

December 1977

# Reinstatement and revision of Salicorniaceae J. Agardh (Caryophyllales)

A. J. SCOTT

Department of Plant Biology, University of Birmingham, Birmingham\*

Accepted for publication July 1977

---

The family Salicorniaceae J. Agardh is reinstated and includes 12 genera of succulent, apparently leafless plants formerly contained in the Chenopodiaceae. One of the genera is new and contains 15 species throughout the world, formerly placed in either *Salicornia* or *Arthrocnemum*. The remaining species of *Salicornia* are placed in 3 sections. The classification, origin and evolution of the family are discussed and the typification of *Kalidiopsis*, here reduced to a synonym of *Kalidium*, and the lectotypification of *Arthrocnemum* are examined.

KEY WORDS:— Salicorniaceae — *Salicornia* — *Sarcocornia*.

## CONTENTS

Introduction . . . . .	357
Historical survey of the genera . . . . .	359
The classification . . . . .	363
Key to the families of the suborder Chenopodiineae . . . . .	363
Key to the tribes, subtribes and (in <i>Salicornia</i> ) sections of the Salicorniaceae . . . . .	363
Taxonomic descriptions . . . . .	365
Acknowledgements . . . . .	372
References . . . . .	373

## INTRODUCTION

The Salicorniaceae is a small family of only 12 genera, closely related to the other families in the suborder Chenopodiineae: Amaranthaceae, Chenopodiaceae and Salsolaceae (Scott, 1977). The family was described by Agardh (1858) with only the succulent genus *Salicornia* L.; however since then it has been included in the Chenopodiaceae, either as a tribe (Bentham & Hooker, 1880; Volkens, 1893) or as a subfamily (Ulbrich, 1934).

Williams & Ford-Lloyd (1974) proposed the division of the Chenopodiaceae into three groups. Although they describe these groups as subfamilies they supply names with tribal endings: Beteae, Chenopodieae, and Salsoleae. Their preliminary survey was based only on 18 characters for 36 genera, using data

\* Present address: The Herbarium, Royal Botanic Gardens, Kew.

extracted from published descriptions. Many of the characters used are of doubtful value since they have been found to vary within the larger genera and even within certain species, as, for example, number of stamens, number of stigmas and seed orientation. Among the characters they used, only embryo curvature clearly distinguishes the Salsoleae from the other two groups, and a further two characters, ovary position and operculum presence, occur only in the Beteae. A large number of important characters was omitted, such as stem articulation, stamens attachment and nature of pericarp; this clearly limited the value of the study.

The re-evaluation of the status of this group as a distinct family is the result of a taximetric investigation of the Chenopodiaceae (Scott, 1975) in which it was demonstrated that the Salicorniaceae differed greatly from the Chenopodiaceae *sensu stricto* in a number of correlated characteristics.

The suborder Chenopodiinae is considered to consist of five groups which are treated as families or subfamilies:

- (1) Chenopodiaceae *sensu stricto*
- (2) Salicorniaceae
- (3) Amaranthaceae subfamily Amaranthoideae
- (4) Amaranthaceae subfamily Gomphrenoideae
- (5) Salsolaceae.

The Chenopodiaceae are particularly abundant in the Southern and Northern temperate regions, and usually have herbaceous perianths, as in *Chenopodium* or *Beta*, while in some genera, such as *Atriplex* the perianth is absent in pistillate flowers and replaced by bracteoles. The perianth is sometimes accrescent and appendaged as in *Maireana* and *Scerolaena*. The family differs from the Salicorniaceae in that the flowers are basically 5-merous with 5 stamens and the stems are entire, not articulated.

The Salsolaceae are chiefly an Asian and Mediterranean group, distinguished by the spiral embryo, absence of endosperm, the narrow-succulent leaves, the typically axillary inflorescence and the usually accrescent, winged perianth.

The Amaranthaceae subfamily Amaranthoideae (including the Polycnemoideae) are mainly tropical and distinguished from the Chenopodiaceae chiefly by the scarious perianth and bracteoles or (in *Celosia*) by the several seeded fruits. The subfamily Gomphrenoideae are chiefly South American in distribution and are distinguished from the Amaranthoideae by the 1-celled anthers, the *Gomphrena*-type of pollen, and the scarious, tube-like staminal disc with conspicuous staminodes.

The most remarkable features of the family Salicorniaceae are their succulent, articulated and apparently leafless stems, with photosynthesis taking place in the fleshy cortex of the stem. The nature of this fleshy cortex has been the subject of numerous investigations. It is generally assumed to be foliar in origin, either through the downward prolongation of the base of the leaf (Duval-Jouve, 1868; Ungern-Sternberg, 1876; Cooke, 1911; De Fraine, 1912; Halket, 1928) or by the fusion of opposite leaves and their adnation to the stem (Leysley, 1949; Backer, 1949; Keller, 1951; James & Kyhos, 1961; Tölken, 1967), although the view has also been taken that the cortex represents the true cortex of the stem and that the leaves are absent (Fahn & Arzee, 1959; Fahn, 1963). I am grateful to I. K. Ferguson (pers. comm.) for pointing out

that the presence of an abscission layer in *Salicornia pusilla* J. Woods is strong evidence for the foliar origin of the cortex. Articulated stems also occur in related genera in the Salsolaceae such as *Anabasis* L., *Arthrophytum* Schrenk, and *Haloxyton* Bunge. Bisalputra (1961) even suggested dividing the family Chenopodiaceae into an articulated group and a non-articulated group on the basis of stem anatomy. Such grouping is not supported by the anatomical structure of the articulated stem, which has been shown to differ in *Salicornia* and *Anabasis* (Fahn & Arzee, 1959). In addition there are many structural differences in the flower and fruit, as well as leaf structure (Carolin, Jacobs & Vesk, 1975). Thus articulated genera such as *Anabasis* are connected with non-articulated genera such as *Salsola* L., while the genera of Salicorniaceae show no close relationship with other genera of Chenopodiaceae.

Other features unique to the Salicorniaceae are the spike-like inflorescence of sessile, 3-flowered cymes, the reduced flowers, which usually consist only of a 2-4 lobed calyx tube with 1-2 stamens, and the subannular or curved embryo.

#### HISTORICAL SURVEY OF THE GENERA

Linnaeus recognized only one genus, *Salicornia* L., which he described to include all succulent and apparently leafless, chenopodiaceous plants. The next genus described was *Halocnemum* by Bieberstein (1819), based on the Mediterranean species *Salicornia strobilacea* Pallas. *Sarcathria* was next described by Rafinesque (1837), and distinguished only by its possession of two stamens as against one in *Salicornia*. This is a most unreliable character as shown by the unnatural collection of species placed in *Sarcathria* by Rafinesque. The six species included by Rafinesque were *Salicornia ambigua* Michx., *S. indica* Willd., *S. procumbens* Sm., *S. radicans* Sm., *S. strobilacea* Pallas (spelt *S. strobilacca*), and *S. virginica* L. Two of these, *S. virginica* L. and *S. procumbens* Sm., are now considered to be synonyms of *Salicornia europaea* L.; *S. ambigua* Michx. and *S. radicans* Sm. are synonyms of *Sarcocornia perennis* (Miller) A. J. Scott; *Salicornia indica* Willd. is now included in *Arthrocnemum*, while *S. strobilacea* Pallas is the type of *Halocnemum*. Merrill (1949) suggests that *Sarcathria strobilacea* Rafin. is based on *Salicornia strobilacea* Delile, a synonym of *Haloepelis perfoliata* (Forsk.) Bunge ex Schweinf. However, this species has a single stamen and entire stems which does not agree with the brief generic description given by Rafinesque. The genus *Sarcathria* is therefore superfluous, since it contains the type of an earlier genus, and it is a synonym of *Halocnemum*, as indicated by Index Nominum Genericorum (card no. 10/11570).

