

The Species of *Arthrocnemum* and *Salicornia* (Chenopodiaceae) in Southern Africa

by

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ABSTRACT

In the genus *Arthrocnemum*, ten species and three varieties are recognized. The new species and combinations are: *A. mossianum*, *A. terminale*, *A. xerophilum*, *A. decumbens*, *A. natalense* var. *affine* (Moss) (*A. affine* Moss), *A. pillansii* var. *dunense* (Moss) (*A. dunense* Moss). *A. perenne* var. *lignosum* is a new record for South Africa. In *Salicornia*, of the three species dealt with, one is new: *S. uniflora*. Two keys are provided for the identification of fertile and sterile material respectively. The anatomy is discussed. The presence or absence, and the type and shape of sclereids were found to have taxonomic significance. Twenty-four naturally occurring hybrids in the genus *Arthrocnemum* and one in the genus *Salicornia* are recognized on the basis of sterility and pollen irregularities.

INTRODUCTION

Throughout the world this taxonomically critical group has provided difficulties at both specific and generic levels. Moquin (1840) separated the genus *Arthrocnemum* from the genus *Salicornia* L. on the basis of only one character, viz. the perennial habit of the former as against the annual habit of the latter. Although he later (Moquin, 1849) attempted another circumscription of the two genera, based mainly on endosperm characters which proved to be unreliable, it was Ungern Sternberg (1866) who formulated *Arthrocnemum* to include species with endospermous seeds while those with ex-endospermous seeds were placed in *Salicornia*.

This definition was adopted by Bentham & Hooker (1880), Volkens (1894), Paulsen (1918), Chevalier (1922) and Ulbrich (1934). However, doubts soon arose as to whether the genera should be separated on a single character such as this. In addition, the absence of seeds in many specimens makes it difficult to ascribe them to either genus and, even recently, species have been somewhat indiscriminately transferred from one genus to the other.

Wright (1912) in *Flora Capensis* probably followed Ungern Sternberg's circumscription of the two genera when he upheld three species and three varieties of *Salicornia*. His delimitation of the species soon proved to be unsatisfactory, while the names of two European species, *S. herbacea* and *S. fruticosa*, were incorrectly used when applied to South African species.

Since then the main student of the *Salicorniae* in South Africa has been C. E. Moss, who had previously worked on this group in Europe (Moss, 1911; 1912; 1912b; Moss & Salisbury, 1914), before he came to South Africa. Unfortunately he did not bring his notes on the South African species to finality before his death in 1930. Adamson eventually undertook the task of editing and publishing the notes (see Moss 1948 and 1954). In the former, Adamson clearly accredits the work to Moss when he states that "the following descriptions are practically as they were drawn up by their author". I have not seen Moss's manuscript dealing with the *Salicorniae* and have based my interpretations entirely on Adamson's publications. Unfortunately Moss's notes, possibly due to their being edited and published posthumously, proved

to be insufficiently critical. In addition, the keys to the species soon proved to be unsatisfactory, while in some cases the nomenclature and typification may not have been presented as Moss would have desired. The need thus became apparent for a further taxonomic revision of the two genera in Southern Africa and the present review became urgently required as a result of recent ecological studies of estuaries.

Moss (1948; 1954) accepted Moquin's original circumscription of the two genera and added that the flowers of *Arthrocnemum* are protogynous and have bifid stigmas while those of *Salicornia* are protandrous and have tufted stigmas. This separation proved to be effective as applied to the South African species and is accepted as a basis for the present study, although it may be mentioned that Dalby (1962), Ball (1964) and Ferguson (1964) have queried whether some of the floral characters can be used for distinguishing the genera.

In the revision of the two genera (Moss, 1954), two species of *Salicornia* and fifteen species of *Arthrocnemum* were recognized. The genus *Arthrocnemum* was subdivided into two subgenera and two sections. In my opinion, however, the affinities are rather different from the concept presented by Moss (1954), and the subdivisions he proposed were not adhered to in the present study. His species order was also changed following the affinities revealed by morphological and anatomical information but, unfortunately, technical difficulties did not permit the application of cytological evidence to these problems.

The subgenus *Angianthemum*, for instance, was separated by Moss from the subgenus *Gymnanthemum* on the basis of its hidden flowers and the presence of endosperm. However, no endosperm was observed in *A. africanum* and *A. affine*, both now placed as synonyms of *A. natalense*, and their inclusion together with *A. indicum* in the subgenus *Angianthemum*, on the basis of the hidden flowers only, is unfortunate. If affinities are evaluated, it becomes obvious that *A. indicum* is different, both anatomically and also in its seed structure, from the other species of *Arthrocnemum* and *Salicornia* in Southern Africa. Experiments have shown that the seeds do not germinate as readily as those where a fully developed embryo with chlorophyll and no endosperm is found. It seems, therefore, that the character, endosperm present or absent, is not an isolated character, as indicated earlier, and that its significance in the dissemination biology seems to be much more complex than was realized by Moss (1954). However, further investigations on a world-wide basis are needed before the generic delimitations can be reliably evaluated.

Anatomical and seed characters appear to be of taxonomic value and show a remarkable coincidence when used for the grouping of the species. Although *A. natalense*, for instance, is superficially very similar to *A. indicum*, it is different in the seed structure and the anatomy, which are more like those of all the other species of *Arthrocnemum* and *Salicornia* investigated. Yet the complete absence of sclereids in the palisade tissue, as well as passage cells, which, at least in some cases, are undeveloped sclereids (see p. 261), is peculiar. Sclereids, in particular the spirally thickened sclereids, are very characteristic of the species of *Salicornia* and *Arthrocnemum*.

