The ecology and identification of the southern African Salicornieae (Chenopodiaceae)

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The Salicornieae is represented in southern Africa by three genera: *Sarcocornia* A.J. Scott (nine species), *Salicornia* L. (four species) and *Halosarcia* P.G. Wilson (one species). Approximately 500 specimens of this tribe from the four major herbaria in South Africa (STE, BOL, NBG, PRE), as well as living populations, were examined. The peculiar anatomy, morphology, habitat and ecological features are discussed. Keys based on morphological and habitat characters are presented to facilitate identification. Many of the specimens were previously incorrectly identified and a relatively high proportion were hybrids.

In suidelike Afrika word die Salicornieae verteenwoordig deur drie genera: *Sarcocornia* A.J. Scott (nege spesies), *Salicornia* L. (vier spesies) en *Halosarcia* P.G. Wilson (een spesie). Ongeveer 500 eksemplare van die vier hoofherbaria in Suid-Afrika (STE, BOL, NBG, PRE), asook lewende populasies, is bestudeer. Die besonderse anatomiese, morfologiese, habitat- en ekologiese eienskappe word bespreek. Sleutels gebaseer op morfologiese en habitatkenmerke word aangebied. 'n Groot aantal van die eksemplare is voorheen verkeerd geïdentifiseer en 'n relatief hoë proporsie is hibriedes.

Keywords: Chenopodiaceae, *Sarcocornia, Salicornia, Halosarcia*, identification, ecology.

Introduction

The taxonomy and identification of the Salicornieae have proved to be difficult since the last century (Moquin 1840). The South African species were revised by Moss (1948, 1954) to include two genera: *Arthrocnemum* Moq. (15 species) and *Salicornia* L. (2 species). The taxonomic history and validity of the specific concepts were discussed by Tölken (1967) in his review of the South African species of *Arthrocnemum* (10 species) and *Salicornia* (three species).

Tölken's concept of *Arthrocnemum indica* (Willd.) Moq. was placed in the genus *Halosarcia* P.G. Wilson by Wilson (1980) by virtue of the absence of sclereids in the palisade tissue and the adaxial position of the stamen. The remaining nine species of *Arthrocnemum* were placed in the genus *Sarcocornia* A.J. Scott by Scott (1977) on the basis of membranous or hairy testa and the absence of endosperm in the seed.

Brenan (1988) described *Sarcocornia mossambicensis* Brenan whose distribution seems to be restricted to the Mozambique coast. However, this new species is similar to *Sarcocornia perennis* (Mill.) A.J. Scott and some specimens of *S. perennis* from the northern Natal coast, might in fact be *S. mossambicensis*. I have not seen specimens which have been definitively identified as *Sarcocornia mossambicensis* and, as it seems to have a very restricted distribution, I have not included it in the present study.

Tölken (1967) discussed two forms of *Salicornia pachystachya* Bunge ex Ung.-Sternb. The first has an erect habit with all branches ending in a spike which is 20 – 30 (50) mm long. The second has a nearly decumbent habit and flowers appear first at the end of the main branch. Flowers may appear later or not at all on the lower branches. The flowering spikes are 20 – 50 (80) mm long. This second form was recognized as a distinct species by Brenan (1988), although he did state that this taxon (*Salicornia perrieri* A. Chev.) was unsatisfactory and further study was required.

A number of criticisms might be raised regarding these taxonomic developments. For example, the stem anatomy of *Halosarcia indica* is different to all the other Salicornieae, whereas the absence of sclereids and the covering of the flowers by the subtending bract place this species close to *Sarcocornia natalensis* Bunge ex Ung.-Sternb. Furthermore, the distinction of *Sarcocornia mossambicensis* from *S. perennis* is based on a difference in hairiness of the seed testa and a tapering as opposed to non-tapering inflorescences. In my experience, these degree differences are not easily distinguished.

This study is not an attempt to revise these taxa, rather it is an attempt to facilitate their identification. This is to be achieved through a practical key which highlights the morphological and ecological features which are useful in identifying the Southern African Salicornieae. For this purpose it is assumed that the taxa are acceptable and, notwithstanding subsequent taxonomic developments, the specimens identified by Tölken (1967) for his study are correctly named and can be used as reference.

Anatomy, morphology and ecology

Superficially, the Salicornieae appear to have succulent, jointed, leafless stems containing chlorophyll. The flowers are small, inconspicuous and sessile, subtended by a bract, and usually occur in groups of three or more. Inflorescence, perianth, stamens and ovaries do not have a high taxonomic value as there is little variation between the species. Stigma and seed characters are more useful, but these are easily lost or destroyed in specimen preparation.

These plants are usually found in wetland habitats which are highly stressful and unpredictable environments. The different species show similar adaptations to the environmental stresses, but must remain plastic to survive the variability. As a result, the species are similar in appearance and

the morphology of each species is highly variable.

Furthermore, these species hybridize easily. Tölken (1967) recorded 24 putative hybrids between 8 species of *Sarcocornia*.

Flowering is often dependent on environmental factors. Each species generally has a four to six month flowering period, usually during summer to autumn. However, the flowering period of a particular population may be relatively short, depending on the occurrence and duration of conditions favourable for flowering. For example, an estuary mouth might remain closed during most of the flowering season resulting in the vegetation being flooded and not being able to flower. Only if the floodwaters recede for some reason will the vegetation be induced to flower. Favourable flowering conditions might prevail for a short period only, might occur out of normal flowering season, or might not occur for a number of years.

Salicornia, Sarcocornia and *Halosarcia* (to a lesser extent) are cosmopolitan genera. Most of the species are sympatric with wide dibtribution ranges. However, each species is restricted to a particular habitat, a feature which can assist in identification. Unfortunately, taxonomic literature seldom defines these habitats to the degree that is required for recognition in the field.

Floral features form the basis of most taxonomic keys. However, the floral anatomies of many of the Salicornieae are similar and seed, morphological and anatomical characters are also used (Brenan 1988; Tölken 1967; Wilson 1980, 1984). Because many of the specimens in herbaria lack flowers, these keys are not always easily applied. For this reason, Tölken (1967) produced a second key based on vegetative and anatomical features. These keys are not easy to use owing to difficulty in obtaining information about the specimen (*e.g.* the presence or absence of sclereids in the palisade tissue and their features) or because of poorly defined terms.