The first study to try and embrace all the species included by Dumortier (1827) in the tribe Salicornieae was that of Moquin-Tandon (1840), who included the 17 species known to him in only three genera: *Salicornia*, with six species; *Halocnemum*, with six species, and five species in a new genus, *Arthrocnemum*. Many of the species of this period were poorly discriminated, the distinguishing characters being largely vegetative and the species and generic limits vague, for example *Halocnemum sensu* Moquin-Tandon (1840) included species now placed in *Kalidium*, *Haloepelis*, and *Heterostachys*. Moreover *Arthrocnemum* was not clearly differentiated from *Salicornia*.

*Salicornia caspica* Pallas, a large shrubby species from south-west Asia was

next transferred to *Halostachys* by Schrenk (1843), taking up the name of Meyer (1838), together with two further species, *H. songarica* Schrenk, now treated as a synonym of *Halopeplis pygmaea* (Pallas) Bunge ex Ung.-Sternb., and *H. nodulosa* (Delile) Schrenk, a synonym of *Halopeplis amplexicaulis* (Vahl) Ung.-Sternb.

Moquin-Tandon (1849) further examined the group, and described another genus, *Kalidium*, placing the 22 species recognized by him in five genera: *Salicornia*, with six species; *Halocnemum*, with two species; *Halostachys*, with five species; *Arthrocnemum*, with seven species, and *Kalidium*, with two species.

Only the circumscription of *Kalidium* now remains unchanged. Thus by the middle of the 19th century there was no clear concept of the genera in the Salicornieae and hardly any guide to the characters of importance in delimiting species.

The first critical assessment of the characters in the Salicornieae was that of Ungern-Sternberg (1866) who redefined *Arthrocnemum*, transferring several species, including *Salicornia fruticosa* (L.) L. to *Salicornia* subgenus *Arthrocnemoides*, and adding two new genera, *Spirostachys* and *Halopeplis*. The name *Spirostachys* was later rejected since it was a homonym of an earlier name in the Euphorbiaceae, and was replaced by *Heterostachys*. In a subsequent monograph (1876) the anatomy, floral and fruit morphology were dealt with in great detail, and the genera clearly delimited with 25 species placed in eight genera: *Salicornia*, with eight species; *Arthrocnemum*, with six species; *Kalidium*, with four species; *Halopeplis*, with three species; and *Halocnemum*, *Halostachys*, *Heterostachys* and *Microcnemum*, all with one species.

A more natural separation of the genera is evident and to the present day the definition of many genera remains unchanged. In addition *Arthrocnemum* was separated from *Salicornia* by the absence of an endosperm, by the hairy seeds and by the conduplicate embryo present in *Salicornia*.

Three further genera were added, *Allenrolfea* Kuntze (1891) based on the American species, *Halostachys occidentalis* S. Watson, and two Australian genera, *Tecticornia*, based on *Halocnemum cinereum* F. Mueller, and *Pachycornia*, based on *Salicornia robusta* F. Mueller, both by Hooker fil. in Bentham & Hooker fil. (1880).

Ulbrich (1934) in his account of the Chenopodiaceae elevated the tribe Salicornieae to a subfamily, recognizing two tribes, Halopeplideae and Salicornieae, dividing the latter into two subtribes, Halostachyinae and Salicorniinae, based chiefly on the shape of the embryo and the arrangement of the bracts. This classification was accepted by Yale Dawson (1945), but the separation of the two subtribes based on the fusion of the bracts was criticized by Wilson (1972) because both free and connate bracts occur in Australian species of *Arthrocnemum*.

Another genus included by Ulbrich (1934) in the Salicornieae was *Halophytum* Speg. This genus had been described by Spegazzini (1902) to include a single succulent species in South America, based on *Tetragonia ameghinoi* Speg. Soriano (1946) placed this genus in a separate family, Halophytaceae, a view supported by the pollen morphology (Scott, 1975; Nowicke, 1976) and the sieve-tube plastid anatomy (Hunziker, Dietmar-Benke, Eifert & Mabry, 1974) which show that *Halophytum* is not closely related to the Salicorniaceae.

One more genus, *Kalidiopsis*, was added by Aellen (1967a). This was described as differing from *Kalidium* only in that the flowers fall from the axis, while Aellen (1967b) reported that specimens of *Kalidium* available to him had flowers fused to the inflorescence axis. Comparison of specimens of *Kalidium* available with the isotype of *Kalidiopsis wagenitzii* Aellen, the type of the genus, at Edinburgh show that this difference is not consistent and that in both genera the flowers finally fall from the axis of the inflorescence.

As discussed by Ball (1964a) *Salicornia* and *Arthrocnemum* really contain three groups:

Group A e.g. *Salicornia europaea* L.

Group B e.g. *Salicornia fruticosa* (L.) L.

Group C e.g. *Arthrocnemum glaucum* (Delile) Ung.-Sternb.

Group A consists of herbs in which the flowers are unequal in size and arranged in a triangle and the seeds are membranous and hairy without endosperm. Group B resembles Group A in the structure of the seeds but are shrubs with the flowers more or less equal in height. In Group C the flowers are equal in height but are usually hidden by the bracts, and the seeds are glabrous with a crustaceous testa and contain abundant endosperm.

In the original publication of the genus *Arthrocnemum*, Moquin-Tandon (1840) included the names of species now considered to belong to four genera: *Arthrocnemum*, *Halostachys*, *Pachycornia*, and *Sarcocornia*. It is therefore necessary that this genus is lectotypified and in a manner which accords best with Moquin-Tandon's original intention and with current taxonomic practice.

The species included by Moquin-Tandon (1840) in the genus *Arthrocnemum* were: *A. fruticosum* (L.) Moq., *A. ambiguum* (Michx.) Moq., *A. belangerianum* Moq., *A. arbuscula* (R.Br.) Moq., and *A. indicum* (Willd.) Moq. Under *A. fruticosum* he listed three varieties, var. *radicans* (Sm.) Moq., var. *macrostachyum* and var. *glaucum* (Delile) Moq.

In 1849 Moquin-Tandon re-defined the genus and transferred *A. belangerianum* to *Halostachys*. The circumscription was later further modified by Ungern-Sternberg (1866); of the taxa originally included by Moquin-Tandon, only *A. indicum*, *A. arbuscula* (with a query), and *A. fruticosum* var. *macrostachyum*, which he recognized as a distinct species *A. macrostachyum* (Moric.) Bunge ex Ung.-Sternb., were retained. The interpretation of the genus provided by Ungern-Sternberg was followed by Hooker (1880), Volkens (1894), and Ulbrich (1934). This interpretation also agrees well with Moquin-Tandon's generic description which was evidently based largely on the '*macrostachyum*' component. Therefore, as understood by most taxonomists at the end of the 19th century the genus *Arthrocnemum* contained only species belonging to Group C as described above.