Also, the two very similar species *A. mossianum* and *A. terminale* differ from the rest in the shape of their uniformly thickened sclereids, the almost black, glabrous seeds and odd stigma behaviour. The absence of chloroplasts in the secondary cortex of the old branches separates these two species from other shrubby species (*A. pillansii*, *A. littoreum*, *A. xerophilum*) which, again, are similar to one another. On the other hand *A. decumbens* and *A. capense*, the other two South African species with uniformly thickened sclereids, exhibit greater affinities to *A. perenne*, a species with spirally

thickened sclereids, than to *A. mossianum* and *A. terminale*. The four species with spirally thickened sclereids are very similar to one another although each tends to grow in a different habitat. An evaluation of the affinities of the South African species of the two genera with those from other countries is extremely difficult as the descriptions of these plants in many floras are inadequate.

The revision presented here is based mainly on fresh or preserved specimens collected by the author, and on extensive habit and habitat observations. Although most of the material was collected in the salt marshes at Milnerton near Cape Town, I have investigated various populations of *Arthrocnemum* and *Salicornia* species at many different localities from Lüderitz Bay around the coast to Durban. Preserved specimens from Lourenco Marques and Swakopmund were also at my disposal.

In this treatment, Southern Africa is delimited by the Kunene River on the west coast and the Limpopo River on the north-east coast. This delimitation seems to cover the main centre of distribution of this group of plants in Southern Africa. Immediately to the north of this area only *S. pachystachya* and *A. indicum* are recorded on the east coast, and *A. indicum* and possibly also *A. natalense* var. *affine* on the west coast.

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TAXONOMIC VALUE OF SOME CHARACTERS

The species of *Arthrocnemum* and *Salicornia* are extremely variable in habit and in the shape and size of the different organs. In addition, a description from which living plants as well as herbarium material can be identified, is a requirement not easily met in succulent plants. Therefore measurements given in the descriptions are rarely of taxonomic value and usually a range is given which includes the dimensions of a particular character in both the living as well as dried plants. Clear-cut diagnostic characters are rare in this group and consequently it is important to know the range of variability of the characters used.

1. Adventitious Roots

Adventitious roots are commonly found in the species of *Arthrocnemum* with prostrate growth, but they have also been observed in all salt marsh species of this genus, if the stems are buried. Normally, adventitious roots are absent in the erect and shrubby species, especially in herbarium material, because specimens are usually collected from the top of the plants. König (1960) records several cases of rooting at the nodes in the genus *Salicornia* in Europe, if the branches are buried by dune sand, but this behaviour has not been observed in South African species.

2. Succulent Leaf Sheath

If the anatomy, and in particular the vascular traces of the succulent stems of the *Salicornia*, is investigated it is found that "the succulent cortex which covers the internodes of a *Salicornian* shoot is foliar in origin" (De Fraigne, 1911). In fact the 'cortical envelope' of the segments of the stems seems to represent inverse dorso-ventral (in comparison with the general use of the term), opposite leaves which have enlarged and fused laterally and of which the abaxial sides have expanded vertically to cover the whole internode below the respective node. According to the recurved upper leaf traces, the whole abaxial surface of the leaf has experienced a downward movement. A difference between the tissues of the leaves and those of the stem cannot be ascertained.

In herbarium material the dried leaves often develop characteristic shapes and colours. The characteristic spinescent appearance of *A. mossianum*, which distinguishes this species from all the other shrubby species of *Arthrocnemum*, is due to the markedly spreading leaf apex. It must also be mentioned at this stage that a distinction must be made between dried leaves of herbarium material and dead leaves which are normally adhering to the branches of living plants. For example, in *A. capense*, the dried leaves are cylindrical to obconical with a spreading leaf apex, whereas the dead leaves are barrel-shaped and cork-like.

The lateral ridges of a segment are the vertical colourless ridges along the central axis on the upper half of the leaf rudiments. Sometimes they are pronounced ridges but often only a colourless line below the leaf apex.

3. Colour of the Segments

In *Salicornia*, Moss and Salisbury (1914), Ball and Tutin (1959) and Aellen (1961) have used the colour of the segments for distinguishing some of the species. However, König (1960) considered segment colour useless in the delimitation of the species as he found no clear-cut distinctions.

Colours of the fleshy segments were found to be useful field characters in separating species of *Arthrocnemum*, but it is very difficult to describe these colours. If plants are observed from a distance of about two metres a specific tinge can often be recognized. However, if the plant is investigated from nearby, a full range of colours is found. Colour differences are most noticeable in the red range. Here it is immediately realized that *A. littoreum* and *A. perenne* var. *lignosum* produce no red colouration, or only a light tinge. Their segments fade to yellow, whereas in the other species a brownish-red or a bluish-red coloration can be observed.

These colours were found to be a useful hint in the identification of the parents of putative hybrids. Good examples of this are the two hybrids between *A. natalense* and *A. pillansii*.

4. Anatomy of the Branches

In this study further work has been done on the anatomy of the different taxa in an attempt to discover additional characters on which they might be separated. For detailed accounts of the anatomy of this group of plants, one may refer to De Fraigne (1911), Baumgärtel (1917) and Metcalf and Chalk (1950). For purposes of identification, I found transverse sections of the succulent stems sufficient. All South African species of *Arthrocnemum* and *Salicornia* are very similar in the basic arrangement of the tissues except *A. indicum*. This species has, in contrast to all the other species, only one layer of palisade cells, equal in size and each one about twice as long as wide. A single layer of isodiametric cells, which normally become lignified with age, is found to the inside of the palisade tissue. This layer was not observed in other species investigated.

Two characters were found to be of taxonomic value in the other species of *Arthrocnemum* and *Salicornia*. They are the sclereids in the palisade tissue, and the nature of the secondary cortex.

(i) *Sclereids and Passage Cells in the Palisade Tissue*

Although the sclereids in the palisade tissue were mentioned by Moss (1954), no use was made of them in the delimitation of species, as is done here. Basically two types of sclereids can be distinguished and both types, even in young stages, do not contain chlorophyll.

Firstly, there are uniformly thickened sclereids, i.e. a sclerenchyma cell, varied in form, and having thick lignified walls with many pits. They are often long and slender or even branched in *A. mossianum*. Into this group fall *A. capense*, *A. decumbens*, *A. mossianum* and *A. terminale*.

