Ecuador, primarily in Guayas province, extending south to departamento Tumbes in N Peru. It probably also occurs further north in Ecuador to Manabi province in the vicinity of Pedernales at about latitude 0° (Cornejo 2014) and further south in Peru in departamento Piura in the disjunct San Pedro de Vice mangrove (latitude 5°42'S). The mangroves in these two areas are similar to those in which *Mangleticornia* occurs (Cornejo 2014), but no specimens have been seen to confirm their presence. Vegetative specimens can be identified by the raised stomata, whereas *Salicornia neei* which occurs further south in Peru has sunken stomata.

Ecology — Ecologically *Mangleticornia ecuadorensis* is a typical element of the Equatorial-Pacific mangroves as defined by Cornejo (2014). These mangroves are co-dominated by *Avicennia germinans* (L.) L. and occur in areas that have an average annual rainfall of less than 600 mm and definite wet and dry seasons, the wet season being from late December to May. The plants occur in the following habitats: as understory under *A. germinans*; in open, disturbed mangroves; on the drier edge of mangroves on muddy soils; on sandy-grassy beaches close to mangroves; or in salt marshes on the landward side of mangroves. They grow in both shade and full sun and usually occur at or slightly above high tide mark, where they are regularly but briefly inundated by seawater. They are often dominant in open habitats. *Mangleticornia ecuadorensis* does not occur further north; in N Ecuador, Colombia and SW Costa Rica mangroves are in areas that have substantially higher rainfall (an average annual rainfall of 1000 mm or more), so they are regularly inundated by fresh water. Salt marshes and similar saline habitats do not occur adjacent to such mangroves (Cornejo 2014).

Conservation status — *Mangleticornia ecuadorensis* occurs in reasonably large numbers in mangrove ecosystems that are legally conserved and protected in Ecuador