The choice of lectotype should be made from the three species retained by Ungern-Sternberg. Of these, *A. arbuscula* was only included with a query; it does not agree with Moquin-Tandon's description, and is now considered to be generically distinct from the other two taxa; it should therefore be excluded from the choice.

The first person to lectotypify the genus appears to have been Standley (1916) who cited as type "*A. fruticosum* Moq.". It is evident that he intended by this *A. fruticosum* [non (L.) Moq.] Moq. since *Salicornia fruticosa* (L.) L.,

which is based on the same type as is *A. fruticosum* (L.) Moq., was included by Standley in the genus *Salicornia* (see also Standley, 1914). This typification was accepted by Ulbrich (1934) with the comment that '*A. fruticosum* Moq.' was a synonym of *A. glaucum* (Delile) Ung.-Sternb.

I consider that the taxa which were included by Moquin (1840) under *A. fruticosum* belong to three species as follows: *A. fruticosum* var. *radicans* (Sm.) Moq., based on *Salicornia radicans* Sm., which is treated here as a synonym of *Sarcocornia perennis* (Miller) A. J. Scott; *A. fruticosum* var. *macrostachyum* (Moric.) Moq. and *A. fruticosum* var. *glaucum* (Delile) Moq., which are both treated as synonyms of *A. glaucum* (Delile) Ung.-Sternb; and *A. fruticosum* (L.) Moq. *sensu stricto* which is transferred to the genus *Sarcocornia*.

Two of the four taxa included by Moquin-Tandon (1840) under the name *A. fruticosum* are thus recognised as being referable to *A. glaucum* and it is this species that both Standley and Ulbrich selected, by implication, as lectotype. This species also agrees well with Moquin-Tandon's original description, which emphasizes the character of abundant endosperm, and with the circumscription usually given to the genus.

In 1954, Moss stated that the type of the genus *Arthrocnemum* is "*A. fruticosum* (L.) Moq.", as did Tölken (1967). This lectotypification is also given in the Index Nominum Genericorum (card no. 10/09162) with a reference back to Ulbrich, but as noted above, this was not Ulbrich's intention.

The erection of *A. fruticosum* as lectotype would make *Arthrocnemum* congeneric with the newly described genus *Sarcocornia*. It would be contrary to the understanding of Moquin-Tandon and Ungern-Sternberg and to the intention of Standley and Ulbrich. Therefore, the lectotype here selected is *A. fruticosum* var. *macrostachyum* (Moric.) Moq. (= *A. glaucum* (Delile) Ung.-Sternb.).

The name *Arthrocnemum* is thus only applied to species belonging to Group C. However, Moss (1954) also included in *Arthrocnemum*, species belonging to Group B, restricting *Salicornia* to annual species. The work of Moss was published posthumously and was in many ways incomplete; several of the characters used by Moss were shown by Dalby (1962) and Ferguson (1964b) to be very variable in British species. However this definition of *Arthrocnemum* and *Salicornia* was that accepted by Ball (1964b) and Tölken (1967). The narrow definition of *Salicornia* is retained here and a third genus, *Sarcocornia*, is described to include species belonging to Group B.

Ball (1964a, b) also recognized that *Salicornia* contained two distinct series of species in Europe, one of which was diploid and the other tetraploid, associated with which were several morphological differences, such as the ability to produce red pigmentation, the number of stamens and the position of the three flowers. In the British Isles, several other characters also appear correlated with this division, such as seed diameter, anther size and pollen diameter (Ball & Tutin, 1959; Ferguson, 1964a). These differences also appear to be consistent in some species examined from Europe, North and South America in which chromosome numbers are not known. These two groups are recognized as the sections, *Salicornia* and *Dolichostachyae*. *Salicornia pusilla*, although a diploid, does not appear to be similar to section *Salicornia* since the flowers are solitary and the stems of the inflorescence disarticulate, and this species is placed in section *Pusillae*.

THE CLASSIFICATION

*Key to the families of the suborder Chenopodiineae*

1. Embryo spiral, endosperm absent. Perianth often accrescent with wings or spines. Flowers usually 1-3, clustered in the axils of leaf-like bracts, rarely ament-like; bracteoles present. Stamens attached to the base of the perianth or on a fleshy ring. Leaves mostly linear to filiform, terete, sometimes scale-like. . . . . Salsolaceae
- 1'. Embryo annular to conduplicate, endosperm usually abundant. Perianth rarely accrescent, or if accrescent with wings or spines then ebracteolate. Flowers usually in spicate or paniculate inflorescences, rarely few in sessile axillary clusters. Stamens free or attached on a membranous, scarious or fleshy disc. Leaves mostly broad, sometimes narrow and fleshy or scale-like. . . . . 2
  2. Free part of leaf reduced to a scale or tubercle. Leaves opposite, connate and articulate or alternate and amplexicaul. Perianth 2-4-lobed, herbaceous or membranous, with 1-2 free stamens, not accrescent in fruit. Flowers ebracteolate, usually in groups of 3, sunk into cavities in the axis of the spicate inflorescences. . . . . Salicorniaceae
  - 2'. Leaves not reduced to tubercles or scales, alternate or opposite, not connate. Perianth mostly 4-5-merous, stamens 5 or fewer, free or often on a disc. Bracteoles present or absent, flowers not sunk into cavities in the axis. . . . . 3
3. Perianth and bracteoles scarious. Staminal disc scarious, often tube-like with staminodes. Ovules 1 or several. Anthers 1 or 2-locular. . . . . Amaranthaceae
- 3'. Perianth herbaceous or membranous, sometimes accrescent and appendaged in fruit. Staminal disc membranous or fleshy, without staminodes, or stamens free. Ovules 1. Anthers 2-locular. . . . . Chenopodiaceae

*Key to the tribes, subtribes, genera and (in Salicornia) sections of the Salicorniaceae*

1. Leaves opposite, connate. Stems articulated. Embryo semi-annular, conduplicate or straight. . . . . tribe Salicornieae. 2
- 1'. Leaves alternate, amplexicaul. Stems entire. Embryo semi-annular. . . . . tribe Halopeplideae. 13
  2. Small shrubs or herbs. Leaf lamina tubercle-like or scale-like. Bracts opposite, free or connate, tubercle-like or scale-like, persistent. . . . . subtribe Salicorniinae. 3
  - 2'. Small trees or shrubs. Leaf lamina scale-like. Bracts spiral or opposite, free, scale-like, deciduous. . . . . subtribe Halostachyinae. 10
3. Flowers exerted from the bracts. Testa membranous, hairy, tubercled, papillose or smooth. . . . . 4
- 3'. Flowers more or less concealed by the bracts. Testa crustaceous, granular or smooth. . . . . 8

