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TAXONOMIC AND PHYLOGENETIC STUDIES ON SALICORNIOIDEAE (AMARANTHACEAE)

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ACADEMIC DISSERTATION

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LIST OF ORIGINAL PUBLICATIONS

This PhD thesis is based on the following manuscripts, which are referred to in the text by their Roman numerals:

I Piirainen, M. 1991: Flora Nordica notes I. *Salicornia* (Chenopodiaceae) in northern Europe: typification and taxonomic notes. Ann. Bot. Fenn. 28: 81–85.

II Kadereit, G., Piirainen, M., Lambinon, J. & Vanderpoorten, A. 2012: Cryptic taxa should have names: Reflections in the glasswort genus *Salicornia* (Amaranthaceae). Taxon 61: 1227–1239.

III Piirainen, M. 2015: Pattern of morphological variation of *Salicornia* in north Europe. Nordic J. Bot. 33: 733–746. DOI: 10.1111/njb.00848

IV Piirainen, M. 2015: Typification of the name *Salicornia deserticola* (Amaranthaceae/Chenopodiaceae). Phytotaxa 201(1): 106–108. DOI: 10.11646/phytotaxa.201.2.11

V Piirainen, M. 2015: Proposal to conserve the name *Halostachys* (*Chenopodiaceae* s.str.; *Amaranthaceae* sensu APG: *Salicornioideae*) with a conserved type. Taxon 64: 386–387. DOI: 10.12705/642.20

VI Piirainen, M., Liebisch, O. & Kadereit, G. 2017: Phylogeny, biogeography, systematics and taxonomy of Salicornioideae (Amaranthaceae/Chenopodiaceae) – A cosmopolitan, highly specialized hygrohalophyte lineage dating back to the Oligocene. Taxon 66: 109–132. DOI: https://doi.org/10.12705/661.6

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Original idea	**MP**	JL, AV	**MP**	**MP**	**MP**	GK, **MP**
Study design	**MP**	GK, JL, **MP,** AV	**MP**	**MP**	**MP**	GK, **MP**
Data gathering / preparation	**MP**	GK, JL, **MP,** AV	**MP**	**MP**	**MP**	GK, OL, **MP**
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Manucript preparation	**MP**	GK, JL, **MP,** AV	**MP**	**MP**	**MP**	GK, **MP**

JL = Jacques Lambinon, GK = Gudrun Kadereit, OL = Oskar Liebisch, **MP**= Mikko Piirainen, AV = Alain Vanderpoorten

ABSTRACT

This dissertation handles the taxonomically challenging subfamily Salicornioideae (Amaranthaceae in APG IV taxonomy), consisting of 11 genera and some one hundred species of obligatory halophytes with a reduced morphology. Habitats include coastal and inland salt marshes from tropical mangroves to the subarctic; a few shrubby species inhabit xeric conditions. The species in the subfamily are known for their modified morphology with succulent and often articulated stems and highly reduced leaves and flowers. The reduced morphology, together with a remarkable phenotypic plasticity, has caused much confusion in the morphology-based taxonomy. In addition, identifying taxa is further complicated by that these plants lose many of their diagnostic characters upon drying.

The study starts with the morphology, taxonomy and nomenclature of the genus Salicornia in northern Europe, extends to cover the whole Eurasian continent and use of molecular data and finally proceeds to a comprehensive DNA-based phylogeny and phylogeography of the subfamily.

An acceptable taxonomy ought to reflect a plausible phylogeny, using monophyly as the main criterion. At the same time, it should be workable enough to be useful as a practical everyday tool for field botany, floristic work and conservational purposes, among others. The new taxonomy of the annual Eurasian *Salicornia* presented aims to meet these demands. Several taxa with a limited geographical distribution are neither supported in the molecular analysis nor morphologically separable and are thus placed in synonymy. On the other hand, unresolved clades combined under *S. perennans*, cryptic speciation between *S. europaea* and *S. perennans* and the fact that all involved taxa were not available in the molecular analysis offer a challenge for future studies.

The monophyly of Salicornioideae is confirmed by the phylogenetic analysis. Five clades are found well supported in the subfamily, but are unresolved at deeper nodes: 1) *Kalidium*, 2) *Halopeplis*, 3) *Halocnemum*/*Halostachys* and 4) *Allenrolfea*/*Heterostachys*. All of them are highly supported except for *Allenrolfea*, which is moderately supported. *Halostachys* and *Halocnemum* are found to be sister genera, as were *Allenrolfea* and *Heterostachys*. 5) The remainder of the subfamily forms the fifth clade, in which the highly supported Eurasian *Arthrocnemum macrostachyum*, *Microcnemum*, the North American *Arthrocnemum subterminale* and *Tecticornia* form an unresolved polytomy. *Sarcocornia* and *Salicornia* also form a monophyletic clade in which the American and Eurasian species of *Sarcocornia* and *Salicornia* respectively form well-supported clades. However, the Southern and Eastern African and Australian *Sarcocornia* are only moderately supported.

Salicornioideae probably originated in Eurasia during the late Eocene to early Oligocene. The divergence of the early main clades took place in the middle Oligocene. Long-distance dispersal has taken place several times to the Americas (*Allenrolfea*/*Heterostachys*, *Arthrocnemum subterminale*, *Salicornia*/*Sarcocornia*), South Africa (*Halopeplis*, *Salicornia*/*Sarcocornia*) and Australia (*Tecticornia*, *Salicornia*/*Sarcocornia*).

Based on these results, an updated generic classification of Salicornioideae is proposed with two main novelties: 1) the two species of *Arthrocnemum* are separated and described as two different genera, *Arthrocaulon* and *Arthroceras*, 2) *Sarcocornia* is treated as congeneric with *Salicornia*. In addition, all Australian genera (*Halosarcia*, *Pachycornia*, *Sclerostegia*, *Tecticornia*, *Tegicornia*) are treated under *Tecticornia* as proposed earlier by Australian researchers. For *Salicornia* (incl. *Sarcocornia*) a new infrageneric classification is proposed to accommodate the four phylogenetically and geographically well-supported lineages within the genus.

Nomenclatural questions are given special emphasis. Thirty new nomenclatural combinations and one *novem novum* are published, and thirteen lectotypifications and one epitypification are made in the papers included in the work.

TIIVISTELMÄ

Revonhäntäkasvien (heimo Amaranthaceae) alaheimoon Salicornioideae kuuluu 11 sukua ja noin sata lajia, jotka ovat erikoistuneet kasvamaan suolapitoisella alustalla trooppisilta mangrovesoilta aina subarktisille merenrannoille; monet lajit kasvavat sisämaan ajoittain tulvanalaisilla suolamailla, muutama myös kuivilla paikoilla. Ryhmän kasveja luonnehtivat mehivartisuus, pieniksi ja suomumaisiksi surkastuneet lehdet sekä hyvin pienet ja huomaamattomat kukat, jotka sijaitsevat suomumaisten tukilehtien hangassa tavallisesti kolmen kukan ryhminä. Kuivattaessa kasvit yleensä menettävät suuren osan vähistäkin käyttökelpoisista tuntomerkeistään. Kasvien määrittäminen, sukujen ja lajien rajaaminen ja niiden sukulaissuhteiden selvittäminen on näistä syistä ollut erityisen vaikeaa.

Tämä väitöstyö on edennyt vaiheittain pohjoiseurooppalaisten suolayrttien (*Salicornia*) morfologian, nimeämisen ja luokittelun selvittämisestä ensin koko Euraasiaan, mistä tutkimus laajennettiin selvittämään koko alaheimon alkuperäalueita, fylogeniaa (polveutumista) ja polveutumisen ajoitusta.|

Tutkimuksessa esitetään euraasialaisten suolayrttien uusi luokittelu, joka pohjautuu DNA-tutkimukseen, morfologiaan ja maantieteeseen. Pohjois- ja Itä-Euroopan suolayrttien osoitetaan kuuluvan kahteen perimältään toisistaan eriytyneeseen ns. kryptiseen lajiin, joita ei ulkoisten tuntomerkkien avulla pystytä erottamaan toisistaan.