Terminology

The Salicornieae have a peculiar anatomy and some of the descriptive terms are confusing. The succulent parts of these plants are jointed and divided into longitudinal segments containing chlorophyll. Although a number of theories have been proposed for the origin of this photosynthetic material, it is generally accepted as foliar in origin (Scott 1977; Tölken 1967). It seems that these segments represent inverse, dorsi-ventrally opposite leaves which have enlarged and fused laterally. The abaxial sides of the leaves have expanded vertically to cover the entire internode (Tölken 1967). The adaxial side of this structure is fused to the stem. In other words, the bottom surface of what is normally understood to be the leaf has turned uppermost and fused with the stem. The lateral margins of each leaf have fused with their opposite counterparts, thus forming a cylinder. The palisade tissue is situated to the outside of this cylinder. This cylinder has elongated down the stem to cover the space between each set of leaves.

The apex of each leaf can be distinguished as it usually overlaps the base of the succeeding segment. Two lateral ridges often run down the segment, one from the centre of each apex. This ridge may be pronounced to form a distinct keel just below the apex, or may be poorly developed and not distinguishable in dried material. It can, however, usually be distinguished as a colourless line in fresh material (Figure 1).

In some species, the older segments die. These dead segments may remain attached to the plant or may be lost. In herbarium material, distinction must be made between dead leaves (those that died prior to sampling) and dried leaves. Aerial parts of the plant that do not have succulent leaf sheaths are referred to as stems.

The inflorescence, in the form of a spike, consists of numerous bracts which are anatomically similar to the leaves, although usually shorter. A cymule, consisting of usually three or more flowers, is found in the axil of each bract (Figure 1).

Methods

Of 507 specimens from four of the major herbaria in South Africa (BOL, NBG, PRE, STE), 230 had been identified by Tölken for his revision (Tölken 1967). The morphology, habit, habitat and distribution of these 230 specimens were carefully studied and a tentative key was compiled. All the remaining specimens were identified according to this tentative key. Of these remaining specimens, the identity of 67 were deemed tentative owing to poor specimens and 220 were selected and identified using Tölken's (1967) keys as a test of the above-mentioned tentative key.

To study sclereids in the palisade tissue, Tölken (1967) recommended the use of hand-cut sections. However, I found that the sclereids were extremely difficult to observe in hand-cut sections. A freezing microtome was therefore used to make 200 μm thick cross- and longitudinal sections

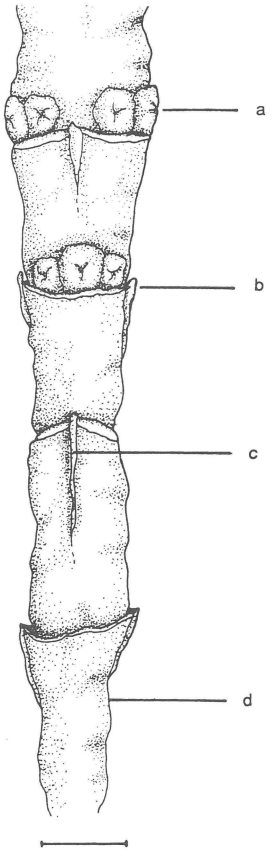

Figure 1 Herbarium material of *Sarcocornia* showing (a) cymule consisting of 3 flowers, (b) leaf apex, (c) keel and (d) segment (scale bar, 10 mm).

of the segments after samples of the dried specimens had been soaked in a 30% alcohol solution for seven days. Staining was not necessary.

Results and Discussion

From the work of the authors quoted above it is realized that of the 15 species in southern Africa, only 11 are common in the temperate regions. *Halosarcia indica, Sarcocornia mossambicensis, Salicornia pachystachya* and *Salicornia perrieri* are primarily tropical plants. If found in South Africa, they would be restricted to the extreme northern Natal coast.

When identifying southern African Salicornieae, the first problem encountered is the distinction between the genera. Of the specimens studied, four were found to be incorrectly placed in the genus *Sarcocornia* and six in the genus *Salicornia*. A total of 10 specimens (4.5 percent) had been identified as the wrong genus.

Salicornia

In southern Africa, all the species of *Salicornia* have an annual life-cycle whereas all the *Sarcocornia* and *Halosarcia* species are perennial. *Salicornia* consequently do not form adventitious roots. Usually the whole *Salicornia* plant, together with a short tap root, is collected as a specimen.

Morphologically, the *Salicornia* form two distinct groups: *S. pachystachya* and *S. perrieri* are robust whereas *S. meyeriana* and *S. uniflora* have a more delicate appearance. With the exception of *S. perrieri*, all the branches end in spikes. In the younger stages, *Salicornia* tends to have a distinct twist at the base of the main stem and the plants usually turn red and die in late summer to autumn.

Salicornia pachystachya Bunge ex Ung.-Sternb. and *S. perrieri* A. Chev.

These are both woody shrublets and were regarded by Tölken (1967) as being only different forms of *S. pachystachya* or possibly, *S. perrieri* was a hybrid of *S. pachystachya*. Brenan (1988) regarded *S. perrieri* as an unsatisfactory taxon.

The two species can be distinguiushed firstly by their habit. *S. pachystachya* grows up to 400 mm tall with suberect lateral branches forming an angle of less than 45° with the main stem. The main stem is longer than the lateral branches. *S. perrieri* has a more decumbent habit, it is more branched and the lateral branches are often taller than the main stem. Secondly, all the branches of *S. pachystachya* end in flowering spikes which become thickened and cork-like when fruiting. When dried, the inflorescence maintains a regular appearance and is cylindrical with a blunt end. In contrast, the inflorescence of *S. perrieri* also becomes thickened, but not as much as that of *S. pachystachya*. In dried material, the inflorescence of *S. perrieri* does not maintain its regular appearance and it tapers far more than that of *S. pachystachya*. Furthermore, not all the branches of *S. perrieri* end in spikes. The inflorescences on the branches near the top of the main stem develop in June. Inflorescences on the lower branches may develop later or not at all.

Both species occur along the tropical East African and Madagascan coasts, but *S. perrieri* mainly in the southern parts. *S. pachystachya* may be found in the mangroves and in the salt-marsh patches which develop amongst the mangroves, whereas *S. perrieri* does not seem to enter the mangrove itself. *S. perrieri* also seems to be found in slightly wetter areas. Neither of these species is common in South Africa, being restricted to the sub-tropical northern Natal coast.

Illustrations may be found in the article by Brenan (1988).

Salicornia meyeriana Moss and *S. uniflora* Toelken

Although *S. meyeriana* can reach at height of 400 mm, it is scarcely woody. These two species can easily be separated from each other when in flower. *S. uniflora* has only one flower per cymule. *S. meyeriana* has three flowers per cymule. However, care must be taken as the central flower in *S. meyeriana* is usually much larger than the lateral flowers. These lateral flowers often meet behind and can be hidden by the large central flower.