4. Annual herbs, all branches ending in an inflorescence. Central flower exceeding the lateral pair forming a triangle, or flowers solitary. . . . . *Salicornia*. 5
- 4'. Perennials with vegetative branches. All flowers more or less equal in height and in a row. . . . . 7
5. Cymes 1-flowered; inflorescence disarticulating. . . . . *Salicornia* section *Pusillae*
- 5'. Cymes 3-flowered; inflorescence not disarticulating. . . . . 6
6. Stamens mostly 1, sometimes not exerted; central flower much exceeding the laterals; anthocyanin commonly produced. . . . . *Salicornia* section *Salicornia*
- 6'. Stamens mostly 2, exerted; central flower not much exceeding the laterals; anthocyanin rarely produced. . . . . *Salicornia* section *Dolichostachyae*
7. Endosperm abundant. Pericarp woody. Lateral flowers staminate, central bisexual. . . . . *Pachycornia*
- 7'. Endosperm absent. Pericarp membranous. Flowers bisexual or pistillate. . . . . *Sarcocornia*
8. Perianth of two succulent segments, free or joined only at the base. Inflorescence of compact, lateral and terminal spikes. . . . . *Tecticornia*
- 8'. Perianth lobes 3-4, connate above the middle. Inflorescence usually of lax terminal spikes. . . . . 9
9. Annual herb. Flowers minute, perianth lobes connate almost to the apex. Flowers free from the axis. . . . . *Microcnemum*
- 9'. Shrubs. Flowers larger, distinctly 3-4-lobed. Flowers partially adnate to the axis. . . . . *Arthrocnemum*
10. Flowers solitary. Perianth segments 4, the two lateral segments much larger than the dorsal and ventral segments. Radicle lateral or ascending. . . . . *Heterostachys*
- 10'. Flowers in groups of 3. Perianth 3-4-lobed. Radicle inferior. . . . . 11
- 11 Perianth 4-lobed. Bracts spiral. Stamens 1-2. . . . . *Allenrolfea*
- 11'. Perianth 3-lobed. Bracts opposite. Stamen 1. . . . . 12
12. Large shrubs or small trees. Perianth segments connate to below the apex, fleshy, membranous in fruit and distinctly 3-angled. . . . . *Halostachys*
- 12'. Small shrubs. Perianth segments connate below the middle, the lateral pair gibbous, green and herbaceous. . . . . *Halocnemum*
13. Perianth tube 3-lobed. Flowers hidden by the ovate, scarious margined bracts, fused to each other and to the bracts. . . . . *Halopeplis*
- 13'. Perianth tube 4-lobed. Flowers sunk in cup-like depressions. Bracts small and herbaceous. . . . . *Kalidium*



*Taxonomic descriptions*

Salicorniaceae J. Agardh, *Theoria Systematis Plantarum*, 357 (1858) (as 'Salicornieae').

Chenopodiaceae tribe Salicornieae Dumortier, *Florula Belgica*, 23 (1827).

Chenopodiaceae subfamily Salicornioideae Ulbrich, in Engler & Harms, *Die Natürlichen Pflanzenfamilien*, ed. 2, 16c, 449, 543 (1934).

Succulent herbs, shrubs or small trees. Leaves opposite, connate and articulated or alternate and amplexicaul, the free lamina very short or tubercle-like. Flowers bisexual and unisexual, sessile, commonly in groups of 3, rarely solitary or up to 12, in the axils of scale-like bracts, without bracteoles, often immersed in the axis of the inflorescence, forming a spike-like thyrs. Perianth segments 2, 3 or 4, usually connate to below the apex, rarely free, herbaceous, membranous in fruit or becoming succulent, spongy or hardened. Stamens 1 or 2, free; anthers 2-celled, unappendaged. Stigmas 2, rarely 3; ovary superior; ovule solitary, attached by a basal funicle or sessile. Pericarp membranous, scarious or thickened. Testa hard or membranous. Seeds vertical, radicle usually inferior; embryo semi-annular, hippocrepiform, conduplicate or straight, endosperm abundant or absent.

*Type. Salicornia* L.

## Tribe Salicornieae

Shrubs or herbs with succulent, articulated stems. Leaves opposite, connate, reduced to tubercles or scales. Flowers bisexual or unisexual, 1-3-12 in spicate inflorescences. Perianth segments initially herbaceous, free or connate. Bracts spiral or opposite, free or connate. Embryo semi-annular, conduplicate or straight.

## Subtribe Salicorniinae

Small shrubs or herbs. Leaves reduced to lobes or absent. Flowers usually in groups of 3, rarely solitary or up to 12, in the axils of short bracts. Bracts opposite, free or connate, persistent, usually forming a spicate inflorescence. Perianth persistent, divided into 2-4 lobes or segments; herbaceous or becoming spongy and adnate to the axis. Embryo hippocrepiform, conduplicate or straight; endosperm abundant or absent.

*Salicornia* L., *Species Plantarum*, 3 (1753).

*Synonym. Belotropis* Rafin., *American Monthly Magazine and Critical Review*, 1: 543 (1817) *nomen nudum*.

Annual leafless herbs, usually erect, not rooting at the nodes. Flowers exserted, usually 3, rarely solitary, arranged in a triangle with the laterals meeting below the central flower. All branches terminating in a spicate inflorescence. Flowers fused to each other and with the bracts, partially immersed in the axis of the inflorescence. Perianth herbaceous, 3-4-lobed, lobes connate almost to the apex, becoming hard and spongy in fruit. Stamens 1-2. Stigmas 2, papillose. Pericarp membranous. Testa membranous, covered with hooked hairs. Embryo conduplicate, endosperm absent.

*Type. Salicornia europaea* L.

About 13 species on coastal salt marshes throughout the world except Australia.

#### Section *Salicornia*

*Synonyms.* *Salicornia* subgenus *Boreali-americana* Ung.-Sternb., *Versuch einer Systematik der Salicornieen*, 52 (1866). *Type.* *Salicornia virginica* Nuttall (= *Salicornia bigelovii* Torrey). *Salicornia* subgenus *Vulgata* Ung.-Sternb., l.c. 43. *Type.* *Salicornia herbacea* L. (= *Salicornia europaea* L.).

Cymes 3-flowered. Inflorescence not disarticulating. Stamens usually 1, anterior, often not exerted. Central flower much exceeding the laterals. Anthers less than 0.6 mm diameter. Pollen 20-31  $\mu\text{m}$  diameter. Seeds (1.0-) 1.2-1.5 (-1.7) mm diameter. Anthocyanin commonly produced. ( $2n = 18$ .)

About six species in Europe, Asia, West Africa, North and South America: *Salicornia europaea* L., *S. bigelovii* Torrey, *S. depressa* Standley, *S. prostrata* Pallas, *S. ramosissima* J. Woods, and *S. rubra* A. Nelson.

#### Section *Dolichostachyae* A. J. Scott sect. nov.

Cyma 3-flora. Inflorescentia non disarticulata. Stamina vulgo duo. Flos centralis flores laterales vix excedens. Anthocyaninium raro evolutum.

Cymes 3-flowered. Inflorescence not disarticulating. Stamens mostly 2, exerted. Central flower not much exceeding the laterals. Anthocyanin rarely produced. Anthers greater than 0.6 mm diameter. Pollen 28-39  $\mu\text{m}$  diameter. Seeds (1.3-) 1.4-2.0 (-2.3) mm diameter. ( $2n = 36$ ).

*Type.* *Salicornia dolichostachya* Moss.