Alaheimon monofyleettisyys (polveutuminen vain yhdestä kantamuodosta ja eriytyminen kaikista sukulaisistaan) pystyttiin vahvistamaan DNA-pohjaisessa fylogeneettisessä tutkimuksessa. Alaheimon kaikki 11 sukua ovat kukin monofyleettisiä ja muodostavat yhdessä viisi suurempaa polveutumishaaraa. Ryhmän kantavanhemmat ovat todennäköisesti kehittyneet Euraasiassa myöhäiseoseenin ja varhaisen oligoseenin aikana, ja ryhmän viisi haaraa ovat syntyneet oligoseenikauden lopulla. Alaheimon kasveja levisi kaukokulkeutumisen seurauksena useana eri ajankohtana Etelä- ja Pohjois-Amerikkaan, Etelä-Afrikkaan ja Australiaan, missä sukujen ja lajien eriytyminen vauhdittui. Näiden tulosten pohjalta tutkimuksessa esitetään alaheimon uusi luokittelu, joka poikkeaa aikaisemmista kahdessa pääkohdassa: 1) suolasormion (*Arthrocnenum*) suku jaetaan kahteen uuteena kuvattavaan sukuun, *Arthrocaulon* (Euraasia) ja *Arthroceras* (Pohjois-Amerikka); 2) suolasormikit (*Sarcocornia*) siirretään suolayrttien sukuun. Lisäksi kaikki viisi australialaista, usein erillisinä pidettyä endeemistä sukua (*Halosarcia*, *Pachycornia*, *Sclerostegia*, *Tecticornia*, *Tegicornia*) käsitellään yhtenä nivelsarvien (*Tecticornia*) sukuna.

Tutkimuksessa kiinnitetään erityistä huomiota ryhmän usein sekavankin tieteellisen nimistön selvittämiseen ja nimistöhistorian yksityiskohtiin. Osajulkaisuissa tehdään yhteensä 30 nimistöteknistä kombinaatiota, julkaistaan yksi korvaava nimi ja valitaan 14 nimistöteknistä tyyppiä.

1 INTRODUCTION

1.1 THE SUBFAMILY SALICORNIOIDEAE

The taxonomy of the Angiosperm Phylogeny Group (the most recent version APG IV 2016) has widely been accepted in taxonomic literature in recent years. In this taxonomy, the traditional family Chenopodiaceae is included in Amaranthaceae, which then consists of approximately 165 genera and 2040 species (Christenhusz & Byng 2016). However, the status of Chenopodiaceae has been debated. In their comprehensive treatment of Caryophyllales, Hernández-Ledesma & al. (2015) maintained Chenopodiaceae arguing that its merging into Amaranthaceae had been made without robust phylogenetic data. As the focus of this thesis is in the subfamily level, no position on the status is taken here and the taxonomy of APG IV (2016) is formally followed.

Chenopodiaceae sensu Hernández-Ledesma & al. (included in Amaranthaceae by APG IV 2016) comprise 104 genera and ca. 1700 species (Hernández-Ledesma & al. 2015). It has an exceptionally high proportion of halophytes among eudicots, with an estimated 381 species (Flowers & Colmer 2008) and 44%–50% of its genera (Flowers & al. 1986, Glenn & Brown 1999) include species with salt tolerance. All species in subfamily Salicornioideae are halophytes representing one third of the total number of salt tolerant species in the family. With highly specialized adaptations to saline environments these remarkable plants inhabit tidal flats and periodically flooded habitats in coastal or inland salt marshes worldwide (except for arctic areas, where the climate is too cold and growing season too short). Inland habitats also include other poorly drained saline soils, such as periodically flooded depressions and around temporary springs in arid areas. Only a few shrubby species occur in xeric conditions (Kadereit & al. 2006).

Succulence and salt tolerance are likely ancestral conditions in Salicornioideae and Suaedoideae (Kadereit & al. 2012). Salt tolerance was probably present in the common ancestor of Salicornioideae, Suaedoideae, Camphorosmoideae and Salsoloideae already during the Paleocene – Late Oligocene 61–35 million years ago. The analysis of Kadereit & al. (2012) resolved Salicornioideae as monophyletic and sister to *Bienertia* Bunge ex Boiss. (Suaedoideae); the two together resolved sister to the rest of Suaedoideae. However, their sampling was limited so no taxonomic conclusions were made on this basis.

Salicornioideae are well known for their modified morphology with highly reduced leaves and flowers and often articulated stems. The subfamily was characterized by Kühn & al. (1993) as containing succulent plants with frequently articulated stems, reduced leaves, flowers usually in groups of three, sunken into cavities in the axis of spiciform inflorescences, often with a two- to four-lobed perianth and annular or curved (rarely straight) embryo. The reduced morphology, combined with a wide phenotypic plasticity, has until recently caused much confusion in the delimitation of species and genus and morphological systematics in the subfamily. In addition, many morphological traits are difficult or impossible to observe in normally preserved herbarium material, as the fleshy tissues shrink and squeeze during desiccation. Preservation of at least some flowering or fruiting parts of the plants in alcohol or another preserving liquid, when collecting material from the field, is highly recommended, but usually not routinely performed.

The origin of the articulated succulent stem in Salicornioideae has been interpreted in two different ways. The most widely accepted view—which is also accepted here—is that the fleshy outer layer or "cortex" of the stem is of foliar origin, formed through the elongation of decurrent leaf bases, which are fused with the true stem to form an articulated structure as convincingly shown by, e.g. Fraine (1913), James & Kyhos (1961) and Grigore & al. (2014), based on anatomical evidence. However, Fahn (1963) and some other authors are of the opinion that the fleshy articulated stem represents a modified true stem.

In their comprehensive phylogenetic study of the subfamily, Kadereit & al. (2006) accepted 11–15 genera and ca. 90 species, forming a well-supported monophyletic group with Suadoideae as the sister group. Shepherd & Wilson (2007) reduced the number of genera by incorporating the Australian genera *Halosarcia* Paul G.Wilson, *Pachycornia* Hook.f., *Sclerostegia* Paul G.Wilson, and *Tegicornia* Paul G.Wilson into the single genus *Tecticornia* Hook.f. During the last decade, several new species have been described in *Tecticornia* (Shepherd 2007a, 2007b, 2008; Shepherd & van Leeuwen 2007, 2011; Shepherd & Lyons 2009), *Salicornia* L. (Akhani 2008, Yaprak & Yurdakulol 2008), *Sarcocornia* A.J.Scott (Steffen & al. 2009, de la Fuente & al. 2011, 2013; Yaprak 2012) and *Arthrocnemum* Moq. (Sukhorukov & Nilova 2016). The reinstatement of an older synonymized taxon, *Halocnemum cruciatum* (Forssk.) Tod. (Bacchetta & al. 2012, Biondi & al. 2013) added another species to *Halocnemum* M.Bieb., which was previously considered to be monotypic. After these changes, Salicornioideae comprise 11 genera (Hernández-Ledesma & al. 2015) and more than a hundred (108–113) species. The discovery of a new genus from the tropical mangroves of southwestern Ecuador and adjacent northern Peru during the preparation of this manuscript added another genus and species to these figures (Ball & al. 2017).

1.2 HISTORY OF GENERA AND MORPHOLOGY BASED CLASSIFICATION IN SALICORNIOIDEAE

Linnaeus (1753) included all five taxa of succulent, articulated species known to him (later assigned to Salicornioideae) in the genus *Salicornia*. Only *S. europaea* L. and *S. virginica* L. remain in the genus as we circumscribe it today. Two Linnaean taxa, *S. arabica* L. and *S. caspica* L., were synonymized under *Kalidium caspicum* (L.) Ung.-Sternb., while *S. europaea* var. *fruticosa* L. was elevated to species rank and later placed in the genus *Sarcocornia* as *S. fruticosa* (L.) A.J.Scott. New genera were described in the subfamily during the following 160 years; see Table 1.