Distinction between these two species is more difficult in the vegetative state. *S. meyeriana* grows taller than *S. uniflora*. The main branches of *S. meyeriana* are erect and the secondary branches arise at an acute angle to the main branches. These secondary branches tend to spread and are longer than the main stem. This results in an ovoid to narrowly ovoid shape of the plant, particularly noticeable in younger stages. In *S. uniflora*, the lateral branches do not arise at an acute angle, do not spread and are fastigiate, giving an obconical shape to the plant (Figure 2). Furthermore, the segments of *S. uniflora* have a fairly distinct keel and lateral ridge whereas the keel of *S. meyeriana* is faint or absent. In fresh material, distinction is possible because the stomata of *S. meyeriana* protrude whereas those of *S. uniflora* are sunken.

S. meyeriana is common along the coast from Vanrhynsdorp to Durban and is occasionally found inland. *S. uniflora*

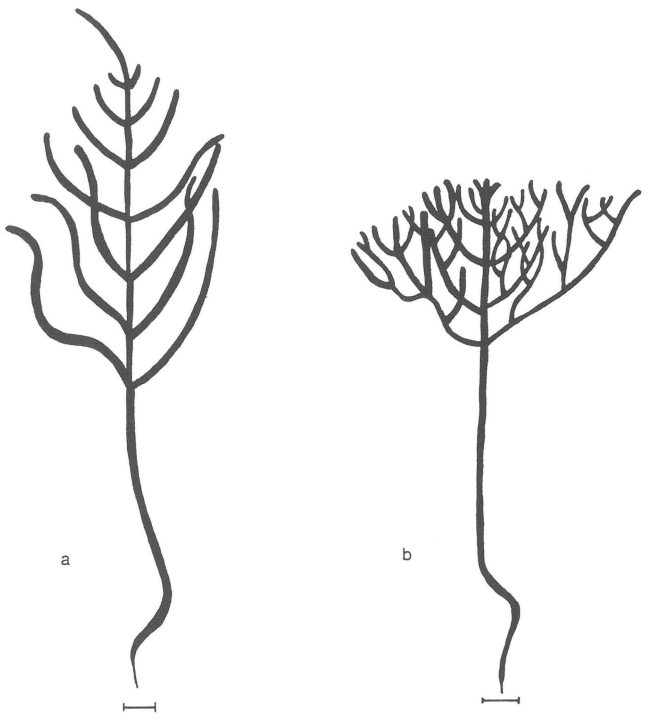

Figure 2 (a) *Salicornia meyeriana* and (b) *Salicornia uniflora* showing different habits (scale bar, 10 mm).

is less common and is restricted to Lüderitz Bay and the Malmesbury district. The habitat of both species is similar: open or disturbed areas in the middle reaches of the marshes in estuaries or around vleis. *S. uniflora* does not seem to tolerate salt concentrations as high as those tolerated by *S. meyeriana*.

Halosarcia

With flowering material, *Halosarcia indica* is easily distinguished from the *Sarcocornia* species. The cymule is covered by the lower bract which is similar to the situation in *Sarcocornia natalensis*. However, the flowers of *H. indica* are usually well fused with both the lower and upper segments. The seeds are glabrous and fruits are only released once the segments decay. The flowers of *S. natalensis* are not fused with the segments, the seeds are papillose and fall easily from the inflorescence. With non-flowering material, this species is easily distinguished from *Sarcocornia* by the unique segment anatomy [as described by Tölken (1967) and Wilson (1980)].

Failing access to anatomical features, *H. indica* might be deemed similar to *S. perennis*. They are ecologically very similar: both are found on intertidal mudflats and show similar morphological features. Both form decumbent mats, but the *H. indica* mats are open with individuals about 600 mm in diameter. The individuals of *S. perennis* are much smaller and many individuals grow together to form dense mats. The older segments of both species adhere to the plants, become slightly corky with age and later disintegrate. However, the segments of *H. indica* are keeled with a lateral ridge, those of *S. perennis* are only faintly keeled.

The inflorescence of *H. indica* is corky and broader than the barren segments below. This is similar to *S. decumbens*. However, in *H. indica*, it is the flowering segments (bracts) which are cork-like whereas in *S. decumbens*, it is the perianth lobes which are corky. The inflorescence of *H. indica* disintegrates with just the corky segments remaining to form separated discs around the central stem. The apices are clearly seen as points on the upper edge of the segment. Furthermore, *H. indica* has 3 flowers per cymules whereas *S. decumbens* has up to 9 flowers per cymule.

H. indica is found in tropical areas around the Indian Ocean, including Australia and the east coast of Africa. In South Africa, it might be found on the Northern Natal coast.

Illustrations may be found in the article by Brenan (1988).

Sarcocornia

The species of *Sarcocornia* can be identified according to their habitat and the shape of the leaves after pressing and drying. However, the habitat is often not easily discernable from the literature or is difficult to recognize in the field. Furthermore, many of the species are rather variable, particularly *S. natalensis* (Bunge ex Sternb.) A.J. Scott and *S. pillansii* (Moss) A.J. Scott. For this reason other characters need also to be taken into account.

Of the 220 specimens studied (*i.e.* those not identified by Tölken), 147 (66.8%) had been placed in the incorrect genus and 42 (19.1%) had not been identified to the species level.

1. *Sarcocornia mossiana* (Toelken) A.J. Scott

This is a woody shrub up to 500 mm tall and one of the most distinctive species. The segments are very short (2 – 3 mm long) with a distinct keel. The apices are widely spread to give a fine thorny appearance to the plant. The distal edge of the segment is concave and gives a champagne-glass appearance to the dried segment (Figure 3a). The dead leaves do not adhere to the stems which are often laterally compressed. The bark is rough which gives a gnarled appearance to the stems.