Secondly, there are the spirally thickened sclereids which are sclerenchymatous cells normally longer and wider than the palisade cells, becoming lignified in spiral striations. Sclereids of this type are found in *A. pillansii*, *A. xerophilum*, *A. littoreum*, *A. perenne* and the South African species of *Salicornia*.

De Fraine (1911) reported finding intermediate forms between the two types in *A. perenne* and some species of *Salicornia*. In the case of plants with spirally thickened sclereids, uniformly thickened sclereids are also found around the stele. However, the sclereids around the stele are always of the uniformly thickened type, except in *A. xerophilum*. In this species spirally thickened sclereids or uniformly thickened sclereids with additional trabecula-like bars of lignin occur frequently around the stele especially at the nodes.

It was observed that in South African species either the one or the other type of sclereids is found, if the sclereids in the palisade tissue only are considered. No intermediates were observed. Young stages where the spiral striations are still incomplete should not lead to confusion as the walls are either not lignified or not lignified uniformly. This is often found in *A. perenne* var. *lignosum* where spirally thickened sclereids rarely develop fully.

Also, sclereids are often found in flowering spikes in the water tissue surrounding the flowers. Their form and development suggest that they are merely lignified parenchyma cells. However, sometimes, especially in *A. decumbens*, the pit canals are narrowly widened at their mouth in such a way as to give the appearance of incomplete striations in surface view.

The faint spiral striations usually found in *A. pillansii* are almost perpendicular to the lateral walls. This character, which is used to separate this species from other species with spirally thickened sclereids, cannot be applied to putative hybrids involving *A. pillansii*. In such hybrids the spiral striations are always oblique to the lateral walls.

Sclereids in the palisade tissues of putative hybrids were studied extensively and three main groups were distinguished among such hybrids.

(a) Hybrids in which *A. natalense* is one parent usually develop no sclereids, irrespective of the sclereids exhibited by the other parent. Only in hybrids of *A. natalense* with *A. mossianum* were uniformly thickened sclereids present.

(b) Hybrids between species having the same type of sclereid also exhibit that type of sclereid. In such cases, if there is a difference in shape between the sclereids of the parents, usually an intermediate shape of sclereid is found in the hybrid.

(c) Hybrids from parents having different types of sclereids, show intermediate types in the progeny, i.e. in such instances sclereids with more or less complete striations overlaying otherwise uniformly thickened walls are produced (Fig. 2: 6). Again, *A. mossianum* is the exception as, in the hybrid *A. mossianum* × *A. pillansii*, sclereids similar to those of *A. mossianum* are found.

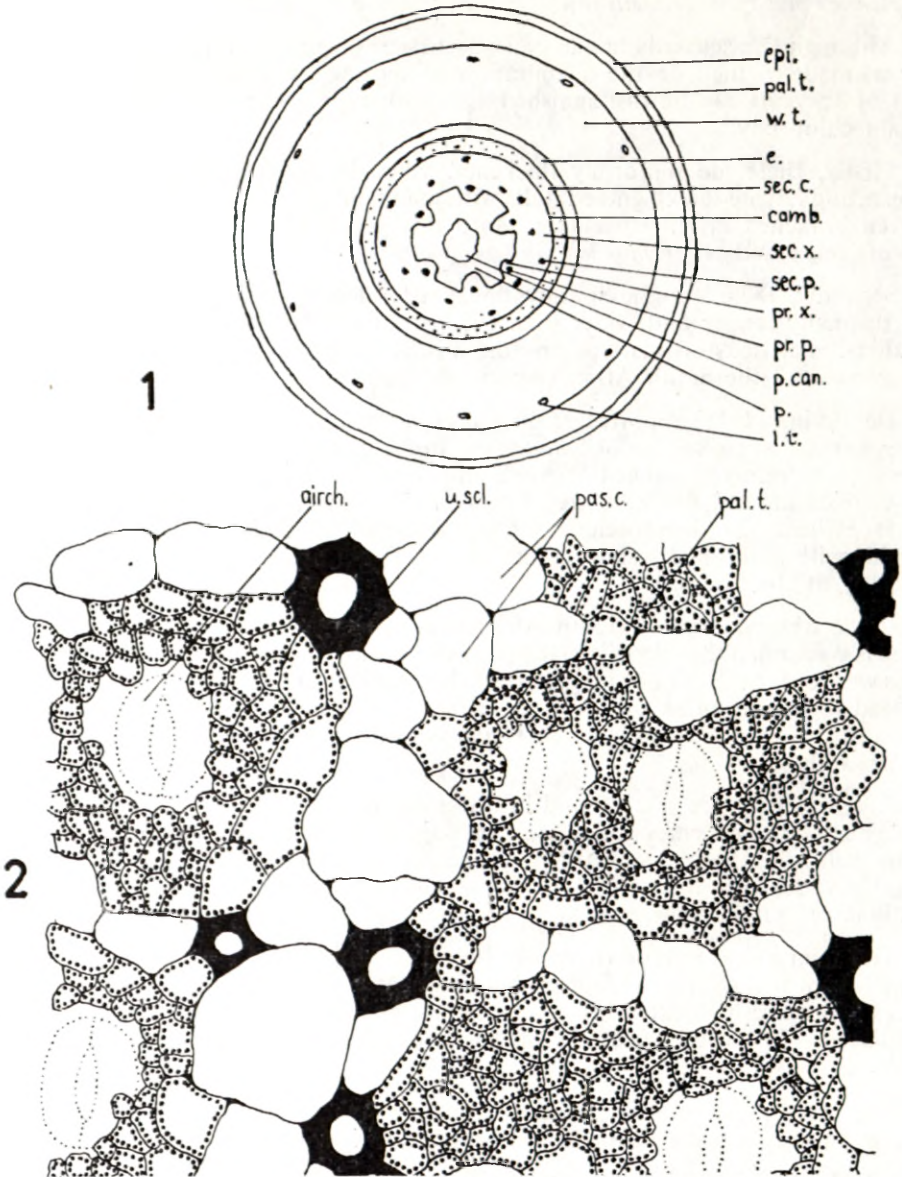


FIG. 1.—1, Diagram of a transverse section through an internode of *Arthrocnemum* and *Salicornia*. 2, *Arthrocnemum capense*, paradermal section of a segment illustrating the distribution of the palisade tissue, passage cells and sclereids. The stomata are at right angles to the axis. airch.—air chamber below stomata; camb.—cambium; e.—endodermis; epi.—epidermis; l.t.—vascular leaf traces; p.—pith; pal.t.—palisade tissue; pas.c.—passage cells; p.can.—pith canal; pr.p.—primary phloem; pr.x.—primary xylem; sec.c.—secondary cortex; sec.p.—secondary phloem; sec.x.—secondary xylem; u.scl.—uniformly thickened sclereids; w.t.—water tissue.