Kalidiopsis was synonymized under *Kalidium* by Scott (1977), a placement confirmed by Kadereit & al. (2006) using molecular data. *Halosarcia*, *Pachycornia*, *Sclerostegia* and *Tegicornia* were synonymized under *Sclerostegia* by Shepherd & Wilson (2007). Many new species were first described in the genus *Salicornia* and only afterwards placed in their current genera. To date, there are 154 scientific names described in the genus *Salicornia* in IPNI (http://www.ipni.org/index.html, accessed 3.3.2017; duplicate records removed). Following the generic delimitations of Scott (1977) only 13–17 accepted species remain in the genus.

Table 1. *The genera of Salicornioideae with a reference to their original publication*

Genus	Described by
Salicornia L.	Linnaeus (1753)
Halocnemum M.Bieb.	Bieberstein (1819)
Arthrocnemum Moq.	Moquin-Tandon (1840)
Halostachys C.A.Mey. ex Schrenk	Schrenk (1843)
Kalidium Moq.	Moquin-Tandon (1849)
Halopeplis Bunge ex Ung.-Sternb.	Ungern-Sternberg (1866)
Heterostachys Ung.-Sternb.	Ungern-Sternberg (1876)
Microcnemum Ung.-Sternb.	Ungern-Sternberg (1876); first as *Spirostachys* Ung.-Sternb. nom. illeg. Ungern-Sternberg (1866)
Pachycornia Hook. f.	Hooker in Bentham & Hooker (1880)
Tecticornia Hook. f.	Hooker in Bentham & Hooker (1880)
Allenrolfea Kuntze	Kuntze (1891)
Kalidiopsis Aellen	Aellen (1967a, 1967b)
Sarcocornia Scott	Scott (1977)
Halosarcia Paul G.Wilson	Wilson (1980)
Sclerostegia Paul G.Wilson	Wilson (1980)
Tegicornia Paul G.Wilson	Wilson (1980)

Augier (1801) placed *Salicornia* in a separate family under the invalid name “Salicornes” (ICN Art. 18.4; McNeill & al. 2012). This family contained unrelated dicots and monocots and was thus most unnatural according to modern taxonomic understanding. Martinov's later validation of the name (Martinov 1820) was questioned by Sennikov & al. (2015), because in their view Martinov did not explicitly accept the name as required in the nomenclatural code (Art. 33.1.; McNeill & al. 2012). According to this view, the first taxonomically acceptable classification was published by Dumortier (1827), whereby he described the tribe Salicornieae Dumort., diagnosed by the undivided hooded perianth. It was represented by only one genus, *Salicornia*, which included both annuals (*Salicornia* sensu stricto) and the perennial *S. fruticosa* (L.) L. (= *Sarcocornia fruticosa*). Dumortier's tribe was raised to the rank of subfamily as Salicornioideae Kostel. by Kosteletzky (1835). The species of the subfamily, included under *Salicornia* and *Halocnemum* at the time, are today partly placed in *Halopeplis*, *Kalidium* and *Tecticornia*. Agardh (1858) reinstated the family Salicorniaceae, with only one genus, *Salicornia*, diagnosed by opposite branches and spike-like inflorescences. This act has not received wide acceptance in later treatments except for Scott (1977), who preferred to separate Salsolaceae and Salicorniaceae from the traditional Chenopodiaceae based on vegetative, floral and embryological characteristics. Neither has it received any phylogenetic support in later studies, as Salicornioideae was found deeply nested in Chenopodiaceae (Kadereit & al. 2003, Müller & Borsch 2005, Kadereit & al. 2012).

In more recent classifications (Table 2) Ulbrich (1934) divided Salicornioideae into two tribes, Salicornieae and Halopeplideae Ulbr. The latter was defined as having alternate bracts and an annular, semi-annular or curved embryo, and it consisted of *Allenrolfea*, *Halopeplis*, *Heterostachys* and *Kalidium*. The genera with opposite bracts, included in Salicornieae, were grouped into two subtribes, Halostachyinae (*Halocnemum*, *Halostachys*, *Tecticornia*) with free peltate bracts and Salicorniinae (*Arthrocnemum, Microcnemum, Pachycornia, Salicornia*) with pairwise fused bracts. Ulbrich's Salicorniinae also included *Halophytum* Speg., which was later separated to a monospecific family, Halophytaceae (Soriano 1946 invalidly, validated by Soriano 1984, and accepted by APG IV 2016), because it was found to belong to the portulacid clade. Scott (1977) mainly accepted Ulbrich's (1934) classification without *Halophytum*, and he reinstated Agardh's (1858) Salicorniaceae and reassigned *Allenrolfea* and *Heterostachys* under Halostachyinae and *Tecticornia* under Salicorniinae. Kühn & al. (1993) restored Salicornioideae as a subfamily of Chenopodiaceae. They accepted the tribal division suggested by Scott (1977), but discarded Ulbrich's (1934) subtribes of Salicornieae.

Later, molecular phylogenetic studies helped clarify the classification, but the tribal classification based on morphology had to be rejected (Shepherd & al., 2005; Kadereit & al., 2006; Kapralov & al., 2006). Kadereit & al. (2006) found the morphological differences used by Scott (1977) and Kühn & al. (1993) inconsistent and leading to unnatural groupings not supported by molecular data.

Table 2. Classification of Salicornioideae by Ulbrich (1934), Scott (1977), Kühn & al. (1993), Kadereit & al. (2006) and Paper VI of this study.

Ulbrich 1934	Scott 1977	Kühn & al. 1993	Kadereit & al. 2006	Paper VI
Salicornioideae (c. 61 spp.)	**Salicorniaceae** (c. 57 spp.)	**Salicornioideae** (c. 80 spp.)	**Salicornioideae** (c. 90 spp.)	**Salicornioideae** (c. 100 spp.)
Halopeplideae	**Halopeplideae**	**Halopeplideae**	**Salicornieae**	**Salicornieae**
Allenrolfea	*Halopeplis*	*Halopeplis*	*Allenrolfea*	*Allenrolfea*
Halopeplis	*Kalidium*[2]	*Kalidium*[2]	*Arthrocnemum*	*Arthrocaulon*[4]
Heterostachys	**Salicornieae**	**Salicornieae**	*Halocnemum*	*Arthroceras*[4]
Kalidium	**Halostachyinae**	*Allenrolfea*	*Halopeplis*	*Halocnemum*
Salicornieae	*Allenrolfea*	*Arthrocnemum*	*Halosarcia*	*Halopeplis*
Halostachyinae	*Halocnemum*	*Halocnemum*	*Halostachys*	*Halostachys*
Halocnemum	*Halostachys*	*Halosarcia*	*Heterostachys*	*Heterostachys*
Halostachys	*Heterostachys*	*Halostachys*	*Kalidium*[2]	*Kalidium*[2]
Tecticornia	**Salicorniinae**	*Heterostachys*	*Microcnemum*	*Microcnemum*
Salicorniinae	*Arthrocnemum*	*Microcnemum*	?*Pachycornia*	*Salicornia*[3]
Arthrocnemum	*Microcnemum*	*Pachycornia*	*Sarcocornia*	subg. *Afrocornia*[6]
Halophytum[1]	*Pachycornia*	*Salicornia*[3]	*Salicornia*	subg. *Amerocornia*[6]
Microcnemum	*Salicornia*	*Sclerostegia*	?*Sclerostegia*	subg. *Arthrocnemoides*[6]
Pachycornia	*Sarcocornia*	*Tecticornia*	?*Tecticornia*	subg. *Salicornia*
Salicornia	*Tecticornia*	*Tegicornia*	?*Tegicornia*	*Tecticornia*[5]

[1] separated as a monospecific family, Halophytaceae, by Soriano (1984);
[2] incl. *Kalidiopsis*;
[3] incl. *Sarcocornia*;
[4] *Arthrocnemum* auct., non Moq., p.p. (*Arthrocnemum* Moq. = *Salicornia* L.);
[5] incl. *Halosarcia, Pachycornia, Sclerostegia, Tegicornia*;
[6] *Sarcocornia* p.p.