About five species in Europe, East and southern Africa, Madagascar and India: *Salicornia dolichostachya* Moss, *A. fragilis* P. W. Ball & Tutin, *S. meyerana* Moss, *S. nitens* P. W. Ball & Tutin, and *S. pachystachya* Bunge ex Ung.-Sternb.

#### Section *Pusillae* A. J. Scott sect. nov.

Flores solitarii. Inflorescentia disarticulata. Stamen unum. Anthocyaninium evolutum.

Cymes 1-flowered. Inflorescence disarticulating. Stamen solitary, anterior. Anthocyanin usually produced. Anthers less than 0.6 mm. ( $2n = 18$ .)

*Type.* *Salicornia pusilla* J. Woods.

One species in north-west Europe. (*S. uniflora* Tölken from southern Africa may also belong to this section).

#### *Sarcocornia* A. J. Scott gen. nov.

*Synonyms.* *Salicornia* subgenus *Arthrocnemoides* Ung.-Sternb., *Versuch einer Systematik der Salicornieen*, 54 (1866). *Lectotype.* *Salicornia fruticosa* (L.) L. (= *Sarcocornia fruticosa* (L.) A. J. Scott).

*Salicornia* section *Perennes* Duval-Jouve ex Moss, *The Journal of Botany, British & Foreign*, 49: 178 (1911). *Lectotype.* *Salicornia perennis* Miller (= *Sarcocornia perennis* (Miller) A. J. Scott).

Frutex parvus, caules erecti vel prostrati, articulata, succulenti, saepe ad nodos radicanes. Folia opposita, connata, ad tubercula parva deminuta.

Inflorescentiae thrysos spiciformes efformantes, cymae 3-12-florae in axillarum cavitatibus immersae; bracteae lobiformes; bracteolae deficientes; flores aequales, bracteam excedentes. Flores bisexuales vel polygami, omnes raro pistillati. Ovulum unicum, funiculus brevissimus; stigmata 2 vel 3, papillosa vel plumosa. Stamina 1 vel 2. Perianthii tubus in lobos 3 vel 4 divisus, herbaceus, spissescens et semen continens. Pericarpium membranaceum. Testa membranacea, pilis curvatis vel papillis vestita; endospermium nullum; embryo conduplicatus; semen erectum; radícula infera.

A *Arthrocnemum* Moq., seminibus sine endospermio, testa membranacea pilosa, floribus bracteam excedentibus differt. A *Salicornia* L., habitu perenni, floribus aequalibus distinguenda.

*Type.* *Salicornia perennis* Miller, *The Gardeners Dictionary*, ed. 8 (1768).

Small prostrate or erect shrubs with succulent, articulated stems, often rooting at the nodes. Leaves opposite, connate and reduced to small tubercles. Inflorescence a spike-like thyrse of sessile, 3-12-flowered cymes sunk in cavities in the axis, bracts lobe-like; bracteoles absent; flowers of equal height and exserted. Flowers bisexual or polygamous, rarely all pistillate. Ovule solitary on a short funicle; stigma bifid or trifid, papillose or plumose. Stamens 1 or 2. Perianth tube with 3 or 4 lobes, herbaceous, becoming thickened and containing the seeds. Pericarp membranous. Testa membranous, covered with curved hairs or papillose; endosperm absent; embryo conduplicate; seeds vertical, radicle inferior.

Differs from *Arthrocnemum* Moq., in the seeds lacking endosperm with a membranous, hairy testa and the flowers exserted. Differs from *Salicornia* L. in being perennial with the flowers of equal height.

Fifteen species throughout the world.

*Type.* *Sarcocornia perennis* (Miller) A. J. Scott comb. nov.

*Basionym.* *Salicornia perennis* Miller, *The Gardeners Dictionary*, ed. 8 (1768).

*Synonyms.* *Salicornia ambigua* Michaux, *Flora Boreali-Americana*, 1: 2 (1803).

*Salicornia radicans* Sm., *English Botany*, t. 1691 (1807).

*Arthrocnemum ambiguum* (Michaux) Moq., *Chenopodearum Monographica Enumeratio*, 112 (1840).

*Arthrocnemum perenne* (Miller) Moss, *Memoirs Botanical Survey of South Africa*, 20: 20 (1941).

*Arthrocnemum variiflorum* Moss, *The Journal of South African Botany*, 14: 39 (1948).

Distribution: Europe, Africa, and North America.

*Sarcocornia fruticosa* (L.) A. J. Scott comb. nov.

*Basionym.* *Salicornia europaea* L. var. *fruticosa* L., *Species Plantarum*, 3 (1753).

*Synonyms.* *Salicornia fruticosa* (L.) L., *Species Plantarum*, ed. 2, 5 (1762).

*Arthrocnemum fruticosum* (L.) Moq., *Chenopodearum Monographica Enumeratio*, 111 (1840).

*Salicornia peruviana* Kunth, in Humb., Bonpl. & Kunth, *Nova Genera et Species Plantarum*, 2: 193 (1818).

Distribution. Europe, Asia, North and South America.

- Sarcocornia natalensis*** (Bunge ex Ung.-Sternb.) A. J. Scott comb. nov.  
*Basionym.* *Salicornia natalensis* Bunge ex Ung.-Sternb., *Versuch einer Systematik der Salicornieen*, 62 (1866).  
*Synonyms.* *Arthrocnemum natalense* (Bunge ex Ung.-Sternb.) Moss, *The Journal of South African Botany*, 20: 15 (1954).  
*Arthrocnemum africanum* Moss, *The Journal of South African Botany*, 14: 37 (1948).  
*Arthrocnemum affine* Moss, *The Journal of South African Botany*, 20: 8(1954).  
*Distribution.* Southern Africa.
- Sarcocornia mossiana*** (Tölken) A. J. Scott comb. nov.  
*Basionym.* *Arthrocnemum mossianum* Tölken, *Bothalia*, 9: 281 (1967).  
*Distribution.* Southern Africa.
- Sarcocornia terminalis*** (Tölken) A. J. Scott comb. nov.  
*Basionym.* *Arthrocnemum terminale* Tölken, *Bothalia*, 9: 281 (1967).  
*Distribution.* Southern Africa.
- Sarcocornia pillansiae*** (Moss) A. J. Scott comb. nov.  
*Basionym.* *Arthrocnemum pillansii* Moss, *The Journal of South African Botany*, 14: 38 (1948).  
*Synonyms.* *Arthrocnemum dunense* Moss, *The Journal of South African Botany*, 20: 14 (1954).  
*Arthrocnemum hottentoticum* Moss, *The Journal of South African Botany*, 20: 10 (1954).  
*Arthrocnemum namaquense* Moss, *The Journal of South African Botany*, 20: 15 (1954).  
*Distribution.* Southern Africa.
- Sarcocornia xerophila*** (Tölken) A. J. Scott comb. nov.  
*Basionym.* *Arthrocnemum xerophilum* Tölken, *Bothalia*, 9: 286 (1967).  
*Distribution.* Southern Africa.
- Sarcocornia littorea*** (Moss.) A. J. Scott comb. nov.  
*Basionym.* *Arthrocnemum littoreum* Moss, *The Journal of South African Botany*, 14: 38 (1948).  
*Distribution.* Southern Africa.
- Sarcocornia capensis*** (Moss) A. J. Scott comb. nov.  
*Basionym.* *Arthrocnemum capense* Moss, *The Journal of South African Botany*, 14: 38 (1948).  
*Distribution.* Southern Africa.
- Sarcocornia decumbens*** (Tölken) A. J. Scott comb. nov.  
*Basionym.* *Arthrocnemum decumbens* Tölken, *Bothalia*, 9: 293 (1967).  
*Distribution.* Southern Africa.
- Sarcocornia quinqueflora*** (Bunge ex Ung.-Sternb.) A. J. Scott comb. nov.  
*Basionym.* *Salicornia quinqueflora* Bunge ex Ung.-Sternb., *Versuch einer Systematik der Salicornieen*, 59 (1866).