In the genus *Salicornia* only spirally thickened sclereids have so far been found. The European species *S. dolichostachya* and *S. strictissima*, have no sclereids at all (Nannfeldt, 1955).

Large non-chlorophyllose cells often occur around the sclereids in the palisade tissue (Fig. 2). They are referred to as passage cells as this appears to be their function. They are twice or three times as wide as the surrounding palisade cells. Usually a row of two or three such cells extends across the palisade tissue from the epidermis to the water tissue. It seems significant that these passage cells are most commonly found in species with uniformly thickened sclereids, whereas in species with spirally thickened sclereids they are rare or completely absent. In species with the latter type of sclereid, the initial stages of the sclereids and the passage cells are very alike. In fact, the passage cells are only undeveloped spirally thickened sclereids, as found in *A. perenne* var. *lignosum*. Normally, however, the passage cells become about twice as wide as the sclereids.

Bäumgartel (1917) found that no sclereids are formed if the seedlings are cultivated under very moist conditions. The present author observed that usually in very old segments of such plants growing in more moist regions, e.g. *A. decumbens* at Lourenco Marques as opposed to Mossel Bay, eventually at least some sclereids are formed. However, dry conditions and apparently also high salt concentrations seem to promote the formation of sclereids.

Paradermal sections reveal that the sclereids in general are arranged singly or in groups in the palisade tissue between the stomata. They occur only occasionally almost next to the air chambers below the guard cells, but are never in contact with them. In *A. capense* the sclereids together with the passage cells produce an almost complete reticulation around a clump of palisade cells below the respective stomata (Fig. 1: 2).

(ii) Secondary Cortex

Towards the outside the cambium produces a parenchymatous secondary cortex. In species with a shrubby habit and spirally thickened sclereids, such as *A. pillansii*, *A. littoreum* and *A. xerophilum*, the cells of the secondary cortex of old stems contain chlorophyll, but this does not occur in those species with uniformly thickened sclereids, such as *A. mossianum* and *A. terminale*.

In *Salicornia* the thickness of the secondary cortex appears to be a useful taxonomic character. As it is applicable only to older specimens, it might be partly due to the much stouter nature of *S. pachystachya*, which exhibits a thicker secondary cortex than do the other two species, *S. meyerana* and *S. uniflora*.

5. Inflorescence

The inflorescence or the "spike" of *Arthrocnemum* and *Salicornia* is a compound inflorescence consisting of three- or more-flowered, sessile cymules in the axils of the opposite decussate bracts. Perhaps the term spike-like thyrse is more appropriate. A recent tendency has been to substitute "spike" by "pseudo-spike" (Scheinähre in König, 1960; Aellen, 1961). This might point out the wrong use, but it is still not the correct morphological term. As the term "spike" has been so widely used in taxonomic treatments of this group, this terminology is used in the present study.