1.3 PHYLOGENETICS OF SALICORNIOIDEAE

Kadereit & al. (2006) studied nuclear (ITS) and plastid (*atpB-rbcL* spacer) DNA sequences for their phylogenetic study of Salicornioideae. They confirmed the results of Kadereit & al. (2003), Pratt (2003) and Müller & Borsch (2005), showing that Salicornioideae represent a clade sister to Suaedoideae. The relationships between the early branching groups in Salicornioideae, consisting of *Allenrolfea, Halopeplis, Halocnemum, Halostachys, Heterostachys* and *Kalidium* could not be resolved. This was interpreted as evidence that the major lineages of Salicornioideae likely underwent a rapid radiation in a relatively short period of time. *Arthrocnemum* and *Microcnemum* were either resolved as sister to each other (ITS, with low support) or forming a grade with *Microcnemum* placed sister to all higher taxa (*atpB-rbcL*). The sister group relationship of *Arthrocnemum* and *Microcnemum* was supported by morphological similarities such as opposite and fused leaves and bracts forming cup-like structures and three-flowered cymes of nearly equal-sized, slender flowers that are free from each other and the bracts. However, the two genera also differ from each other, as *Arthrocnemum* contains shrubs with a four-lobed perianth and two stamens and *Microcnemum* is a small annual with a small perianth rudiment and only one stamen. Among the remaining taxa the Australian lineage represented by *Tecticornia, Halosarcia* and *Pachycornia* was moderately supported as monophyletic and sister to the *Salicornia*/*Sarcocornia* clade, but only with low support. While the *Salicornia*/*Sarcocornia* clade was well-supported, a monophyletic *Salicornia* was nested in *Sarcocornia*, rendering the latter genus paraphyletic.

Kapralov & al. (2006) confirmed the sister group relationship between Salicornioideae and Suaedoideae, using six genomic regions from both nuclear and plastid markers. Their sampling in Salicornioideae was limited to a small number of species in *Allenrolfea, Halocnemum, Halostachys, Kalidium, Salicornia* and *Sclerostegia*, but all the included genera were resolved as monophyletic with high support. According to their results, *Allenrolfea* was resolved sister to all other taxa, *Salicornia* and *Sclerostegia* placed sister to each other and together, sister to *Kalidium*, which was in turn sister to *Halocnemum+Halostachys*, all of these with high support. Their topology differed clearly from that of Kadereit & al. (2006), which may largely be due to the limited sampling of Kapralov & al. (2006). On the other hand, statistical support for early branching clades was low and the two markers showed partly conflicting results in Kadereit & al. (2006).

In their ETS analysis of *Salicornia*, Kadereit & al. (2007) confirmed the paraphyly of *Sarcocornia* in relation to *Salicornia*. They found a geographical signal within *Sarcocornia*, with separate Eurasian, American and African/Australian clades. The same result was reached by Steffen & al. (2015) using ETS, *atpB-rbcL* and *rpL32-trnL*.

Other recent phylogenetic studies have concentrated on single genera and/or a limited geographical area, e.g. Murakeözy & al. (2007; Atlantic coasts of France), Kadereit & Yaprak (2008; *Microcnemum*), Kaligarič & al. (2008; *Salicornia*, Gulf of Trieste in N Italy), Teege & al. (2011; *Salicornia*, NW and W Europe), Slenzka & al. (2013; *Salicornia*, South Africa), de la Fuente & al. (2013, 2015; *Sarcocornia*, Western Mediterranean Europe).

1.4 THE GENUS *SALICORNIA*

The genus *Salicornia*, as circumscribed in most modern floras according to the taxonomy of Scott (1977), comprises only annual species with a decussate phyllotaxy and pairwise fused leaves and bracts. Its growth habit and the number of branches it produces are variable. The main stem and all branches end in a spike-like thyrse ("terminal spike"), usually composed of one sterile and two to 25 fertile segments, each formed from two opposite cymes of (one to) three flowers arranged in a triangle and immersed in the succulent axis. The fruit is a nut with a membranous pericarp. The seed coat is membranous and covered with curved or hooked hairs, rarely with only rudimentary remnants of hairs.

Taxonomically useful morphological characters in *Salicornia* are limited: the succulent leaves are fused with the internodes, leaving only a narrow scarious rim free, and the flowers are composed of fused tepals. Species have been circumscribed based on continuously variable characters such as colour, difference in size and form between central and lateral flowers of the same cyme, shoot architecture and length of the inflorescence. On the other hand, the phenotypic variation of *Salicornia* species is considerable. Much of it can be explained by salinity, nutrient content and moisture of the soil (Seliskar 1985, Ungar 1987) or other external factors such as tidal activity (Wiehe 1935). When crowded in dense stands or in dense vegetation of other species, *Salicornia* plants may become unbranched and slender with unusually long sterile internodes. However, at least some part of the morphological differences has been shown to have a genetic basis (Teege & al. 2011). Herbarium material is problematic in taxonomic studies because the colours are often lost and many other characters such as the relative size of central and lateral flowers are no longer measurable.

In standard floras and checklists (e.g. Ball & Akeroyd 1993, Piirainen 2009), the genus is often divided in two species groups according to their ploidy: the diploid *S. europaea* group and the tetraploid *S. procumbens* group, both containing several microspecies differing in minor characteristics and usually with a limited geographical range. Although supported also by phylogenetic data (Kadereit & *al.* 2007, Murakeözy & *al.* 2007, Teege 2009, Vanderpoorten & *al.* 2011), the division is much more complicated (Kadereit & *al.* 2007). Diploid *Salicornia* are cleistogamous or chasmogamous and protandrous, tetraploid taxa are often chasmogamous and protogynous. Diploid taxa are probably self-pollinating by rule (Ball & Tutin 1959, Dalby 1962, Ball 1964, Ferguson 1964, Jefferies & al. 1981, Jefferies & Gottlieb 1982) and there is evidence that this also happens in tetraploid taxa (Teege 2009 and citations therein). Outbreeding may in some cases be a rare event as shown by Noble & *al.* (1992) in a population in Norfolk, U.K., in their rDNA analysis of 38 maternal plants and 2112 of their progeny with no evidence for outcrossing. Especially diploid plants tend to form self-pollinating, pure lineages with small morphological differences (Dalby 1955, 1962, Cristofolini & Chiapella 1970, Jefferies & Gottlieb 1982, Wolff & Jefferies 1987a, Vanderpoorten & al. 2011). Most taxonomic studies of the genus concern only limited areas, which has led to description of species on a local basis and with no true insight of the variation at a wider geographic range or across the genus as a whole.

Salicornia and *Sarcocornia* differ only in life form and inflorescence characters. *Salicornia* is always annual and the individual flowers are arranged in a triangle, with two smaller lateral flowers that are in contact below the larger central flower. In *Sarcocornia*, the plants are woody perennials (only young parts fleshy), and the flowers are arranged in a horizontal row (lateral flowers are separated from each other by the central one); the number of flowers may be as high as 13.