This species has only been recorded between Caledon and

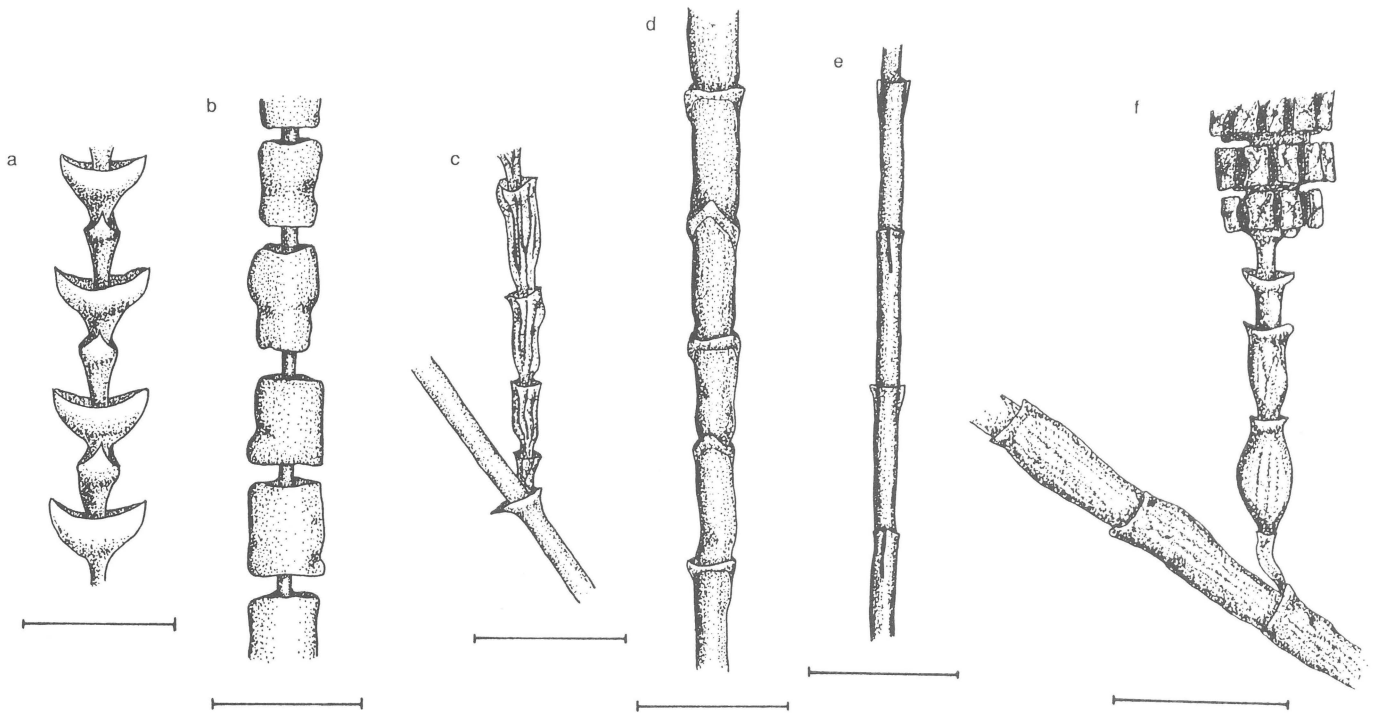

Figure 3 Details of herbarium material of (a) *Sarcocornia mossiana*, (b) *Sarcocornia xerophila*, (c) *Sarcocornia terminalis*, (d) *Sarcocornia littorea*, (e) *Sarcocornia capensis*, and (f) *Sarcocornia decumbens* (scale bar, 10 mm).

Riversdale. It is not found in maritime marshes and cannot withstand high salinities. It occupies the highest zone in inland marshes and along river banks.

2. *Sarcocornia xerophila* (Toelken) A.J. Scott

This fairly distinctive species forms a shrub up to 500 mm tall. The dead leaves do not adhere to the stems which, although rough, are not laterally compressed. The distinctive feature is the way the segments shrink to form short (5 – 7 mm long, 4 – 6 mm broad) discs or cylinders between which the stem can be seen (Figure 3b).

This is the only species in South Africa which is not found in moist areas, but rather on dry rocky slopes in the Knersvlakte of the Vanrhynsdorp district. It also flowers early in the summer season, between September and October.

3. *Sarcocornia terminalis* (Toelken) A.J. Scott

This shrub grows up to 1 m tall. The apices of the narrow (2 – 3 mm broad) segments spread much like *S. mossiana*, but the segments are much longer (5 – 12 mm long). When dried, these segments tend to shrink in a regular way showing faint longitudinal grooves (Figure 3c). Although the main branches may be erect or decumbent, the lateral branches are always erect and fastigiate. The name refers to the flowering spikes which are consistently terminal on secondary branches.

This is an uncommon shrub found high on river banks in Namaqualand, above the *S. pillansii* zone. *S. terminalis* can easily be confused with *S. pillansii*, but may be distinguished by its consistently terminal spikes (*S. pillansii* has lateral and terminal spikes) and the cylindrical shape of the spikes (*S. pillansii* has tapering spikes).

4. *Sarcocornia littorea* (Moss) A.J. Scott

This species reaches a height of 1 m and has numerous erect woody stems. It is distinctive as it is restricted to rocky shores along the southern and south-western Cape coast, extending into Namaqualand. It is often exposed to salt spray and may even become inundated at extremely high tides. One exeption has been found [also mentioned by Tölken (1967)] on the western shores of Langebaan Lagoon where this species grows on the upper marsh with *S. pillansii* [possible reasons for this exception are discussed by O'Callaghan (in prep. a)]. The dead leaves do not adhere to the stems which are relatively thick (30 – 80 mm at the base, rarely laterally compressed, and with a smooth light-coloured bark. The secondary branches are fastigiate giving a truncate appearance to the whole plant. The leaf segments are restricted to the upper 200 mm and dry to a light-green to light-yellow colour with apices that tend to spread (Figure 3d).

5. *Sarcocornia capensis* (Moss) A.J. Scott

S. capensis is a decumbent or prostrate species which forms dense mats or irregular rosettes up to 250 mm tall. It often roots at the nodes and dead leaves adhere to the stems. The distinctive feature of this species is the thin tough branches with distinctly keeled leaf apices. The segments are long (10 – 16 mm), thin (2 – 3 mm), and cylindrical. When prepared as a herbarium specimen, the segments usually do not flatten. The segments have a somewhat formal or regular appearance and often have a reddish tinge (Figure 3e).

S. capensis grows in sandy soils along the banks of rivers or vleis where there is very little salt. It is found mainly in the vicinity of Cape Town (Noordhoek, Rondevlei, Milnerton, Mamre and Kuils River), but isolated patches have been found along the southern Cape coast (Uilkraals River and Port Elizabeth).

6. *Sarcocornia decumbens* (Toelken) A.J. Scott

Although this shrub mainly has a decumbent growth form, it can attain a height of 500 mm. The main stems are fairly thick (up to 15 mm), erect and not laterally compressed. The old leaves adhere to the stems and often become thickened or corky. The apices of the young leaves tend to spread slightly on drying to give a long funnel-shaped appearance with a fairly distinct keel. The older segments are cylindrical, or barrel-shaped when corky (Figure 3f).