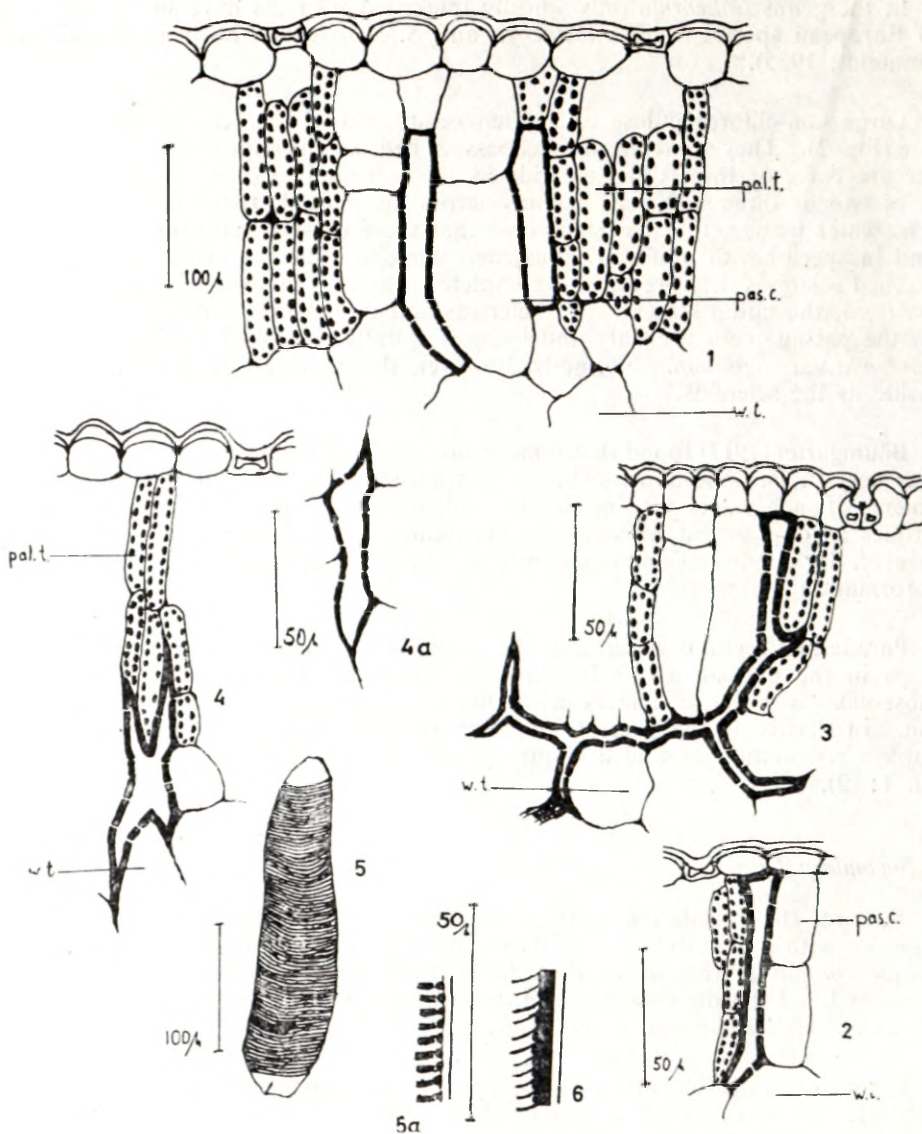


FIG. 2.—Scledeids of the palisade tissue in relation to the stomata and passage cells. 1, *Arthrocnemum decumbens*, sclereids usually rectangular, not reaching the epidermis. 2, *A. capense*, sclereids usually narrower in the middle, reaching the epidermis. 3, *A. mossianum*, branched sclereids reaching the epidermis and into the water tissue. 4, *A. terminale*, branched sclereids not reaching the epidermis but into the water tissue; 4a, sclereids not branched. 5, *A. pillansii*, spirally thickened sclereids; 5a, detail of the cell wall showing lignin deposited in striations. 6. *A. decumbens* × *A. pillansii*, lignified walls plus spiral striations.

pal.t.—palisade tissue; pas.c.—passage cells; w.t.—water tissue.

The bracts are anatomically similar to the leaf with the exception that, in the former, more sclereids are often found both in the palisade tissue and around the stele. The internodes do not elongate as much as the barren branches, which results in a condensed inflorescence. Characters such as tapering spikes, fruiting segments thicker than the

barren segments or bulging segments are often good indications of species concerned. Spike length on the other hand must be used with care, as it is often very variable, especially in species of *Arthrocnemum*.

In *A. natalense* a continuation of vegetative growth above the spike has often been observed. Alternating vegetative and fruiting growth may be repeated up to three times. This terminal proliferation was also recorded, but much less frequently, in *A. pillansii* and *A. capense*.

Another phenomenon which is thought to be lateral proliferation is the presence of lateral branches of spikes, frequently observed in a form of *S. meyerana*. Lateral branches may develop in this form in the position normally occupied by one or both lateral flowers of the cymule. Another branch below the central flower can also occur with all three flowers developed. The central flower is never absent. These lateral branches always bear flowers.

A similar arrangement of the branches has been observed in the axils of non-fruiting segments of the same form of *S. meyerana*. Here the maximum of eight branches per node is possible, yet seldom found, but up to six branches in various combinations are not uncommon at a node. It is remarkable that a whole population of this odd form was found at Saldanha Bay.

6. Cynules

In all the species of *Arthrocnemum* investigated, the flowers are completely sessile, but in *A. natalense* a bulge indicates the pedicel of the flower. However, in all the species a vascular strand, one or two tracheids thick, is visible at the base of each flower.

In *Arthrocnemum* all the flowers are approximately equal in height, whereas in most of the species of *Salicornia* the central flower is bigger and does not completely separate the two lateral flowers. Only in the Australian species *S. blackiana* (which should be placed in *Arthrocnemum*) are two to three flowers often found below the central flower. Cynules are usually three-flowered but up to sixteen flowers per cymule have been recorded for *S. australis* Sol. ex Benth. (Cooke, 1912). The number of flowers may vary greatly and Moss (1954) grossly overrated the usefulness of this character in delimiting *A. variiflorum* and, even more so, in separating the section *Trianthemum* and *Polyanthemum* on the number of flowers per cymule only. Moss (1954) must have been aware of this as he admits that "*A. variiflorum* forms a connecting link between the sections . . .". However, there are certain species, such as *A. indicum* and *A. capense*, with consistently three flowers per cymule.

7. Flowers

In all species of *Arthrocnemum* and *Salicornia* the perianth tube exhibits a number of segments at the apex. The number of segments at the apex of the perianth tube is constantly three or four in the genera *Arthrocnemum* and *Salicornia* in South Africa. Black (1919) does not regard these segments as perianth lobes in *S. australis*, but considered them to be the result of bursting open of the perianth. If this view is correct, one would expect irregular segments as the result of fragmentation. In South African species these perianth lobes are already visible before anthesis. In the two species with laterally compressed perianth tube, namely *A. indicum* and *A. natalense*, usually only three lobes are seen. In all the other species of *Arthrocnemum* and *Salicornia* where the truncate perianth tube is found, usually four segments were observed, rarely only three in lateral flowers.

Furthermore, in all the species except *A. indicum*, an abscission layer is formed at maturity of the seeds well above the tissues of the bracts, so that a ridge outlining the flower remains when the nodes have fallen out.

A useful additional character for separating some species, e.g. *S. meyerana* from *S. pachystachya*, was found to be whether the perianth becomes cork-like when mature or shrivels up. However this character must be used with care, since in certain species, such as *A. perenne*, a cork-like perianth is often an indication of a specimen grown under unfavourable conditions.

8. Stamens

The number of stamens was never found to exceed two. The record of four or five stamens by McCann (1952) in the Australasian species of *Salicornia* is open to doubt since Allan (1961) failed to find more than two in the New Zealand species also investigated by McCann. However, sometimes one or no stamens are produced in functionally female plants as recorded for *A. pillansii* and *A. mossianum*.

The size of the anthers as a taxonomic character has been investigated in *Salicornia* in Europe (Ball, 1964), but does not give workable results in South Africa.