2 OUTLINE AND THE AIMS OF THIS STUDY

The focus of this thesis is to study the systematics and taxonomy of Salicornioideae, especially the genus *Salicornia*, with particular emphasis on nomenclatural questions. The aim of Paper I is to clarify the taxonomy and nomenclature of *Salicornia* in the Nordic Countries in connection with the account of the genus for *Flora Nordica* (Piirainen 2001), mainly based on morphological studies. Paper II extends this study of *Salicornia* to cover the entire Eurasian continent and applies molecular data to provide a revised classification of Eurasian taxa. Paper III continues the theme with a detailed morphological analysis of *Salicornia* for the *Flora Nordica* area extending the study to include populations from the White Sea area of Russia. Papers IV and V focus on resolving nomenclatural issues in *Salicornia*/*Sarcocornia* and *Halostachys* as a continuation of the account of the subfamily in the Euro+Med PlantBase project (Piirainen 2009). Finally, Paper VI is a global phylogenetic and phylogeographic study of the whole subfamily Salicornioideae using molecular methods and aiming to come to a well-founded taxonomy of the subfamily based on phylogenetic data.

3 MATERIALS AND METHODS

Collections of *Salicornia* held in all major Nordic herbaria (AAU, BG, C, H, KUO, O, OULU, S, TROM, TUR, TURA and VOA; acronyms following Thiers 2017) were examined for Paper I, Possible type specimens and other important collections were also borrowed from relevant herbaria in the U.K., Germany and Russia (BM, CGE, FD, GOET, LE, LTR, K, KPABG, OXF). New study material of *Salicornia* was collected from saline natural habitats in Denmark, Finland, Norway and Sweden (Papers I and III) and northwestern Russia (Paper III). Morphological measurements were made from both fresh material and components preserved in liquid Formalin–Acetic acid–Alcohol (FAA) for later morphometric study (Papers I and III). Material was also collected and dried in a normal plant-press and later sampled for DNA extraction and molecular analyses (Paper II). Voucher specimens are deposited in the herbarium collections of H and MJG (DNA vouchers). Original material of *S. deserticola* A.Chev. was borrowed from Paris (P) for Paper IV. Paper V was mainly based on survey of historical botanical literature. For the molecular analyses in Paper VI, a comprehensive voucher collection of Amaranthaceae from the field and from different herbaria kept at the Institut für Spezielle Botanik und Botanischer Garten der Johannes Gutenberg-Universität, Mainz (MJG) was used. In addition, specimens were sampled for DNA extraction from herbarium vouchers in Helsinki (H), Mainz (MJG), San Francisco (CAS) and Vienna (W).

The morphology of *Salicornia* was studied from 666 plants and 52 populations, collected for this purpose between 1988 and 2002 (Paper III). The measurements of a total of 21 metric and seven multistate characters were carried out under a dissecting microscope. The data was analyzed as three different datasets under the headings 1) General morphology comprising all characters of 307 plants that covered both the vegetative and flower morphology and six ratios of characters based on them; 2) Reduced general morphology comprising a total of 529 plants that were scored for eight vegetative characters and 13 characters of the terminal spike and four ratios; 3) Spike morphology of all 666 plants, which were scored for 11 fertile segment and flower characters and two ratios. The datasets were analyzed with PCA (principal components analysis) to discover the best combination of uncorrelated variables. After this, the datasets were analyzed with a hierarchical cluster analysis using Ward's method and Euclidean distances. A hierarchical cluster analysis was performed based on the population means of original characteristics to test, if plain population means could be used as a practical tool for species identification.

Phylogenetic evidence derived from ETS sequences from 215 specimens in Paper II was used to propose a new taxonomic treatment of Eurasian *Salicornia*; 101 of the sequences were published as new accessions. For Paper VI, two nuclear DNA markers, ETS and ITS, and two plastid markers, *atpB-rbcL* and *matK-trnK* were used to study the phylogeny, phylogeography and taxonomy of Salicornioideae. A total of 66 taxa of Salicornioideae were sampled for paper VI, including all 11 genera that were accepted at the time of study, 201 new sequences were published, and 143 ingroup as well as 14 outgroup sequences were extracted from GenBank (Benson & al. 2013). The sampling covered all the species except for *Allenrolfea* (2 out of 3 species) and the three largest genera *Salicornia, Sarcocornia* and *Tecticornia*. The monophyly of *Salicornia* and *Tecticornia* and the *Salicornia*/*Sarcocornia* clade was already shown in previous studies. ML (maximum likelihood) phylogenetic analyses was performed using RaxML version 8.2.4 (Stamatakis & al. 2008, Stamatakis 2014). Traits for character optimization were analyzed using the ML criterion in Mesquite (Maddison & Maddison 2011). A molecular clock was applied on a Bayesian tree generated with BEAST v1.8.2 (Bayesian Evolutionary Analysis by Sampling Trees; Drummond & Rambaut 2007), calibrated with the fossil of *Salicornites massalongoi* Principi from Oligocene deposits (35.4–23.3 Mya) in Chiavon, northern Italy (Principi 1926). A biogeographical analysis was conducted with RASP v. 3.01 (Yu & al. 2015).

Nomenclatural issues were surveyed for papers I, II, V and VI, following the rules laid out in the International Code of Nomenclature for algae, fungi, and plants (ICN; McNeill & al. 2012). Historical bibliography was studied particularly for papers V and VI.

4 RESULTS AND DISCUSSION

4.1 SALICORNIA

Four taxa of *Salicornia* were accepted for the *Flora Nordica* area (Denmark, Finland, Iceland, Norway and Sweden) in Paper I, based on morphology, karyology, geography and ecology: *S. europaea*, *S. dolichostachya* Moss subsp. *dolichostachya*, *S. dolichostachya* subsp. *strictissima* (Gram) P.W.Ball and *S. dolichostachya* subsp. *pojarkovae* (Semenova) Piirainen. The latter name was published as a new combination as it was found to belong to the *S. dolichostachya* complex. No reason was found to accept *S. ramosissima* Woods (cf. Hansen & Pedersen 1968) at any taxonomical rank due to a lack of reliable diagnostic characters and because of the continuous variation evident among the diploid *Salicorniae*. Furthermore, it was suggested that the name is provisional and thus invalid (ICBN Art. 34.1b; Greuter & al. 1988). Later I discovered that the epithet had subsequently been validated by Hooker (1870) as *S. herbacea* L. var. *ramosissima* Woods ex Hook.f. and combined at the species level by Marshall (1908) as *S. ramosissima* (Woods ex Hook.f.) E.S.Marshall—these nomenclatural questions were further addressed in Paper II. Regardless of the nomenclatural validation, no support was found to accept *S. ramosissima* as a taxon distinct from *S. europaea* based on morphological or molecular data (Paper II).

Previous studies (Papini & al. 2004, Kadereit & al. 2007, Murakeözy & al. 2007, Kaligaric & al. 2008, Vanderpoorten & al. 2011) demonstrated a relatively clear genetic distinction between diploid and tetraploid species of *Salicornia*. The tetraploid species form a well-defined and well-supported monophyletic group in Europe (the "*Salicornia dolichostachya* clade" in Kadereit & al. 2007). To a large extent, these can also be characterized morphologically, though it is not always possible to classify individual specimens in predetermined morphological groups due to the high phenotypic plasticity (Kaligaric & al. 2008). In the analysis in Paper II however, the tetraploid clade also contains *S. heterantha* S.S.Beer & Demina and *S. iranica* Akhani, which were reported to be diploid (Akhani 2008; Beer & al. 2011), while the diploid clade includes *S. altaica*, which was reported to be decaploid (Lomonosova 2005). Hence, cytotypes cannot define infrageneric groups in *Salicornia* as proposed by Scott (1977). This view is confirmed by the results of Kadereit & al. (2007), where tetraploidy was shown to be a polyphyletic trait on a world-wide scale.