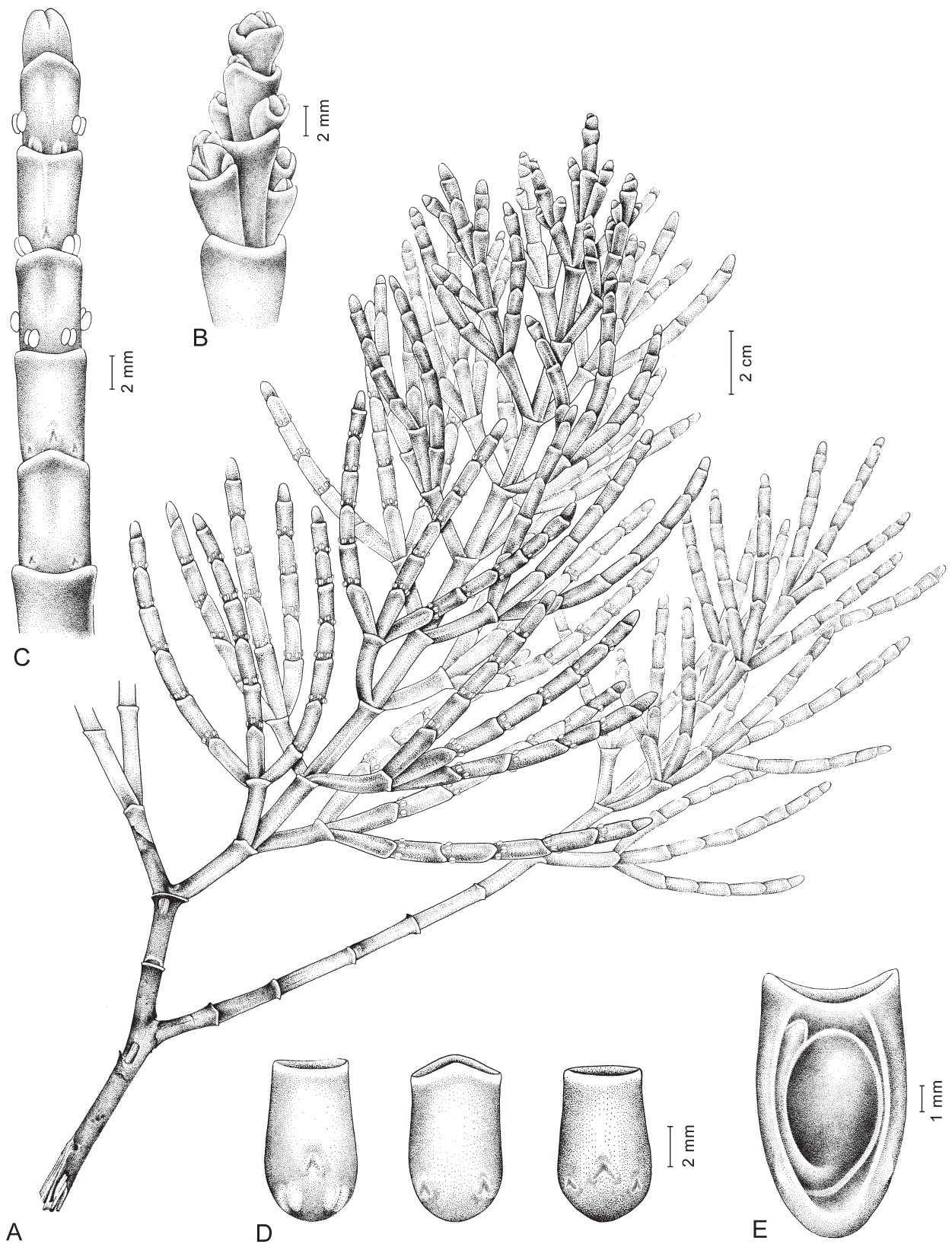


Fig. 2. *Mangleticornia ecuadorensis* – A: whole specimen (holotype); B: vegetative branch; C: inflorescence branch; D: fruiting segments; E: fruiting segment with one side removed to expose seed. – A–C from the holotype, *Madsen 63972* (AAU); D, E from *D. N. Smith 10077* (MO). – Drawn by Maria Geyer.