The most distinctive feature of this species is the flowering spike which is much broader than the barren segment below and the perianth which becomes corky. There can be up to nine flowers per cymule (as opposed to three for all other species). Without flowering material, dried specimens superficially resemble decumbent forms of *S. natalensis* or *S. pillansii*. However, leaves are never pressed completely flat (as in *S. natalensis*) and the distal ends of the segments do not have a gondola shape (as in *S. pillansii*). Furthermore, *S. decumbens* is restricted to the south and east coast in coastal lagoons and the mid to upper levels of estuarine marshes. Its distribution, therefore, does not overlap with the very corky varieties of *S. natalensis* and *S. pillansii*.

The remaining three species are the most common and widely distributed. The environmental conditions in which they grow vary, resulting in a variable morphology. A second variety for each of these species was recognized by Tölken (1967) under *Arthrocnemum* to account for the extreme of this variation. These varieties have been transferred to the genus *Sarcocornia* by O'Callaghan and Oliver (1992).

7. *Sarcocornia perennis* (Mill.) A.J. Scott

This is the species which is most common in the intertidal areas in maritime marshes. It usually has a long decumbent main stem which roots at the nodes. The secondary branches are up to 200 mm long and arise in pairs from swollen nodes. In very wet areas, the plants are often more prostrate and rosette-shaped, *i.e.* without a single main stem. The stems are then very thin (1 mm) with segments only near the ends of the branches. The segments are barrel-shaped to obconical. The older leaves adhere to the secondary branches, but soon disintegrate. The segments tend to become corky in drier areas or further up the shore (Figure 4b).

According to Tölken (1967), one of the important features of this species is spirally thickened sclereids in the palisade tissue. However, he briefly mentioned one specimen which did not seem to have sclereids and was 'probably a plant grown under very moist conditions' (p.269). Sclereids were absent in many of the *S. perennis* specimens investigated in the present study. The majority of these were from marshes in the Langebaan area which are flooded almost twice daily.

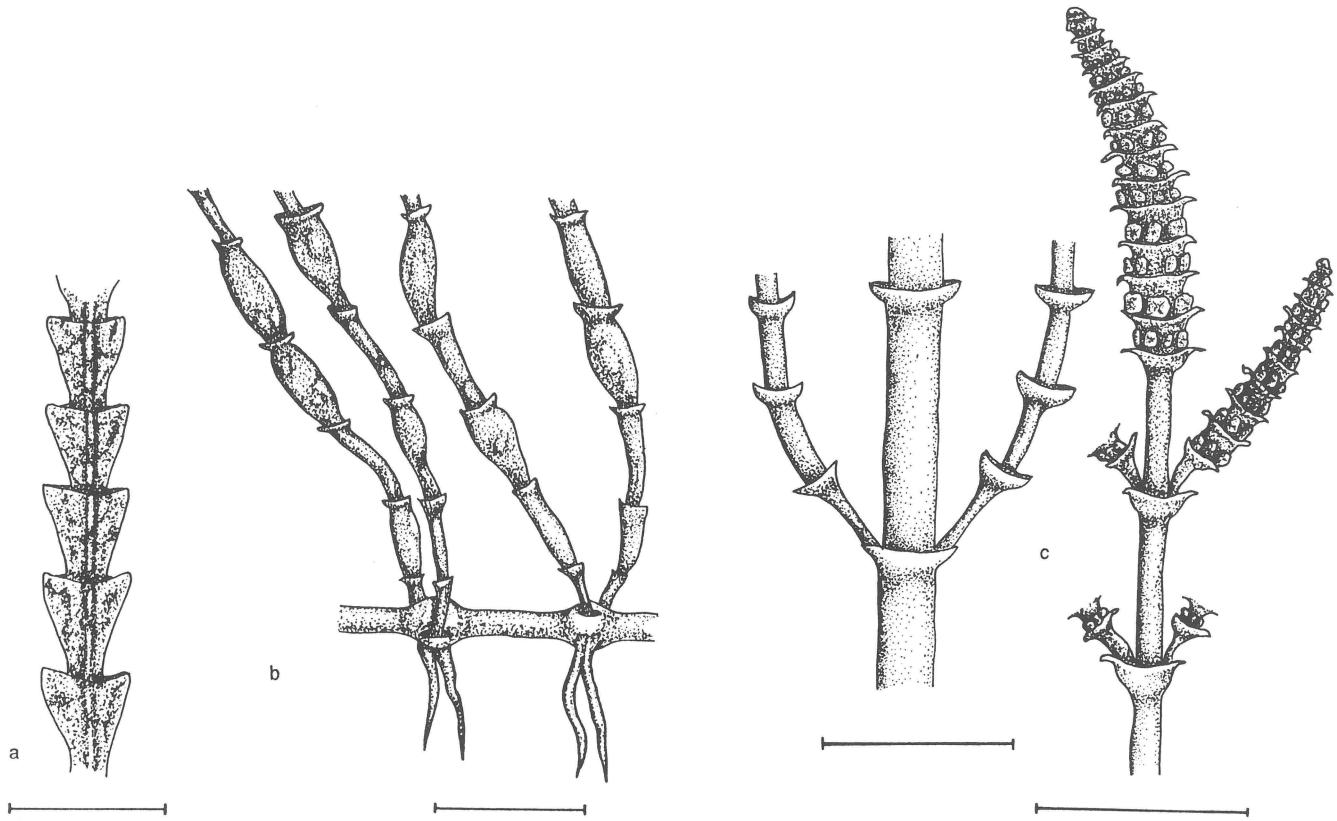

Figure 4 Details of herbarium material of (a) *Sarcocornia natalensis*, (b) *Sarcocornia perennis*, and (c) *Sarcocornia pillansii* (scale bar, 10 mm).

However, the salinity of these areas varies greatly, from 15 parts per thousand (sea water is around 32 p.p.t.) to 140 p.p.t., depending on climatic conditions (O'Callaghan, in prep. b). When the sclereids are absent, the palisade cells tend to enlarge and become more rounded with many not containing chlorophyll. This structure of the palisade easily distinguishes this species from *S. natalensis* and *S. pillansii*, both of which may not have sclereids. *S. natalensis* never has sclereids and the palisade tissue is very narrow and dense. The cells of the palisade are not easily distinguishable and they all contain chlorophyll. When sclereids are absent in *S. pillansii*, only a few cells in the palisade do not contain chlorophyll. The cells are more columnar and regularly arranged, giving a more formal appearance to the organization of the palisade tissue. Sclereids are also absent from *S. decumbens* — however, this species can be distinguished by the features described above.