*Synonyms.* *Arthrocnemum heptiflorum* Moss, *The Journal of South African Botany*, 20: 18 (1954).

*Distribution.* Australia, New Zealand.

***Sarcocornia blackiana*** (Ulbrich) A. J. Scott comb. nov.

*Basionym.* *Salicornia blackiana* Ulbrich, in Engler & Harms, *Die Natürlichen Pflanzenfamilien*, ed. 2, 16c: 552 (1934).

*Synonym.* *Salicornia pachystachya* J. M. Black, *Transactions and Proceedings of the Royal Society of South Australia*, 45: 8 (1921).

*Distribution.* South Australia, Victoria, and Tasmania.

***Sarcocornia utahensis*** (Tidest.) A. J. Scott comb. nov.

*Basionym.* *Salicornia utahensis* Tidest., *Proceedings of the Biological Society of Washington*, 26: 13 (1913).

*Distribution.* Utah.

***Sarcocornia pacifica*** (Standley) A. J. Scott comb. nov.

*Basionym.* *Salicornia pacifica* Standley, *North American Flora*, 21: 83 (1916).

*Distribution.* Pacific coast of North America.

***Sarcocornia pulvinata*** (Fries) A. J. Scott comb. nov.

*Basionym.* *Salicornia pulvinata* Fries, *Nova Acta Regiae Societatis Scientiarum Upsaliensis*, 1: 157 (1905).

*Distribution.* Temperate South America.

*Pachycornia* Hooker fil., in Bentham & Hooker fil., *Genera Plantarum*, 3: 65 (1880).

Small succulent shrubs, the leaves reduced to spreading lobes or to a scarious rim. Flowers in groups of 3, equal, in a row, the central flower bisexual, the two laterals staminate, exerted from the bract. Perianth 2-3-lobed, segments connate to below the apex, membranous or succulent. Stamen 1, abaxial. Stigmas 2, stout, triangular. Pericarp woody, enclosing the seed and in some species becoming embedded in the lignified spike axis. Testa membranous, smooth. Embryo hippocrepiform or straight, radicle inferior or lateral, endosperm abundant.

*Type.* *Salicornia robusta* F. Mueller (= *Pachycornia triandra* (F. Mueller) J. M. Black).

Three described species in Australia: *Pachycornia triandra* (F. Mueller) J. M. Black, *P. tenuis* (Bentham) J. M. Black, and *P. arbuscula* (R.Br.) A. J. Scott comb. nov. (*Basionym.* *Salicornia arbuscula* R.Br., *Prodromus Florae Novae-Hollandiae et Insulae Van-Diemen*, 411 (1810)).

*Microcnemum* Ung.-Sternb., in *Atti Congresso Internazionale Botanica in Firenze 1874*, 280 (1876).

An annual herb, much branched with succulent leafless stems. Flowers in groups of 3, minute, hidden by the scale-like bracts, free from the bracts and each other. Central flower bisexual, lateral flowers pistillate. Perianth membranous gamotepalous, shortly 3-4 lobed. Stamen solitary, anterior. Pericarp membranous. Testa crustaceous, granular. Embryo curved, endosperm abundant.

Type. *Microcnemum fastigiatum* Ung.-Sternb. (= *Microcnemum coralloides* (Loscos & Pardo) Font Quer).

A single species in southern Spain, Turkey and Caucasus: *Microcnemum coralloides* (Loscos & Pardo) Font Quer.

*Arthrocnemum* Moq., *Chenopodearum Monographica Enumeratio*, 111 (1840).

Synonym. *Salicornia* section *Arthrocnemum* (Moq.) Duval-Jouve, *Bulletin de la Société Botanique de France*, 15: 170 (1868).

Small perennial shrubs, erect or ascending, not rooting at the nodes. Leaves reduced to small triangular lobes. Flowers in groups of 3, concealed by the small, scale-like bracts. All flowers of equal height, in a row; central flower bisexual, lateral flowers bisexual or staminate. Flowers free or in some species fused to each other and the upper bract. Bracts opposite, usually connate, rarely free. Perianth membranous, connate to below the apex, 3-4 lobed, becoming succulent or spongy in fruit. Stamen solitary, abaxial. Stigmas 2, slender. Pericarp hyaline or woody. Testa crustaceous, granular or smooth. Endosperm abundant, embryo curved or straight.

Lectotype. *Arthrocnemum fruticosum* (L.) Moq., var. *macrostachyum* (Moric.) Moq. (= *Arthrocnemum glaucum* (Delile) Ung.-Sternb.).

Seven species throughout the world: *Arthrocnemum glaucum* (Delile) Ung.-Sternb. in Mediterranean Europe and North Africa; *A. indicum* (Willd.) Moq. in East Africa, India and northern Australia; *A. ciliolatum* Bunge ex Ung.-Sternb. in Timor, Java and Sumbawa; *A. subterminale* (Parish) Standley in California; *A. halocnemoides* Nees, *A. leiostachyum* (Bentham) Paulson, and *A. lylei* (Ewart & C. T. White) J. M. Black in Australia.

*Tecticornia* Hooker fil., in Bentham & Hooker fil., *Genera Plantarum*, 3: 65 (1880).

Annual herbs or short lived shrubs. Leaves reduced to a narrow rim. Flowers in groups of 3, hidden by the scale-like bracts, arranged in compact, terminal and lateral, spicate inflorescences. Bracts opposite, free with fleshy margins. Flowers free, bisexual. Perianth succulent, consisting of 2 more or less free segments, becoming areolate in fruit. Stamen solitary, abaxial. Pericarp membranous. Testa crustaceous, tubercled or smooth. Embryo straight or curved, endosperm abundant.

Type. *Tecticornia cinerea* (F. Mueller) Hooker fil. ex J. M. Black (= *Tecticornia australasica* (Moq.) P. G. Wilson).

Three species in Australia and New Guinea: *Tecticornia australasica* (Moq.) P. G. Wilson, *T. arborea* P. G. Wilson and *T. verrucosa* P. G. Wilson.

Subtribe Halostachyinae Ulbrich, in Engler & Harms, *Die Natürlichen Pflanzenfamilien*, ed. 2, 16C: 449, 545.

Shrubs or small trees. Leaves reduced to triangular scales. Flowers in groups of 3 or solitary, in the axils of short bracts. Bracts opposite or spiral, free, scale-like, deciduous; forming dense, lateral and terminal, spicate inflorescences. Perianth persistent, not united to the axis. Funicle long. Embryo semi-annular, endosperm abundant.

Type. *Halostachys* C. A. Meyer ex Schrenk.