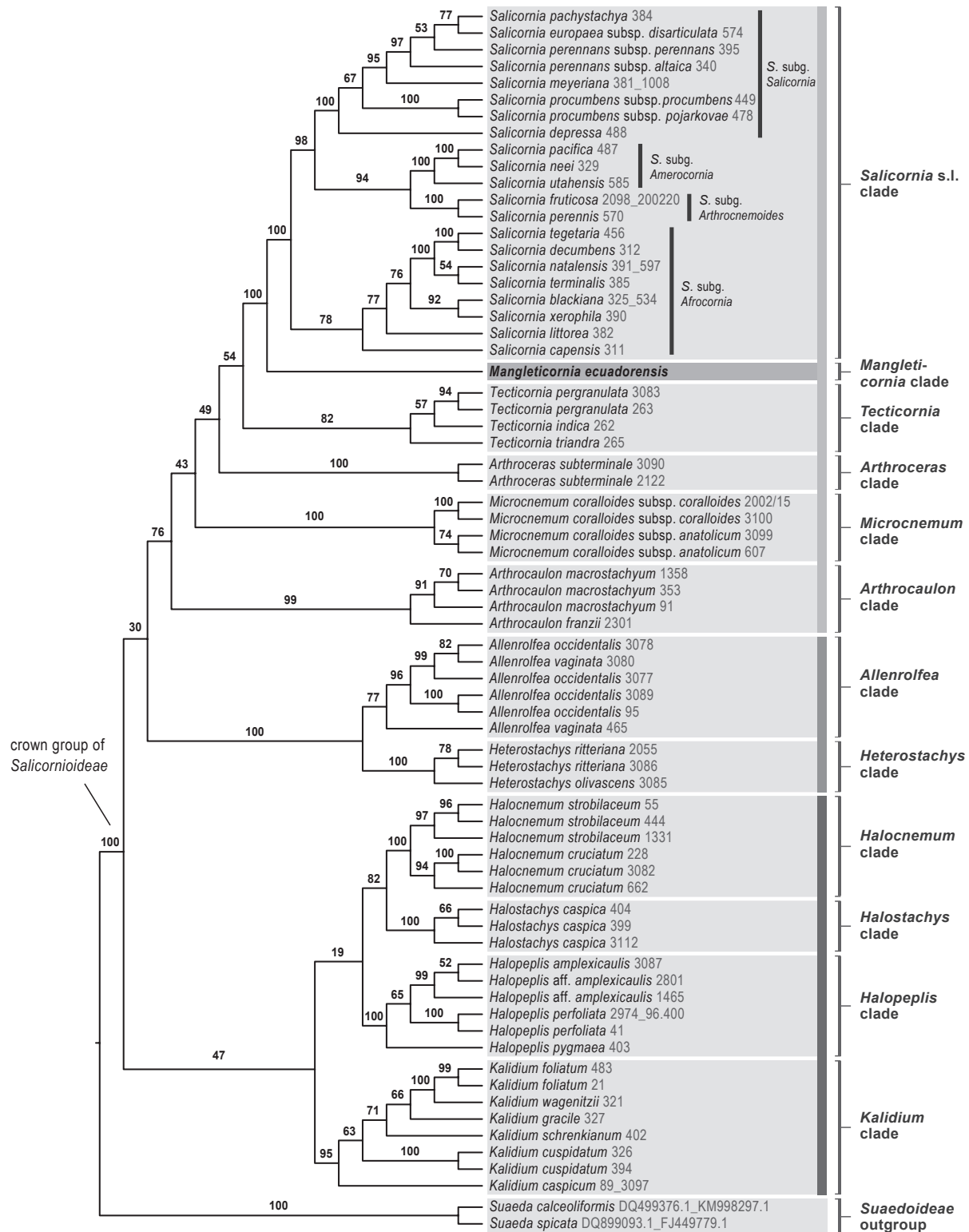


Fig. 3. Phylogenetic tree of *Salicornioideae* based on the two nrDNA markers Internal Transcribed Spacer (ITS) and External Transcribed Spacer (ETS) combined with the two cpDNA markers *atpB-rbcL* spacer and *matK-trnK*. The tree was generated with the same Maximum Likelihood settings (RaxML, Stamatakis 2014) and dataset as used in Piirainen & al. (2017: fig. 1), with the exception that here four sequences (GenBank accession numbers: ETS = KY928651; ITS = KY928650; *atpB-rbcL* spacer = KY928649; *matK-trnK* = KY928648) of the new taxon *Mangleticornia ecuadorensis* were added. DNA extraction, PCR and sequencing followed exactly the methods outlined in Piirainen & al. (2017). Voucher information: *Cornejo & Gallardo 8845* (GUAY; lab No. chen3505) and *Cornejo & Gallardo 8846* (GUAY; lab No. chen3506); see under Additional specimens examined; both samples showed identical sequences. Numbers above branches represent ML bootstrap values. Names of taxa are according to Piirainen & al. (2017).

and Peru. It also occurs, often as a subdominant, in salt marshes and other open coastal-tidal communities, which in recent decades have been diminishing due to encroachment by the shrimp-farming industry. Under these circumstances, the species is provisionally assigned to the IUCN category NT (Near Threatened) (IUCN 2012).

Etymology — The specific epithet refers to the primary country of its occurrence.

Additional specimens examined (paratypes) — ECUADOR: PROV. GUAYAS: entre Playas y Posorja lado sur de la Peninsula, 0–2 m, manglar y bosque seco cerca del mar, arbusto erecto de 3 metros en manglar, 20 Feb 1982, *H. Balsley* 2250 (F 2018430, MO 5753116); 10 km SE from Guayaquil, mangrove swamp, shrub 4 ft high, succulent and green, 21 Jan 1962, *C. H. Dodson & L. B. Thien* 2165 (MO 1782643); mangrove remnants c. 8 km S of Guayaquil, 79°53'W, 02°14'N, 0–2 m, shrub 1–1.5 m, dominating drier parts of mangroves, 22 Jun 1973, *L. Holm-Nielsen & al.* 7259 (AAU, MO 2391187); 5 km S of Guayaquil, 0 m, in standing water, saline or brackish, perennial herb to 8 dm, stem tough, woody, 29 Aug 1938, *H. E. Stork* 8951 (MO 1288108); Hacienda Barcelona, 13–14 km Guayaquil-Salinas, 0 m, mangrove association, shrub to 2 m tall on banks of Estero Salado, “Vidrillo”, 21 Jan 1983, *C. H. Dodson & al.* 13607 (F 2050075, MO 3023221); Isla Puna, from midway Puna Nueva-Zapote and 0–3 km inland, 79°54'W, 02°45'S, shrub to 1.5 m high, common in salt marsh, 29 May 1987, *J. E. Madsen* 63473 (AAU, MO); Guayaquil, Camaronera Aqualit, 17 km via la costa, 0–5 m, bosque seco, tropical, arbusto de 1–2 m alto, comun en camaronera, colectada en bosque de manglar intervenido, Sep 1993, *X. Cornejo & M. Castro* 0287 (GUAY 5265); Reserva de Produccion Faunistica Manglares El Salado, Sep 2016, *X. Cornejo & M. Gallardo* 8845 and 8846 (GUAY; molecular lab No. chen3505 and chen3506, respectively); Guayaquil, Reserva de Produccion Faunistica Manglares El Salado, sector Tres Bocas, 02°13'S, 79°57'W, 5 m, 27 Jan 2017, *X. Cornejo* 8866 (GUAY, MO, NY, TRTE). — PROV. EL ORO: Puerto Bolivar, 80°00'W, 03°16'S, 0 m, mangrove, shrub 1 m, 6 Apr 1980, *L. Holm-Nielsen* 22820 (AAU).

PERU: PROV. TUMBES: estuaries near Puerto Pizarro, sea level, mangrove and grassy sand areas between beach and mangrove, margin between mangrove and grass, shrub 1.2 m, succulent, fr. green, 10 Mar 1985, *D. N. Smith* 10077 (MO 5845906); Tumbes, shrub to 1.5 m tall, 8 Jan 1968, *D. R. Simpson* 602 (F 1897935); Tumbes Dpto. (prior to 1986), *Rafael Lao M. RLM* 5149 (MO 3306725).

Acknowledgements

Our thanks to Margarita Gallardo (Guayaquil) for Fig. 1A and B, Maria Geyer (Mainz) for Fig. 2, Caroline

Bouilly (University of Toronto) for technical assistance, Sylvia Jonitz (Guayaquil) for acting as courier, and the curators of the following herbaria, who enabled us to examine and/or loan their specimens: AAU, F, GUAY and MO. We also thank Kelly Shepherd (Perth), Mikko Piirainen (Helsinki) and an anonymous reviewer for valuable comments on the manuscript, as well as Roy Gereau (St. Louis) for etymological advice on the name of the new genus.

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Willdenowia

Open-access online edition www.bioone.org/loi/will  BioOne

Online ISSN 1868-6397 · Print ISSN 0511-9618 · Impact factor 0.680

Published by the Botanic Garden and Botanical Museum Berlin, Freie Universität Berlin

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