9. Ovary and Stigma

The ovary in all species is very similar except in *A. mossianum*, where two lateral grooves adjoining the anthers are found. This is a very useful character and is clearly visible in hybrids derived from this species.

In *A. natalense* and *A. indicum*, the bifid stigma is papillose and spreading. In *A. pillansii*, *A. littoreum* and *A. xerophilum*, the bifid stigma is plumose and erect, the lobes adhering to one another. In *A. perenne*, *A. capense* and *A. decumbens*, the bifid or trifid stigma is plumose with reflexed lobes, sometimes even adhering to the fleshy segments. In *Arthrocnemum* the stigma was found to be a very reliable character, but unfortunately the stigmata are extremely brittle and are not visible in herbarium material.

10. Seeds and Seed Dispersal

The present author found seed characters, especially the papillae and hairs on the seed testa, very reliable in the delimitation of species. Among the South African species of *Arthrocnemum*, the seeds of *A. indicum* are unique, because they produce a crustaceous pericarp, while endosperm is present. In all the other South African species of *Arthrocnemum* and *Salicornia*, the embryo is conduplicate and without endosperm. At the end of the seed the radicle and the cotyledons are separated by part of the testa which is invaginated. In most of the species this double membrane, resulting from invagination, is not well fused and the radicle can be split from the cotyledons without damaging the seed testa. It appears that embryological studies might reveal interesting data pertaining to the relations of the taxa above the species rank.

In most of the species the perianth tube remains attached to the seeds. Wind and especially rain apparently aid the release of these propagules, which drop onto the ground below the parent plant. If the soil is moist enough, the seeds germinate within two days and the seedlings establish themselves within a week. In the lower zones of salt marshes, the seeds are washed away as the result of tidal movement or river flooding. It is, however, interesting to note that the dried perianth enables the seeds to float. But the question arises how these species can establish themselves if the seeds are washed away. In temporary vleis the seeds have just enough time to

establish themselves before the lower levels of the vleis are submerged after rain. It was noted that seedlings of many species of *Arthrocnemum* and *Salicornia* were able to endure a long period of submergence, during which time the seedlings were not observed to grow.

In contrast with this, endospermous seeds, such as those of *A. indicum*, are released only by the eventual decay of the hard cork-like spike. Also, germination is erratic and takes from a week to three weeks.

11. Flowering Period

In the field it has been observed that all the plants of a species at a given locality usually flower within a very definite period, and that only the hybrids in each population flower at irregular times. Most of the species flower from January to May. Judging from herbarium records, however, there appears to be some variation in the times of flowering at the different localities, which is not unexpected as the species of *Arthrocnemum* and *Salicornia* occur in a wide range of climates. For instance, *A. natalense* seems to flower twice in Natal, namely in December to April, and flowers begin to appear again in June or July. On the other hand *A. natalense* var. *affine* seems to flower throughout the year. Only *A. capense* and *A. xerophilum* are exceptions in the genus *Arthrocnemum* and flower in October and November.

As specimens in the flowering and fruiting stage look so alike, the term flowering period, used in the descriptions, includes both.

12. Habitat and Zonation

Two of the species of *Arthrocnemum* and *Salicornia* in South Africa do not occur in salt marshes. *A. xerophilum* is found on dry slopes in the Knersvlakte (Vanrhynsdorp district) among succulents. The other species is *A. littoreum*, which grows in rock crevices along the sea shore but, in contrast to the previous species, it grows under moist conditions.

All the other species were observed to occur at characteristic levels in salt marshes. Although the limits of the various zones are not always clear-cut, a fairly clear zonation is always noticeable. In fact, the species of *Arthrocnemum* occur at definite levels of the salt marshes and, although this is not of great taxonomic value, it is interesting for the delimitation of the species.

Populations of *Arthrocnemum* and *Salicornia* at lower levels may be subjected to either flooding by fresh water in the rainy season or may be inundated by tidal sea water. According to which is applicable, either *A. natalense* or *A. perenne*, respectively, occur in the lowest zone. This is indicated by the distinction between "inland salt marshes" and "maritime salt marshes". However, in estuarine salt marshes the two types may eventually merge where the effects of the fresh water overlap those of the tidal movement. Inland salt marshes include the temporary vleis in the Cape and also those estuaries which Day (1952) has referred to as "blind estuaries", because their access to the seas has been barred by a sand bank. In these localities, *A. natalense* occupies the lowest zone because of its ability to endure submergence for up to three months. In contrast with this, *A. perenne* can endure only short periods of inundation. At Rugby, near Cape Town, this species occurs together with *A. natalense* in seasonal vleis and it occupies the zone at the highest water level and above. However, this population of *A. perenne* is most unusual because this species normally grows in maritime salt marshes. It is thought that its occurrence at this locality must be attributed to acclimatization, as Day (1952) demonstrated for animals, after these vleis were cut off from the main lagoon.

S. meyerana is generally found in the lower zones of salt marshes. It is a pioneer plant and does not necessarily occur in a definite zone of its own. Plants of this annual species die before enough rain water has accumulated to submerge them in inland salt marshes, but they also occur in maritime salt marshes.

The next zone higher up in the salt marshes is occupied by *A. decumbens*, immediately followed by the *A. pillansii* zone. It appears that there is a strong competition between the two species and the zonation is effected by seasonal flooding, because *A. decumbens* seems to be more tolerant to occasional inundation than *A. pillansii*. Both the varieties of *A. pillansii* always occur outside the reach of the high water level.

Higher up still in the zonation occurs *A. mossianum* and at similar levels, but at different localities *A. terminale* is found. Neither of these species was ever found in localities near the sea. At the higher level the salinity factor seems to be operative.

A. capense also occurs in a zone above *A. pillansii*, and is especially abundant in sandy localities. It is thought that it requires well-aerated soils.