*Halostachys* C. A. Meyer ex Schrenk, *Bulletin de la Classe Physico-Mathématique de l'Académie Impériale des Sciences de St. Petersbourg*, 1: 361 (1843).

Much branched shrub or small tree to 3.5 m with almost leafless stems. Leaves succulent, scale-like. Flowers in groups of 3 in the axils of short, opposite, free, scale-like bracts forming short spicate inflorescences. Perianth 3-lobed, fleshy, membranous in fruit and distinctly 3-angled. Stamen 1, anterior. Stigmas 2, notched. Radicle inferior.

Type. *Halostachys caspica* (Bieb.) C. A. Meyer ex Schrenk.

One species in south-west and central Asia: *Halostachys caspica* (Bieb.) C. A. Meyer ex Schrenk.

*Halocnemum* Bieb., *Flora Taurico-Caucasica*, 3: 3 (1819).

*Sarcathria* Rafin., *Flora Telluriana*, 3: 47 (1837). Lectotype. *Salicornia strobilacea* Pallas.

Small shrub with succulent shoots and obscurely articulated branches. Leaves small, scale-like and succulent, often subtending short globose branches. Flowers 3, rarely 2, in the axils of scale-like, opposite, free bracts, slightly immersed in the axis of the lax spicate inflorescence. Perianth herbaceous, 3-lobed, gamotepalous below the middle, the two lateral segments keeled and slightly exceeding the third. Stamen 1, anterior. Stigmas 2, subulate. Radicle inferior.

Type. *Halocnemum strobilaceum* (Pallas) Bieb.

One species about the shores of the Mediterranean, Red, Caspian and Black Seas: *Halocnemum strobilaceum* (Pallas) Bieb.

*Heterostachys* Ung.-Sternb., *Atti Congresso Internazionale Botanica in Firenze 1874*, 331 (1876).

Synonym. *Spirostachys* Ung.-Sternb., *Versuch einer Systematik der Salicornieen*, 100 (1866). non Sonder (1850). Type. *Spirostachys ritteriana* (Moq.) Ung.-Sternb. (= *Heterostachys ritteriana* (Moq.) Ung.-Sternb.).

Much branched shrubs. Leaves reduced to suborbicular scales. Flowers solitary in the axils of opposite, free, scale-like bracts arranged in short, lateral and terminal spicate inflorescences. Perianth membranous, 4-lobed, the two lateral segments wing-like, exceeding the dorsal and ventral segments. Stamens 2, lateral. Stigmas 2, short. Radicle lateral or ascending.

Type. *Heterostachys ritteriana* (Moq.) Ung.-Sternb.

Two species in South and Central America: *Heterostachys ritteriana* (Moq.) Ung.-Sternb., and *H. olivascens* (Speg.) Molino.

*Allenrolfea* Kuntze, *Revisio Generum Plantarum*, 3: 545 (1891).

Synonym. *Spirostachys* S. Watson, *Proceedings of the American Academy*, 9: 125 (1874), non Ung.-Sternb. (1866).

Much branched, succulent shrubs. Leaves reduced to succulent scales. Flowers in groups of 3, rarely 5, in the axils of succulent, spirally arranged bracts, forming dense terminal spicate inflorescences. Perianth small, 4-lobed, herbaceous. Stamens 1 or 2. Stigmas 2-3, short. Radicle inferior.

Type. *Allenrolfea occidentalis* (S. Watson) Kuntze.

Three species in south-western United States, Central and South America: *Allenrolfea occidentalis* (S. Watson) Kuntze, *A. patagonica* (Moq.) Kuntze, and *A. vaginata* (Griseb.) Kuntze.

Tribe Halopeplideae Ulbrich, in Engler & Harms, *Die Natürlichen Pflanzenfamilien*, ed. 2, 16C: 543.

Low shrubs or herbs, stems entire, leaves alternate, lamina distinct, decurrent or amplexicaul. Flowers bisexual, in groups of 3 in lateral and terminal compact spicate inflorescences. Bracts free, alternate or spiral, scale-like. Perianth segments 3-4, connate to just below the apex; herbaceous, becoming thickened in fruit. Flowers immersed in the fleshy axis of the inflorescence. Stamens 1 or 2, exerted. Funicle long. Endosperm abundant, embryo semi-annular.

Type. *Halopeplis* Bunge ex Ung.-Sternb.

*Halopeplis* Bunge ex Ung.-Sternb., *Versuch einer Systematik der Salicornieen*, 102 (1866).

Herbs or small perennials, with succulent stems. Leaves amplexicaul, reduced to small, succulent scales. Flowers hidden in the axils of ovate, scarious margined bracts. Perianth tube 3-lobed, herbaceous, becoming spongy and hardened in fruit and fused to the bracts and other flowers. Stamens 1 or 2. Pericarp membranous.

Lectotype. *Halopeplis nodulosa* (Delile) Bunge ex Ung.-Sternb. (= *H. amplexicaulis* (Vahl) Bunge ex Ung.-Sternb.).

Three species in Mediterranean Europe, North Africa, South Africa, and Western Asia: *Halopeplis amplexicaulis* (Vahl) Bunge ex Ung.-Sternb., *H. perfoliata* (Forsk.) Bunge ex Schweinf., and *H. pygmaea* (Pallas) Bunge ex Ung.-Sternb.

*Kalidium* Moq., in DC., *Prodromus Systematis Naturalis Regni Vegetabilis*, 13/2: 146 (1849).

Synonym. *Kalidiopsis* Aellen, *Notes from the Royal Botanic Garden Edinburgh*, 28: 31 (1967). Type. *Kalidiopsis wagenitzii* Aellen (= *Kalidium foliatum* (Pallas) Moq.).

Small shrubs with succulent branches. Leaves decurrent, free lamina short, succulent. Flowers sunk into cup-like depressions in the axis of the spicate inflorescence, from which they fall at maturity. Perianth tube 4-lobed, herbaceous, becoming hardened in fruit. Stamens 2. Pericarp membranous.

Type. *Kalidium foliatum* (Pallas) Moq.

Five species in Mediterranean Europe, west and central Asia: *Kalidium foliatum* (Pallas) Moq., *K. caspicum* (L.) Ung.-Sternb., *K. cuspidatum* (Ung.-Sternb.) Grubov, *K. gracile* Fenzl, *K. schrenkianum* Bunge ex Ung.-Sternb.

#### ACKNOWLEDGEMENTS

I am grateful to Dr J. T. Williams for guidance and encouragement, to Mr P. G. Wilson for reading this manuscript and providing additional information,



to the Director of the Royal Botanic Gardens, Kew for the use of the Herbarium and Library, to Drs I. K. Ferguson and H. R. Tölken for helpful discussions, and to Mr H. K. Airy Shaw for correcting the latin descriptions. This work was supported by a Science Research Council Research Studentship.