A new taxonomic treatment of Eurasian *Salicornia* is proposed in Paper II, using monophyly as the main criterion at the species level. At the subspecific level, morphological and karyological criteria are used. Two species are accepted in the *S. europaea* group (*S. europaea* with three subspecies and *S. perennans* with two subspecies). As to *S. perennans*, the criterion of monophyly is not strictly met. The species consists of several unresolved clades, and the strongly supported *S. europaea* seems to be nested in one of them (which, however, has only weak support). As these two taxa seem to be reproductively isolated (Vanderpoorten & al. 2011), they are accepted as two different species. Nevertheless, the problematic situation and need of further investigation is pointed out. In the *S. procumbens* group, *S. dolichostachya* is synonymized under *S. procumbens* Sm., which has nomenclatural priority. This had already been suggested by Dahmen & Wisskirchen (1998). Furthermore, these two taxa could not be separated in the phylogenetic analysis of Kadereit & al. (2007). Two species in the *S. procumbens* group are accepted: *S. procumbens* with four subspecies and *S. persica* Akhani with two subspecies. Four West Asian species, *S. persica* subsp. *rudshurensis* Akhani, *S. perspolitana* Akhani, *S. sinus-persica* Akhani and *S.* ×*tashkensis* Akhani, are regarded as uncertain taxa, the status of which could not be resolved due to a lack of sequences in the analysis.

While *Salicornia europaea* and *S. perennans* represent two clearly distinct DNA chemotypes, they are morphologically indistinguishable (Paper II & III). The conclusion is to regard them as cryptic species. Unfortunately, the material for Paper III was collected and measured before the chemotypes were analyzed and thus the methods for the study could not be planned specifically for this purpose. Further research, with a geographically representative sampling of these two taxa, is required to fully resolve this problem. Slenzka & al. (2013) also demonstrated cryptic speciation in the genus in the South African *S. meyeriana* complex, where phylogenetic tree topology corresponded with geography and ecology, but not with morphology.

Papers I, II and III of the present study concentrate on North Europe and Eurasia. Knowledge of *Salicornia* from a global perspective is still deficient and a worldwide taxonomic revision is required. For example, the study of Kadereit & al. (2007) covered most of the geographical area, but parts of Southwest and East Asia, North Africa and North America were poorly represented. The large number of taxa described in the genus, often on a very local basis, together with the inconsistent application and use of names, do not make the task of completing a global treatment easier.

4.2 SALICORNIOIDEAE: PHYLOGENETIC INFERENCE

The phylogenetic analysis in paper VI confirms the monophyly of Salicornioideae. The results are in line with the conclusions of Kadereit & al. (2006), showing no support for any of the taxonomic subdivisions of the subfamily proposed by earlier authors (Ulbrich 1934, Scott 1977, Kühn & al. 1993; Table 2). The ML analysis resulted in a well-resolved phylogram, which does not conflict with the topology of the Bayesian analysis. Five clades are found to be well supported in the subfamily, but are unresolved at deeper nodes. In these clades all genera, *Kalidium*, *Halopeplis*, *Halocnemum*/*Halostachys* and *Allenrolfea*/*Heterostachys*, are highly or moderately (*Allenrolfea*) supported. *Halostachys* and *Halocnemum* are found to be sister genera, as were *Allenrolfea* and *Heterostachys*. The remainder of the subfamily forms the fifth clade, in which the Eurasian *Arthrocnemum macrostachyum* (Moric.) K.Koch, *Microcnemum*, the North American *Arthrocnemum subterminale* (Parish) Standl. and *Tecticornia* form part of an unresolved polytomy (but resolved in the Bayesian analysis). *Sarcocornia* and *Salicornia* also form a clade in which the American and Eurasian species of *Sarcocornia* and *Salicornia* respectively form well-supported clades. However, the Southern and Eastern African and Australian *Sarcocornia* are only moderately supported.

Based on these results, an updated generic classification of Salicornioideae is proposed that differs from the classification of Kadereit & al. (2006) in three aspects: 1. the two species of *Arthrocnemum* are separated and described as two different genera, *Arthrocaulon* Piirainen & G.Kadereit and *Arthroceras* Piirainen & G.Kadereit, 2. *Sarcocornia* is treated as congeneric with *Salicornia*, and 3. all Australian genera are treated under *Tecticornia* as proposed by Shepherd & Wilson (2007). The separation of the two *Arthrocnemum* species is also supported by the morphological analysis of

Shepherd & al. (2005) and the study of reproductive characters by Sukhorukov & Nilova (2016). For *Salicornia* (incl. *Sarcocornia*) a new infrageneric classification is proposed to accommodate the four phylogenetically and geographically well-supported lineages of *Salicornia*. Two of these subgenera are new and 19 new combinations and one replacement name are published. This decision is also supported by the results of Kadereit & al. (2006) and Steffen & al. (2015). The exact relationships in the large group of Australian *Tecticornia* fall outside the scope of this study, and further research is still needed to understand the species-level relationships in that genus. The main issues causing taxonomic difficulties in *Tecticornia* are lack of informative characters due to rapid radiation and high levels of hybridization and polyploidy (K. Shepherd, in litt.). An overview of the genera and subgenera of Salicornioideae, the number of species and their distribution is given in Table 3.

Table 3. The genera and subgenera of Salicornioideae, species numbers and their distribution as accepted in Paper VI.

Genera and subgenera	No. of species	Distribution
Salicornioideae	107–112	
Allenrolfea	3	Argentina, Mexico, U.S.A.
Arthrocaulon	2	Mediterranean Region, E Africa, SW Asia, Cape Verde
Arthroceras	1	N Mexico, SW U.S.A.
Halocnemum	2	Mediterranean Basin, W and C Asia
Halopeplis	3	Mediterranean Region, W, S and C Asia, South Africa
Halostachys	1	SE Europe, Asia
Heterostachys	2	Argentina, South America, Mesoamerica
Kalidium	6	SE Europe, S, SW, C and E Asia
Microcnemum	1	Spain, W Asia
Salicornia		
subgen. *Afrocornia*	15 or 16	South and East Africa, Australia
subgen. *Amerocornia*	7	South and North America
subgen. *Arthrocnemoides*	7	Atlantic W Europe, Mediterranean Europe, Asia and Africa
subgen. *Salicornia*	13–17	worldwide except for S America and Australia
Tecticornia	44	Australia, S Pakistan, E tropical Africa

4.3 SALICORNIOIDEAE: MOLECULAR CLOCK, ANCESTRAL AREA ANALYSIS AND ML CHARACTER OPTIMIZATION

According to the ancestral area analysis of Paper VI, Asia or a combination of Asia and the Mediterranean Basin are the most likely regions of origin of Salicornioideae. Based on fossil evidence it is known that the crown group of the subfamily existed at least 35.4–23.3 million years ago, which is also the minimum stem age of the main lineages in the subfamily. The common ancestor of the *Allenrolfea*/*Heterostachys* clade dispersed to South America and subsequently this lineage dispersed to North America. The common ancestor of the mainly Asian clade including *Halostachys*, *Halocnemum*, *Halopeplis* and *Kalidium* existed 30.2–15.4 Mya. In the sister branch of this lineage, migration to North America (*Arthrocnemum subterminale*; stem age: 24.9–12.5 Mya) and Australia (*Tecticornia*; stem age: 22.9–11.3 Mya) took place before the divergence of the large *Salicornia*/*Sarcocornia* clade (16.8–8.1 Mya). Migration of *Sarcocornia* to South Africa took place in an early phase (crown age of the South African lineage 13.8–5.5 Mya) and further expansion of the area to East Africa seems to have happened repeatedly. A dispersal event to Australia happened from within the South African lineage (6.6–1.4 Mya). In the analysis, the Australian lineage was represented only by one of three species (*S. blackiana* (Ulbr.) A.J.Scott), which showed almost identical sequences with another Australian species, *S. quinqueflora* (Bunge ex Ung.-Sternb.) A.J.Scott, in the plastid and nuclear analysis. Accordingly, it seems plausible that *Sarcocornia* reached the Australian continent only once. Later long-distance dispersal from the Asian-Mediterranean area took place probably four times to: 1. North America (the American *Sarcocornia* lineage) and further to South America; 2. North America (*Salicornia depressa* Standl.); 3. and 4. to South Africa (*S. meyeriana* Moss and *S. pachystachya* Bunge ex Ung.-Sternb., respectively).