On well-drained or gravelly substrates, the main stem of *S. perennis* tends to thicken (4 – 10 mm), becoming woody with conspicuously swollen nodes, rarely with adventitious roots. This lignification distinguishes the variety *S. perennis* var. *lignosum* (Moss) O'Callaghan (which is not common) from the typical variety. It has only been found at Knysna and Lüderitz Bay.

8. *Sarcocornia pillansii* (Moss) A.J. Scott

S. pillansii is the common shrubby species found on saline and fresh-water floodplains throughout the coastal regions of South Africa. Although it can sometimes be decumbent (for example, when growing in a sedge field), it is generally an upright shrub up to 700 mm tall. The main stem can attain a thickness of 30 mm and is usually laterally compressed, somewhat gnarled and grooved with a light-grey to white bark. The segments are generally long and narrow, but this is variable (4 – 20 mm long, 2 – 6 mm broad). Although Tölken (1967) described the apex of the leaves as scarcely spreading, I have found that they do tend to spread. The distal end of the segment becomes concave giving a gondola shape to the top of the segment (Figure 4c). The inflorescences are clustered at the ends of the branches. The dead leaves adhere to the stems.

Under dry or sandy conditions the segments become corky. This extreme is distinguished as the variety *S. pillansii* var. *dunensis* (Moss) O'Callaghan. Here the plant is usually decumbent and the segments are short and stout (4 – 8 mm long, 4 – 6 mm broad) and barrel-shaped. This variety is restricted to the dry north-western Cape and Namibian coast.

9. *Sarcocornia natalensis* (Bunge ex Ung.-Sternb.) A.J. Scott

S. natalensis is the common decumbent or prostrate shrub which forms dense mats around fresh-water wetlands throughout the entire country — mainly near the coast, but also inland. It is also often found as solitary plants with irregular rosette shapes up to 300 mm tall. If growing near the coast, fresh water must be available from seepage or run-off. The main branches grow along the ground and often root at the nodes, except in the rosette form. The old leaves adhere to the branches unless the plants are submerged for lengthy periods. Under such conditions the thin stems may be bare with leaves only at the ends (similar to *S. perennis* in salt water). The distinguishing character is that the cymule is fully covered by the bract from below. In all other

southern African species the cymules are exposed (the cymules are also covered by the bract in *Halosarcia indica*). Furthermore, sclereids are not found in the palisade tissue which is relatively narrow with all the cells containing chlorophyll. This species is very variable and identification may be difficult without flowering material. Numerous specimens of *S. natalensis* were mis-identified as *S. capensis*. It is helpful to remember that *S. natalensis* is the most herbaceous of the *Sarcocornia* species and the segments often dry very flat with a ridge in the centre denoting the stem (Figure 4a).

In sandy and drier conditions, the segments tend to become corky. The extreme of this adaptation separates the variety *S. natalensis* var. *affinis* (Moss) O'Callaghan from the typical variety. The segments of var. *affinis* are broad, long and cylindrical (15 – 35 mm long, 4 – 6 mm broad) and have a puffed-up appearance. The apices do not spread when dried. This variety is restricted to the Namibian coast and the dry western and north-western Cape coast. It is often covered by drifting coastal sands and may be found around saline coastal pans. A number of specimens collected in the vicinity of Wadrif Soutpan (Clanwilliam district) during September (end of the rainy season) show the typical thickened segments of this variety. However, the young growth on the same plant is typical of the variety *natalensis*. It would appear that the thickening of the segments is an adaptation to arid conditions.

Hybrids

Hybrids can be recognized as the seeds often abort at an early stage or do not contain embryos. The pollen grains are also often irregularly shaped or jagged as opposed to the spherical shape of the true species. In the field, and often in dried material, hybrids can be recognized by their abnormal habit.

Although Tölken (1967) discussed many hybrids, he stated that they make up less than 1 percent of the specimens collected. However, 176 of the 550 specimens examined for the present study were hybrids. This high proportion (32%) could be due to the fact that my own collections comprised the bulk (62.7% excluding those identified by Tölken) of the specimens studied. In the field I endeavoured to collect all possible variations of *Sarcocornia* at any particular site. Nevertheless, this shows that these species hybridize easily.

It is generally accepted that the Chenopodiaceae is an ancient family (Raven & Axelrod 1975; Cronquist 1968). The genus *Sarcocornia* shows many adaptations: reduction and/or specialization of leaves and physiology, reduction of floral parts, unisexual flowers, *etc.* These types of adaptation are regarded by Cronquist (1968) as being advanced. With this amount of specialization, it is easily concluded that the species would be discrete. However, the ability within *Sarcocornia* to hybridize readily might be seen as a result of the variable habitats in which the species are found. To survive such variability, the species must maintain a high degree of genetic plasticity.

As can be seen from Table 1, the species which most often form putative hybrids are the most widespread, have the least specific habitat requirements and are the most morphologically variable. *S. pillansii*, *S. perennis* and *S. natalensis* each consist of two varieties and are widespread throughout the coastal regions of South Africa. *S. pillansii* is found on floodplains where soils may be highly saline or fresh. Flooding may or may not occur bimonthly (neap), biannually (solstice), annually or occasionally by fresh or salt water. *S. perennis* is found on salt marshes and may or may not be flooded twice daily or biweekly by water with a salinity which varies daily and seasonally. *S. natalensis* is found in areas which may or may not be flooded seasonally by fresh water.

Table 1 Putative parents and putative hybrids as a percentage of the total number of hybrids studied

Putative parents		Putative hybrids	
pillansii	91.5%	*pillansii* × *perennis*	38.3%
perennis	44.6%	*pillansii* × *natalensis*	25.5%
natalensis	29.8%	*pillansii* × *decumbens*	12.8%
decumbens	14.9%	*pillansii* × *capensis*	10.6%
capensis	12.8%	*pillansii* × *mossiana*	4.3%
mossiana	6.4%	*perennis* × *capensis*	2.1%
		perennis × *decumbens*	2.1%
		perennis × *natalensis*	2.1%
		natalensis × *mossiana*	2.1%

Identification

Table 2 shows the most characteristic features of each species as a guide to their identification. However, the following is a quick guide to the most common species in South Africa:

1. Decumbent or prostrate shrub to shrublet forming beds on lower estuarine marshes ..... ***Sarcocornia perennis***
2. Bushy shrub on upper marsh or floodplain ..... ***Sarcocornia pillansii***
3. Herbaceous shrub to shrublet in fresh-water marshes ..... ***Sarcocornia natalensis***
4. Annual shrublet in disturbed or open areas ..... ***Salicornia meyeriana***
5. Tall shrub on rocky shores ..... ***Sarcocornia littoralis***

The following key is based on dried herbarium material. However, a number of factors need to be recorded in the field to facilitate the use of this key:

(a) The life cycle of the plant: All southern African *Sarcocornia* and *Halosarcia* species are perennial whereas all *Salicornia* species are annual. This is most easily determined in the field as the annual plant can be easily plucked from the soil with a short tap root. *Sarcocornia* and *Halosarcia* are usually collected without a tap root.