PUTATIVE HYBRIDS

In taxonomic investigations certain intermediate specimens have been recorded. Moss often identified them as hybrids. In the present study, when pollen was investigated, it was found that the grains of these intermediates are often not round as is normal, but are dented and in addition there are much smaller grains without an intermediate range being observed. In the immature pollen it was found that the "tetrads" were abnormal in being composed of more than four grains of varying sizes. Goodspeed (1954) found that a similar phenomenon in hybrids in the genus *Nicotiana* was due to irregularities in meiosis: "The smaller nuclei contain chromosomes which did not reach the poles at the end of anaphase I . . . At the sporal stage two or more lagging chromosomes may become united and are surrounded by a membrane".

In addition, in putative hybrids no seeds develop or these are aborted at an early stage, and in no case was a fully developed embryo found, although often the brown seed membrane can be recognized. The two characters, the presence of abnormal pollen and the absence of seeds, were taken as a criterion for hybrids in this work. Unfortunately it was not possible to substantiate this view by the experimental production of artificial hybrids, as Turesson (1925) could prove in the genus *Atriplex*, also a member of the Chenopodiaceae.

In South Africa it was observed that salt marshes with gently sloping banks and ill-defined zonation often have a higher frequency of hybrids. In a few localities, such as at Milnerton, hybrids appeared to form about a quarter of the population. The large quantity of hybrid plants in this locality is primarily due to the occurrence of the two very vigorous hybrids, *A. pillansii* × *A. natalense* and *A. perenne* × *A. pillansii*. These hybrids produce extensive mats up to three metres in diameter and apparently compete very successfully with their parents.

Since the species of *Arthrocnemum* and *Salicornia* are wind-pollinated and all species flower at about the same time, hybridization is highly likely when they grow together. In species like *A. pillansii*, in which male-sterile plants may occur, the possibility of hybridization is enhanced by the occurrence of purely female plants which must be fertilized with pollen from plants nearby. This may perhaps account for the many hybrids of which *A. pillansii* is one of the parents.

In the genus *Salicornia* in Southern Africa only one putative hybrid has been recorded. This can probably be ascribed to the fact that the different species tend to grow in different localities. In Europe, where more than one species of *Salicornia* may occur at the same locality, hybridization is more likely. However, recent authors such as König (1960), Aellen (1961) and Dalby (1962) could not find any evidence for such hybrids.

Taxonomically the hybrids are not as important as might seem from the treatment now presented, and the number of such specimens seen in herbaria did not constitute more than 1 per cent. When it was realized that these hybrids are sterile, a special search was made for them in order to describe them and avoid later confusion. As a result of this close study, it was found that apparently two types of hybrids may occur between each pair of parents but, nevertheless, I did not succeed in finding all the possible combinations.

In the field, hybrids can be recognized according to several peculiarities which they may exhibit. With some knowledge of the species occurring in an area, hybrids can easily be recognized by their abnormal habit. The branches are often excessively tortuous and lateral branches arise from the main branches at varying angles. Once struck by the odd habit, one immediately recognizes the intermediate character of the plant, while colours are often especially striking. For example, in a population at Bredasdorp containing *A. natalense* and *A. decumbens*, a hybrid showed the habit and colour of *A. natalense* and could be mistaken for this species at first glance. The multi-flowered cymules and the type of flowers of this hybrid indicate that *A. decumbens* is the other parent. Dried material could, however, be mistaken for *A. perenne* or *A. decumbens*.

The stigmata of hybrids were found to be larger and to persist for a longer time even after the pollen is shed, than in the parent plants. Even more characteristic is the irregular flowering of hybrids with odd spikes being produced throughout the year. This presumably has resulted in many collections of hybrids when the species themselves are not flowering. However, the main flowering period for all the hybrids is from February to May, even in putative hybrids of *A. capense*, a species which normally flowers in October and November.

Furthermore the fruiting spikes of hybrids usually dry from the apex downward. The spikes of the parental plants become mature from the lower cymules upwards, and the whole spike dries at more or less the same time. Also the perianth tubes shrink considerably when drying and are, as a rule, not cork-like.

The hybrids are classified in three groups according to the sclereids in the palisade tissue. Hybrids between species with uniformly thickened sclereids and spirally thickened sclereids usually produce an intermediate type of sclereid (Fig. 2: 6). The walls of these sclereids are at first uniformly thickened but produce additional, often incomplete, spiral striations. A separation of specimens with this type of sclereid from those with spirally thickened sclereids would be impractical as sections of herbarium material are often insufficiently clear to distinguish between the two.

A key to the hybrids recognized by the present author, and which probably includes all the commoner combinations, is given below, although this does not exclude the possibility that additional hybrid combinations could be found.

In accordance with Article 1, Appendix 1, of the International Code of Botanical Nomenclature (1961) the names of the putative parents in the formula of the hybrids were placed in alphabetical order. However, in view of the fact that two different types of progeny seem to be possible from the hybridization of a pair of putative parents a type A and a type B were designated, indicating whether the resemblance of the hybrid is considered to be greater to the parent placed first or second in the formula.

KEY TO THE PUTATIVE HYBRIDS

Group A. Hybrids without sclereids in the palisade tissue; flowers usually with ill-defined lateral shield; (usually hybrids with *A. natalense* as one of the parents).

1a. Cymules 3-flowered:

2a. Branches woody, ascending or decumbent:

3a. Branches ascending: segments green..... 1. *A. natalense* × *A. terminale*

3b. Branches decumbent, almost procumbent; segments glaucous 2. *A. natalense* × *A. pillansii*

2b. Branches herbaceous, succulent, prostrate or decumbent:

4a. Barren segments succulent, 3–5 mm thick:

5a. Dried segments light coloured..... 5. *A. capense* × *A. natalense*

5b. Dried segments dark coloured..... 3. *A. natalense* × *A. perenne*

4b. Barren segments scarcely succulent, 2–3 mm thick..... 4. *A. capense* × *A. natalense*

1b. Cymules (3–) 4–7-flowered:

6a. Cymules 3 or 4 (–5)-flowered; flowers with ill-defined lateral shield 6. *A. decumbens* × *A. natalense*

6b. Cymules 4–7-flowered: flowers with clearly defined lateral shield 7. *A. decumbens* × *A. natalense*

Group B. Hybrids with uniformly thickened sclereids.