The common ancestors of Salicornioideae, Suaedoideae, Camphorosmoideae and Salsoloideae were probably already halophytic some 65–35 Mya (Kadereit & al. 2012), during the mid-Palaeocene, Eocene and early Oligocene. Salt tolerance and succulence in the group probably evolved in coastal habitats and might have served as a pre-adaptation for colonization of dry continental inland habitats like steppes and deserts (Kadereit & al. 2012). After the Eocene Optimum, the climate started to cool, ice began to appear at the poles and the continental interiors began to dry out (Pagani & al. 2005), especially at the Eocene/Oligocene boundary. The conditions were probably suitable for the formation and spread of halophytic environments and provoked rapid evolution of salt tolerant plants. The climate during the Oligocene continued to cool and summers became drier. After the early Oligocene climatic deterioration, the global climate was relatively stable through the rest of the Oligocene (Prothero 2009). Salicornioideae probably diverged from Suaedoideae in the late Eocene–early Oligocene (Kadereit & al. 2012, Paper VI). Kadereit & al. (2006) hypothesized that this happened somewhere in Eurasia along the northern margin of the Tethys Sea 38.2–28.7 Mya. At this time, the Tethys Sea was already restricted in its eastern parts because of the formation of the Himalayas after the collision of the Indian subcontinent with Eurasia (Metcalfe 2013). The early adoption of the combination of salt tolerance, succulence and the steady improvement of stress tolerance, together with a dominance in coastal habitats, probably make Salicornioideae the oldest and most widespread hygrohalophyte lineage known among the angiosperms (Kadereit & al. 2012). Further diversification of Salicornioideae is in several cases connected with changes in climatic conditions. Accordingly, the relatively high rate of morphological diversification in the Australian clade is connected with a rapid expansion through the continent during the late Miocene at the time of increased aridity and salinization of the inland lake system (Shepherd & al. 2005b).

The character optimization analysis (Paper VI) shows few transitions for each trait. The ancestral life form for Salicornioideae is a shrubby perennial, the ancestral phyllotaxis is alternate and the ancestor likely had free bracts. Accordingly, the clade containing *Arthrocnemum*, *Microcnemum*, *Tecticornia* and *Salicornia*/*Sarcocornia* with the synapomorphies of opposite leaves and bracts and pairwise fused bracts is considered as the most derived in the subfamily. Whether articulated stems and reduced leaf laminas represent an ancestral character state or not, is ambiguous. However, given the clear ancestry of alternate phyllotaxis we regard it highly unlikely that articulation resulting from the fusion of two opposite leaf bases could be the ancestral condition.

4.4 NOMENCLATURAL QUESTIONS

The long history of describing new taxa based on a very narrow and local focus in Salicornioideae, especially in *Salicornia*, makes it a challenge to apply the principles of nomenclatural priority and nomenclatural stability (ICN; McNeill & al. 2012) to this group. To complicate matters, herbarium specimens are often old and badly preserved or missing diagnostic floral and seed characteristics needed for conclusive identification. Moreover, many if not most of the names have not been typified and thus their exact application is not fixed.

The name *Salicornia dolichostachya* may be given as an example. The name was used in Paper I and in the later account of the genus in *Flora Nordica* (Piirainen 2001) in line with the nomenclature of Flora Europaea (Ball 1964, Ball & Akeroyd 1993). However, it was later synonymized under *S. procumbens* (Dahmen & Wisskirchen 1988, Piirainen 2009). Especially during the preparation of Paper I, the nomenclature of the genus was not stable and the application of several species names, e.g. *S. emerici* Duval-Jouve, *S. oliveri* Moss, *S. procumbens* and *S. stricta* G.Mey. was obscure (Knoerr & Guinochet 1973, Greuter & al. 1984, Ingrouille & al. 1990, Ball & Akeroyd 1993, Kerguélen 1999, Mejden 1999), due to lack of typifications and a wider geographical understanding. Thus, it was not possible to resolve the taxonomy in the tetraploid species group of *Salicornia* based on northern European material alone.

Another example is the case of *Salicornia deserticola* (Paper IV). In connection with the account of Salicornioideae for the Euro+Med Plantbase (Piirainen 2009), a pragmatic decision had to be made on the identity of species described from inland northern Algeria, recognized at species rank in the diploid *S. europaea* aggregate by Greuter & al. (1984). According to its protologue (Chevalier 1934), *S. deserticola* differed from the woody perennial *S. fruticosa* (given as "*S. arabica* L.") mainly due to its biennial life form and more slender stems, while in other characters it approaches the annual species of *Salicornia*. Chevalier's description was insufficient to be taxonomically conclusive, so the identity of the taxon could only be decided on by selecting an appropriate lectotype from the syntypes cited by Chevalier. The specimens in Paris (P) were determinable as *S. fruticosa* (syn. *Sarcocornia fruticosa*), with no characters pointing to the diploid species group, so the decision was to synonymize the name under *S. fruticosa* on the basis of the specimens.

Strict adherence to original typifications may also sometimes cause disadvantageous nomenclatural changes. A good example of this is the genus name *Halostachys*. According to an early and largely neglected typification (Pfeiffer 1874), the name should have been placed in synonymy of another genus, *Halopeplis* and the entity we now know as *Halostachys* should have been given a new name. The proposal to conserve the name *Halostachys* with *H. caspica* as its conserved type (Paper V) aimed to stabilize the use of the names *Halostachys* and *Halopeplis*, which have been in use in their current meaning ever since their separation 150 years ago (Ungern-Sternberg 1866). The proposal was recommended for acceptance by the Nomenclature Committee for Vascular Plants (Applequist 2016).

In all, the following 13 lectotypifications and one epitypification are made in Papers I, II, IV, V and VI in order to fix the application of the names, either accepted or synonymized (the lectotypification of *Salicornia europaea* made in Paper I turned out later to be superfluous, as the name had already been lectotypified by Jafri & Rateeb 1978):

Salicornia dolichostachya Moss (Paper I). – Lectotype: Ireland, Dublin, North Bull, in saltmarsh, 20.VIII.1911, *Ostenfeld* (C)

Salicornia herbacea L. (I). – Lectotype: Sweden, Gotland, *anonymous* (LINN 10.1)

Salicornia herbacea subvar. *brachystachya* G.Mey. (I). – Lectoype Germany, Carolienensiel, VIII.1823 *Meyer*, (GOET)

Salicornia herbacea var. *stricta* G.Mey. (I). – Lectotype: Germany, Carolienen Siel, 26.VIII.1822, *Meyer* (GOET)

Salicornia leiosperma K.Gram (I). – Lectotype: Denmark, Ins. Amager prope Hauniam in prat. marit., 17.IX.1911, *Ostenfeld* (C)

Salicornia strictissima K.Gram (I). – Lectotype: Denmark, West Jutland, Ins. Fanö, pr. urbem Nordby, 25:IX.1911, C. *Raunkiær* (C)

Salicornia europaea L. (II). – Epitype: Sweden, Gotland, W shore of Burgsviken Bay, Näsudden Cape, *Piirainen & Piirainen 4222* (MJG)

Salicornia procumbens Sm. (II). – Type: U.K., Yarmouth, Mr. Backhouse, *anonymous, ex* Smith Herbarium 20.4. (LINN)

Salicornia deserticola A.Chev. (IV). – Lectotype: Algeria, Sud Algérien, Témacine près Touggourt, terrains salés, 15.XII.1931, *Chevalier 42063* (P)

Halostachys C.A.Mey. ex Schrenk, nom. cons. prop. (V). – Type: *H. caspica* (M.Bieb.) C.A.Mey. ex Schrenk

Salicornia subgen. *Oriindica* Ung.-Sternb. (VI). – Type: *S. brachiata* Roxb.

Salicornia subgen. *Vulgata* Ung.-Sternb. (VI). – Type: *S. herbacea* L.

Salicornia L. subgen. *Arthrocnemoides* Ung.-Sternb. (VI). – Type: *S. fruticosa* L.