(b) The habitat of the plant: All the species of *Sarcocornia* can be identified according to habitat (see Table 2).

(c) The habit and growth form: Although the growth forms of the *Sarcocornia* species are variable, it is important to know the overall shape and structural description of the plant.

(d) Shape of segments: The shape of the segments does change with drying. However, some features such as corkiness and the keel can be more easily seen on fresh material.

(e) Bark and stem: Important features for a number of species are the colour of the bark; whether the bark is

Table 2 Comparison of characters useful in the identification of *Sarcocornia* and *Salicornia* species

Name	Life cycle	Flowering time	Habitat	Distribution	Distinctive features	Dried segment features	Sclereide	Other features
pachystachya	ann	?Jun – Oct	mangrove swamps and marsh patches	tropical coast	thickened cylindrical spike	faint keel; lateral ridge	spiral thickening	robust upright shrublet; branches arising at acute angle
perriere	ann	?Jun – Oct	marshes	tropical coast	slightly thickened tapering spike; not all branches flowering	faint keel; lateral ridge	spiral thickening	robust decumbent shrublet
meyeriana	ann	Feb – May	open/disturbed areas higher on the marsh	temperate coast, occasionally inland	3 flowers per cymule; stomata protruding	faint keel	short (not reaching epidermis); spiral thickening	lateral branches spreading & arising at an acute angle; plant ovoid to lanceolate
uniflora	ann	Dec – Jan	open/disturbed areas, higher on the marsh	Lüderitz and Malmesbury coast	1 flower per cymule; stomata sunken	distinct keel	short; spiral thickening	lateral branches erect, fastigiate; plant obconical
indica	pere	Jul – Mar	low on marshes and in mangrove swamps	tropical coast	thickened bracts disintegrating	keel and lateral ridge	uniformly thickened	unique stem anatomy
mossiana	pere	Mar – May	highest zone on marshes and river banks, away from coast	Caledon to Riversdale	segments	short; keeled; apex much spreading to wine-glass shape; thorny appearance	long (to epidermis); uniformly thickened	shrub; bark rough; branches laterally compressed
xerophila	pere	Sep – Dec	dry slopes	Knersvlakte	segments; habitat	cylindrical; shrink to show stem	long; spirally thickened	shrub, bark rough
littorea	pere	Sep – May	rocky beaches	Cape coast	habitat	apex spreads; upper part of segment lighter in colour	spirally thickened	shrub; bark smooth & light in colour; stems fastigiate
capensis	pere	Oct – Apr	high on sandy and fresh marshes; may be submerged seasonally	Cape Town, rarely along south coast	thin tough branches; segments	cylindrical; keeled; very regular appearance	uniformly thickened; long, rectangular, often narrower in middle	decumbent/prostrate; often rooting at nodes
decumbens	pere	Jan – Jun	mid-marsh in estuarine and coastal lagoons	Bredasdorp to Kei River	thick, corky spike; up to 9 flowers per cymule	cylindrical to barrel-shaped; apex of young leaves spreading; cork-like when older	short; rectangular; uniformly thickened	decumbent; rooting at nodes
perennis var. *perennis*	pere	Jan – Jun	lowest zone on estuarine marshes	west to tropical coasts	habitat; dried specimens dark grey; stem swollen at nodes	barrel-shaped to obconical	short; spirally thickened; striations oblique	decumbent; rooting at nodes; old leaves disintegrate
perennis var. *lignosum*	pere	Jan – Jun	lowest zone on estuarine marshes	Knysna; Lüderitz	thick main stem; very swollen nodes	barrel-shaped to obconical	as above	woody main stem
pillansii var. *pillansii*	pere	Jan – Jun	highest zone on estuarine marshes, sometimes inland	temperate coast, rarely inland	habitat; segments	long and narrow; apex often spreads to gondola-shape	spirally thickened; longer and more regular; than perennis, striations perpendicular	decumbent to shrub; old stems much gnarled and laterally flattened
pillansii var. *dunensis*	pere	various, mainly Jan – Feb	brack soils near sea	Namibian coast	habitat; distribution	cork-like; short and stout	as above	decumbent; often covered by sand
natalensis var. *natalensis*	pere	Jan – May	wetlands; often submerged; estuaries if fresh water available	temperate coast and inland	bract covers flowers from below; segments	obconical – cylindrical; soft, flattens entirely	absent	decumbent/prostrate; rosette growth form
natalensis var. *affinis*	pere	Nov – Apr	around saline lagoons; often covered by sand	west and north-west coasts	bract covers flowers from below; segments	obconical – cylindrical; cork-like when older; larger than var. *natalensis*	absent	decumbent/prostrate; rosette growth form

smooth or peeling; whether the stems are smooth or gnarled, laterally flattened or swollen at the nodes.

Key to the South African species of *Sarcocornia* A.J. Scott and *Salicornia* L.