## REFERENCES

- AELLEN, P., 1967a. New Chenopodiaceae from Turkey. *Notes from the Royal Botanic Garden Edinburgh*, 28: 29-34.
- AELLEN, P., 1967b. Chenopodiaceae, In P. H. Davis (Ed.), *Flora of Turkey*, 2: 294-339. Edinburgh: Edinburgh University Press.
- AGARDH, J. G., 1858. *Theoria Systematis Plantarum*. Lund.
- BACKER, C. A., 1949. Chenopodiaceae. In C. G. G. J. Van Steenis (Ed.), *Flora Malesiana*, 4: 99-106. Djakarta: Noordhoff-Kolff N.V.
- BALL, P. W., 1964a. A taxonomic review of *Salicornia* in Europe. *Feddes Repertorium*, 69: 1-8.
- BALL, P. W., 1964b. *Salicornia*. In T. G. Tutin *et al.* (Eds), *Flora Europaea*, 1: 101-102. Cambridge: Cambridge University Press.
- BALL, P. W. & TUTIN, T. G., 1959. Notes on annual species of *Salicornia* in Britain. *Watsonia*, 4: 193-205.
- BENTHAM, G. & HOOKER, J. D., 1880. Chenopodiaceae, in *Genera Plantarum*, 3: 43-78. London: Lovell Reeve, Williams & Norgate.
- BIEBERSTEIN, F. A. M., 1819. *Flora Taurico-Caucasica*. Charkov.
- BISALPUTRA, T., 1961. Anatomical and morphological studies in the Chenopodiaceae. III. The primary vascular system and nodal anatomy. *Australian Journal of Botany*, 10: 13-24.
- CAROLIN, R. C., JACOBS, S. W. L. & VESK, M., 1975. Leaf structure in Chenopodiaceae. *Botanische Jahrbücher*, 95: 226-255.
- COOKE, F. W., 1911. Observations on *Salicornia australis*. *Transactions and Proceedings of New Zealand Institute*, 44: 349-362.
- DALBY, D. H., 1962. Chromosome numbers, morphology and breeding behaviour in the British Salicorniae. *Watsonia*, 5: 150-162.
- DE FRAINE, E., 1912. The anatomy of the genus *Salicornia*. *Journal of the Linnean Society (Botany)*, 41: 317-348.
- DUMORTIER, B. C., 1827. *Flora Belgica*. Tournai.
- DUVAL-JOUVE, M. J., 1868. Des *Salicornia* de l'Hérault. *Bulletin de la Société Botanique de France*, 15: 164-178.
- FAHN, A., 1963. The fleshy cortex of articulated Chenopodiaceae. *Journal of Indian Botanical Society*, 42a: 39-45.
- FAHN, A. & ARZEE, T., 1959. Vascularization of the articulated Chenopodiaceae and the nature of their fleshy cortex. *American Journal of Botany*, 46: 330-338.
- FERGUSON, I. K., 1964a. *A study of the taxonomy of Salicornia L. in Ireland*. Unpubl. thesis, Dublin.
- FERGUSON, I. K., 1964b. Notes on the stigma morphology and flowering behaviour in British Salicorniae. *Watsonia*, 6: 25-27.
- HALKET, A. C., 1928. The morphology of *Salicornia*—an abnormal plant. *Annals of Botany, London*, 42: 525-530.
- HUNZIKER, J. H., DIETMAR-BENKE, H., EIFERT, I. J. & MABRY, T., 1974. *Halophytum ameghinii*: a betalain containing and P-type sieve-tube plastid species. *Taxon*, 23: 537-539.
- JAMES, L. E. & KYHOS, D. W., 1961. The nature of the fleshy shoot of *Allenrolfea* and allied genera. *American Journal of Botany*, 48: 101-108.
- KELLER, B. A., 1951. Extreme salt resistance of higher plants in nature and the problem of adaptation. In *Selected Works*: 212-236. Akad. Nauk S.S.S.R., Moskva.
- KUNTZE, O., 1891. *Revisio Genera Plantarum vascularium omnium*, 2. Leipzig.
- LEYSLEY, F. F., 1949. On the ecology and anatomy of halophytes and xerophytes with reduced leaves. *Botanicheskii Zhurnal SSSR*, 34: 253-266.
- MERRILL, E. D., 1949. *Index Rafinesquianus*. Massachusetts: The Arnold Arboretum of Harvard University.
- MEYER, C. A., 1838. Enumeratio plantarum provinciae talysch et regionum adjacentium. *Bulletin de la Société Impériale des Naturalistes du Moscou*, 11: 239-414.
- MOQUIN-TANDON, A., 1840. *Chenopodearum Monographica Enumeratio*. Paris.
- MOQUIN-TANDON, A., 1849. Salsolaceae. In A. De Candolle, *Prodromus Systematis Naturalis Regni Vegetabilis*, 13.2: 41-219. Paris.
- MOSS, C. E., 1954. The species of *Arthrocnemum* and *Salicornia* in Southern Africa. *Journal of South African Botany*, 20: 1-22.
- NOWICKE, J. W., 1976. Pollen morphology in the order Centrospermae. *Grana*, 15: 51-77.

- RAFINESQUE, C. S., 1837. *Flora Telluriana*. Philadelphia.
- SCHRENK, A., 1843. Chenopodiaceae staticesque novae vel nondum descriptae, quas in itinere ad fluvium Tschu versus. *Bulletin de la Classe Physico-Mathématique de l'Académie Impériale des Sciences de St. Petersbourg*, 1: 360-362.
- SCOTT, A. J., 1975. *The Systematics of the Chenopodiaceae*. Unpubl. thesis, Birmingham.
- SCOTT, A. J., 1977. Proposal to conserve the family name Salsolaceae Moq. *Taxon*, 26: 246.
- SORIANO, A., 1946. Halophytaceae nueva familia del Order Centrospermae. *Notas del Museo de la Plata*, 11: 161-175.
- SPEGAZZINI, C., 1902. Nova addenda ad floram Patagonicam III. *Anales del Museo Nacional de Buenos Aires*, 7: 137-154.
- STANDLEY, P. C., 1914. The genus *Arthrocnemum* in North America. *Journal of Washington Academy of Sciences*, 4: 398-399.
- STANDLEY, P. C., 1916. Chenopodiaceae, in *North American Flora*, 21: 1-93. New York.
- TÖLKEN, H. R., 1967. The species of *Arthrocnemum* and *Salicornia* in Southern Africa. *Bothalia*, 9: 225-307.
- ULBRICH, E., 1934. Chenopodiaceae. In A. Engler & H. Harms (Eds), *Die Natürlichen Pflanzenfamilien*, ed. 2, 16c: 375-584. Berlin: Wilhelm Engelmann.
- UNGERN-STERNBERG, F., 1866. *Versuch einer Systematik der Salicornieen*. Dorpat.
- UNGERN-STERNBERG, F., 1876. *Salicornearum Synopsis*. In *Atti Congresso Internazionale Botanica in Firenze 1874*, 259-543. Florence.
- VOLKENS, G., 1893. Chenopodiaceae. In A. Engler & K. Prantl (Eds), *Die Natürlichen Pflanzenfamilien*, ed. 1, 3.1a: 36-91. Berlin.
- WILLIAMS, J. T. & FORD-LLOYD, B. V., 1974. The Systematics of the Chenopodiaceae. *Taxon*, 23: 353-354.
- WILSON, P. G., 1972. A taxonomic revision of the genus *Tecticornia* (Chenopodiaceae). *Nuytsia*, 1: 277-288.
- YALE DAWSON, E., 1945. Introduction to Salicornieae. *Desert*, 17: 37-43.