Salicornia subterminalis Parish (VI). – Lectotype: U.S.A., Southern California, San Jacinto Plains, VI.1882, *Parish & Parish 1520* (US 00102676)

The taxonomic novelties published in Papers I, II and VI include two new genera, two new subgenera, 19 new combinations at the species level, 9 new combinations at the subspecies level and one *nomen novum* at the species level:

Salicornia dolichostachya subsp. pojarkovae (Semenova) Piirainen, comb. nov. (I)

Salicornia perennans subsp. altaica (Lomon.) G.Kadereit & Piirainen, comb. & stat. nov. (II)

Salicornia persica subsp. iranica (Akhani) G.Kadereit & Piirainen, comb. & stat. nov. (II)

Salicornia procumbens subsp. freitagii (Yaprak & Yardakulol) G.Kadereit & Piirainen, comb. & stat. nov. (II)

Salicornia procumbens subsp. heterantha (S.S.Beer & Demina) G.Kadereit & Piirainen, comb. & stat. nov. (II)

Salicornia procumbens subsp. pojarkovae (Semenova) G.Kadereit & Piirainen, comb. nov. (II)

Arthrocaulon Piirainen & G.Kadereit, gen. nov. (VI)

Arthrocaulon macrostachyum (Moric.) Piirainen & G.Kadereit, comb. nov. (VI)

Arthrocaulon franzii (Sukhor.) Piirainen & G.Kadereit, comb. nov. (VI)

Arthroceras Piirainen & G.Kadereit, gen. nov. (VI)

Arthroceras subterminale (Parish) Piirainen & G.Kadereit, comb. nov. (VI)

Salicornia L. subg. Afrocornia Piirainen & G.Kadereit, subgen. nov. (VI)

Salicornia L. subg. Amerocornia Piirainen & G.Kadereit, subgen. nov. (VI)

Salicornia alpini Lag. subsp. carinata (Fuente, Rufo & Sánchez Mata) Piirainen & G.Kadereit, comb. nov. (VI)

Salicornia capensis (Moss) Piirainen & G.Kadereit, comb. nov. (VI)

Salicornia decumbens (Toelken) Piirainen & G.Kadereit, comb. nov. (VI)
Salicornia decussata (S.Steffen, Mucina & G.Kadereit) Piirainen & G.Kadereit, comb. nov. (VI)
Salicornia dunensis (Moss) Piirainen & G.Kadereit, comb. nov. (VI)
Salicornia globosa (Paul G.Wilson) Piirainen & G.Kadereit, comb. nov. (VI)
Salicornia helmutii Piirainen & G.Kadereit, nom. nov. (VI)
Salicornia hispanica (Fuente, Rufo & Sánchez Mata) Piirainen & G.Kadereit, comb. nov. (VI)
Salicornia lagascae (Fuente, Rufo & Sánchez-Mata) Piirainen & G.Kadereit, comb. nov. (VI)
Salicornia littorea (Moss) Piirainen & G.Kadereit, comb. nov. (VI)
Salicornia mossambicensis (Brenan) Piirainen & G.Kadereit comb. nov. (VI)
Salicornia mossiana (Toelken) Piirainen & G.Kadereit, comb. nov. (VI)
Salicornia natalensis Bunge ex Ung.-Sternb. subsp. affinis (Moss) Piirainen & G.Kadereit, comb. nov.
Salicornia obclavata (Yaprak) Piirainen & G.Kadereit, comb. nov. (VI)
Salicornia pillansii (Moss) Piirainen & G.Kadereit, comb. nov. (VI)
Salicornia pruinosa (Fuente, Rufo & Sánchez Mata) Piirainen & G.Kadereit, comb. nov. (VI)
Salicornia quinqueflora Bunge ex Ung.-Sternb. subsp. tasmanica (Paul G.Wilson) Piirainen & G.Kadereit, comb. nov. (VI)
Salicornia tegetaria (S.Steffen, Mucina & G.Kadereit) Piirainen & G. Kadereit, comb. nov. (VI)
Salicornia terminalis (Toelken) Piirainen & G.Kadereit, comb. nov. (VI)
Salicornia xerophila (Toelken) Piirainen & G.Kadereit, comb. nov. (VI)

5 CONCLUSIONS

In Salicornioideae, adaptation to a narrow ecological niche is connected with considerable morphological reduction. This has caused severe taxonomical difficulties, because of convergence, paucity of useful characters and high phenotypic plasticity. This is especially pronounced in the annual species of *Salicornia*, as demonstrated in Papers I and III of the present study. An acceptable taxonomy ought to reflect a plausible phylogeny, using monophyly as the main criterion. At the same time, it should be workable enough to be useful as a practical everyday tool for field botany, floristic work and conservational purposes, among others. The new taxonomy of the annual Eurasian *Salicornia* presented in Paper II aims to meet these demands. Several taxa with a limited geographical distribution are neither supported in the molecular analysis nor morphologically separable and are thus placed in synonymy. On the other hand, unresolved clades combined under *S. perennans*, cryptic speciation between *S. europaea* and *S. perennans* and the fact that all involved taxa were not available in the molecular analysis offer a challenge for future studies.

To obtain a good understanding of the phylogeny within Salicornioideae, molecular studies across a wide geographical and taxonomical range are necessary. The molecular analyses in Paper VI confirms the main results of other recent phylogenetic studies, but with a better resolution and higher statistic support. Salicornioideae probably originated in Eurasia during the late Eocene–early Oligocene. The divergence of the early main clades took place in the middle Oligocene with the separation of *Allenrolfea*/*Heterostachys*, *Halocnemum*/*Halopeplis*/*Halostachys*/*Kalidium* and *Arthrocnemum*/*Microcnemum*/*Tecticornia*/*Salicornia*/*Sarcocornia* lineages. The latter lineage diversified most and comprises ¾ of the species of the subfamily. The *Arthrocnemum macrostachyum* /*Microcnemum* lineage diverged at the turn of the Oligocene/Miocene – while the *Arthrocnemum subterminale*, *Tecticornia* and *Salicornia*/*Sarcocornia* lineages were all present by the middle Miocene. Long-distance dispersal has taken place several times to the Americas (*Allenrolfea*/*Heterostachys*, *Arthrocnemum subterminale*, *Salicornia*/*Sarcocornia*), South Africa (*Halo-*

peplis, *Salicornia*/*Sarcocornia*) and Australia (*Tecticornia*, *Salicornia*/*Sarcocornia*). Diversification and dispersal of the clades has largely been provoked by changes in the global climate (e.g., aridfication of the interior continental areas) and changes caused by the continental drift (e.g., closure of the Tethys Sea and formation of the Panama Isthmus.).

Most recently accepted genera are well supported in the analyses of Paper VI, with a few exceptions, where some changes in the formerly accepted taxonomy are proposed. *Sarcocornia* is included in *Salicornia*, based on its paraphyletic position in relation to *Salicornia* and lack of sufficient morphological separation. Accordingly, several new nomenclatural combinations and one replacement name are provided. Because of nomenclatural difficulties, the genus *Arthrocnemum* has often been circumscribed to comprise the perennial shrubby species of *Salicornia* (*Sarcocornia*). This is shown to be erroneous, and *Arthrocnemum* is demonstrated to be polyphyletic, consisting of two phylogenetically and morphologically well separable clades. Further, as *Arthrocnemum* is shown to be a later nomenclatural synonym of *Salicornia*, these two clades are described as new genera, *Arthrocaulon* and *Arthroceras*.

Salicornioideae is probably the oldest and most widespread hygrohalophyte lineage known in the flowering plants. Though the subfamily as such or as part of Amaranthaceae has been the subject of several phylogenetic studies, some questions within the group still remain open. The exact relationships within the large group of Australian endemic taxa have not been explained in detail. Also the recent discovery of a new monotypic genus from Ecuadorian mangrove is calling for further study in the tropics, where our knowledge of the group has been proved to be insufficient.

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