1 Shrublets; annual; upright; whole plant usually collected with short tap root; base of the stem usually with a distinctive curve; segments usually less than 4 mm in diameter ..... ***Salicornia***
2 Robust woody shrublets, tall; flowering spikes thickened, 20 – 80 mm long; tropical and subtropical areas
3 Erect growth form up to 400 mm tall; lateral branches arising at an angle of less than 45° from the main stem, but not longer than the main stem; all the branches end in spikes; spikes markedly thickened, cylindrical and regular ..... ***Salicornia pachystachya***
3 Decumbent or semi-decumbent growth form up to 250 mm tall; much branched with lateral branches arising at an angle greater than 45° from the main stem and often longer than the main stem; spikes appear on a few branches near the main stem and the lower branches may flower later or not at all; spikes less markedly thickened, tapering and irregular ..... ***Salicornia perrieri***
2 Delicate scarcely woody shrublets, flowering spikes not thickened, 5 – 30 mm long; temperate areas
4 Plant with ovoid to narrowly ovoid shape; lateral branches spreading; lateral branches arising at an acute angle from the main stem; flowers 3 per cymule, although lateral flowers may be reduced; segments faintly keeled; stomata protruding ..... ***Salicornia meyeriana***
4 Plant with obconical shape; lateral branches fastigiate, not spreading; lateral branches not arising at an acute angle; flowers 1 per cymule; segments distinctly keeled; stomata sunken ..... ***Salicornia uniflora***

1 Shrubs or shrublets; perennial; upright, spreading or decumbent; tap roots rarely collected, but adventitious roots from the nodes may be present; rarely do all branches end in spikes; segments usually more than 45 mm unless segments give a thorny appearance to the plant ..... ***Sarcocornia*** and ***Halosarcia***
5 Plants with a decumbent or procumbent growth form up to 300 mm tall
6 Old segments thick (up to 6 mm), corky and retaining swollen shape; epidermis cracking and/or peeling to give papery appearance
7 Plants forming prostrate dense mats; perianth corky so that the flowering spikes are much thicker than segments; growing in coastal and estuarine lagoons along the east coast ..... **6. *Sarcocornia decumbens***
7 Plants forming solitary upright rosettes; flowering spikes not much thicker than segments; growing on loose sandy substrates along west coast and Namibia
8 Occasionally rooting at the nodes; segments obovate, short and barrel-shaped (4 – 8 mm long, 4 – 6 mm broad); apex of young leaves spreading to boat shape, *i.e.* top of segments concave; often covered with loose sand ..... **8.b. *Sarcocornia pillansii* var. *dunensis***
8 Not rooting at the nodes; segments obconical to columnar (15 – 35 mm long, 4 – 6 mm broad); apex of leaves hardly spreading, top of segments truncate; growing in moist areas and around coastal lagoons ..... **9.b. *Sarcocornia natalensis* var. *affinis***
6 Old segments not retaining swollen shape, although they may become slightly thickened; epidermis usually smooth, not disjunct at the nodes
9 Bracts corky so that the flowering spikes are thicker than the segments; cymules often distintegrate to leave the bracts which form discs around the stem ..... ***Halosarcia indica***
9 Bracts not corky and flowering spikes not much thicker than the segments; cymules do not disintegrate to leave the bracts
10 Plants not rooting at the nodes; plants shrub-like; if woody stems present, then gnarled and laterally compressed; apex often spreading to form boat shape, *i.e.* top of segment concave ..... **8.a. *Sarcocornia pillansii* var. *pillansii***
10 Plants rooting at the nodes; forming dense mats or irregular rosettes; if woody stems present, then smooth, not flattened nor swollen at the nodes; apex hardly spreading and never boat-shaped
11 Top of segment truncate to give obconical appearance (5 – 15 mm long, 1 – 4 mm broad); leaves often spreading slightly; growing in less saline soils and not at coast unless fresh water supply available ..... **9.a. *Sarcocornia natalensis* var. *natalensis***
11 Segments cylindrical to obovate; leaves not spreading in herbarium material
12 Branches thin and tough; segments hardly flattened in herbarium material; leaves strongly keeled; growing on hardly saline soils; mainly found around Cape Town, but also isolated patches along south coast ..... **5. *Sarcocornia capensis***
12 Branches softer; segments flattened in herbarium material; leaves not keeled; growing low on maritime marshes to form beds
13 Stem less than 3 mm in diameter; stem not swollen at the nodes; growing in lowest zone on muddy marshes ..... **7.a. *Sarcocornia perennis* var. *perennis***
13 Older stems up to 8 mm in diameter and swollen at the nodes; growing in lowest zone on gravelly marshes at Lüderitz Bay and Knysna ..... **7.b. *Sarcocornia perennis* var. *lignosum***

5 Plants with an upright, shrubby growth form up to 1 m tall
14 Segments shrinking to expose stem; apex of leaves not spreading in herbarium material, therefore having a columnar or disc shape; not growing near water, but on dry rocky slopes in Knersvlakte ..... **2. *Sarcocornia xerophila***
14 Stem not exposed between segments (although segments may become very narrow at the bottom to have obconical appearance); leaf apices spreading (at least some) in herbarium material; found in wet areas or near water
15 Segments very small (2 – 3 mm long, 2 – 4 mm broad) with distinctly keeled apices; segments giving spinescent appearance to plant; apices spreading

dramatically to a champagne-glass shape in herbarium material ..... **1. *Sarcocornia mossiana***

15 Segments nmch longer than broad; segments not having spinescent appearance

16 Secondary branches various, but not fastigiate; dead leaves adhering to the branches, but older stems bare; older stems much gnarled, laterally compressed and swollen at the nodes; if stems not as above then older segments corky; epidermis of older segments and bark of stems often bursting and/or peeling to give thick papery appearance; segments keeled; tops of segments often spreading to form gondola shape in herbarium material

17 Shrub; upright to 700 mm; stigmas 1 – 2 mm long; older segments thin and long (8 – 20 mm long, 2 – 4 mm broad); upper flood plain along coast or inland .... **8.a. *Sarcocornia pillansii* var. *pillansii***

17 Shrub; decumbent, rarely with ascending branches; stigmas 3 – 4 mm long; segments with dry swollen or puffed appearance; segments barrel-shaped to obovate (4 – 8 mm long, 4 – 6 mm broad); often covered with loose sand; along north-western Cape and Namibian coast .... **8.b. *Sarcocornia pillansii* var. *dunensis***

16 Secondary branches fastigiate; bark smooth, not gnarled, but sometimes peeling thinly; dead leaves not adhering to the branches; segments cylindrical to slightly obconical; top edge of segments straight and not concave; tips of segments rarely spreading

18 Plants tall and twiggy; herbarium material with dark grey appearance; secondary branches sparse and erect to give fastigiate appearance; flowering spikes consistently terminal; segments of herbarium material seem to have shrunk in a uniform way to show faint longitudinal grooves; segments long and thin (5 – 12 mm long, 2 – 3 mm broad); occasional along rivers in Namaqualand .... **3. *Sarcocornia terminalis***

18 Plants with several erect main branches; herbarium material light in colour with segments yellow and bark reddish brown; secondary branches dense and clustered at the end main branches; strongly fastigiate; flowering spikes noticeably broader than barren segments; segments 5 – 8 mm long; 3 – 5 mm broad; growing along rocky shores in Cape .... **4. *Sarcocornia littoralis***

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