1a. Barren segments 8–15 mm long, 3–5 mm thick; branches often rooting at the nodes 11. *A. decumbens* × *A. capense*

1b. Barren segments 3–8 mm long, if longer then narrower than 3 mm; branches not rooting at the nodes:

2a. Plants prostrate or procumbent; barren segments often longer than 5 mm:

3a. Terminal spikes 15–20 mm long..... 8. *A. mossianum* × *A. natalense*

3b. Terminal spikes 20–30 (–70) mm long..... 9. *A. mossianum* × *A. natalense*

2b. Plants ascending rarely decumbent; segments 3–5 mm long.. 10. *A. mossianum* × *A. pillansii*

Group C. Hybrids with spirally thickened sclereids or uniformly thickened sclereids with spiral striations superimposed.

1a. Cymules 3–7-flowered:

2a. Plants ascending, woody..... 21. *A. decumbens* × *A. pillansii*

2b. Plants prostrate, scarcely woody:

3a. Branches straight: cymules 3–5 (–7)-flowered..... 23. *A. decumbens* × *A. perenne*

3b. Branches tortuous: cymules 3- or 4-flowered..... 24. *A. decumbens* × *A. perenne*

1b. Cymules 3-flowered:

4a. Flowers scarcely exposed, somewhat laterally flattened, with ill-defined lateral shield:

5a. Barren segments 8–12 mm long..... 12. *A. natalense* × *A. pillansii*

5b. Barren segments 12–18 mm long..... 13. *A. natalense* var. *affine* × *A. pillansii*

4b. Flowers exposed, obpyramidal, with lateral shield:

6a. Branches becoming woody:

7a. Dead segments barrel-shaped, cork-like:

8a. Plants with ascending branches: spikes cylindrical when fruiting 18. *A. capense* × *A. pillansii*

8b. Plants with decumbent branches, sometimes creeping; spikes tapering when fruiting 17. *A. capense* × *A. pillansii*

7b. Dead segments not barrel-shaped and not cork-like:

9a. Sclereids uniformly thickened with usually incomplete spiral striations 14. *A. terminale* × *A. pillansii*

9b. Sclereids spirally thickened..... 16. *A. pillansii* × *A. perenne*

6b. Branches scarcely woody:

10a. Dead segments barrel-shaped, cork-like:

11a. Fruiting segments bulging:

12a. Spikes often clustered at the end of branches, thicker than barren segments 15. *A. perenne* × *A. pillansii*

12b. Spikes not clustered at the end of branches, not thicker than barren segments 20. *A. capense* × *A. perenne*

- 11b. Fruiting segments not bulging:
 13a. Barren segments 3–4 mm thick; spikes 20–30 mm long 24. *A. decumbens* × *A. perenne*
 13b. Barren segments 2–3 mm thick; spikes 10–20 mm long, if longer than segments not succulent:
 14a. Plants much branched; segments green fading to brown or brownish-red 19. *A. capense* × *A. perenne*
 14b. Plants little branched; segments glaucous fading to bluish-red 17. *A. capense* × *A. pillansii*
- 10b. Dead segments cylindrical or obconical, not cork-like:
 15a. Spikes usually cylindrical when flowering; fruiting segments not bulging 21. *A. decumbens* × *A. pillansii*
 15b. Spikes tapering when flowering; fruiting segments bulging:
 16a. Plants much branched; spikes terminal..... 24. *A. decumbens* × *A. perenne*
 16b. Plants little branched; spikes terminal and lateral.. 15. *A. perenne* × *A. pillansii*

Group A

1. *A. natalense* × *A. terminale*

CAPE.—Vanrhynsdorp: Salt River, Tölken 557.

This hybrid resembles *A. terminale* in producing dull green and brownish-red segment colours and in its shrubby habit, but the spikes are terminal and lateral, the lateral shield ill-defined, the stigmas are spreading and the sclereids in the palisade tissue are absent; all these characters are typical of *A. natalense*.

2. *A. natalense* × *A. pillansii* (Type B)

CAPE.—Peninsula: Milnerton, Tölken 542. Bredasdorp: Seekoeivlei, Tölken 514. Port Elizabeth: Swartkopsrivier, Archibald 4900/3 (GRA).

This hybrid resembles *A. pillansii* in its woody branches and the glaucous green and bluish-red segment colours, but it also exhibits a procumbent habit and spreading stigmas characteristic of *A. natalense*.

3. *A. natalense* × *A. perenne*

CAPE.—Peninsula: Salt River, Moss 8754.

The specimen of this hybrid appears to be one involving *A. natalense*, especially since it exhibits spreading leaf apices and lack of sclereids. However, it has exposed flowers with a definite lateral shield typical of *A. perenne*, another prostrate species. A very similar specimen (Moss 8757) is probably a plant of *A. perenne* grown under very moist conditions, so that the sclereids are not formed. Moss on the sheet described it as *A. capense* × *A. perenne* which is highly unlikely because of the absence of sclereids.

4. *A. capense* × *A. natalense* (Type A)

CAPE.—Peninsula: Kommetjie, Moss 8883b (J).

Most of the specimens on the sheet must be regarded as normal *A. capense*, but one detached branch is certainly a hybrid, although it looks very much like the rest of the collection. The flowers of this specimen contain aborted anthers and no seeds are developed. No sclereids but only passage cells were observed, whereas the rest of the collection has sclereids typical of *A. capense*.

5. *A. capense* × *A. natalense* (Type B)

CAPE.—Peninsula: Kommetjie, Moss 11681 (J).

The specimen of this hybrid resembles *A. natalense* in its fleshy, obconical segments and the absence of the sclereids, but the exposed flowers with a lateral shield resembles those of *A. capense*, the other species present at the locality.

6. *A. decumbens* × *A. natalense* (Type A)

MOZAMBIQUE.—Lourenco Marques: Matola Road, Tölken 1091; Matola Bridge, Tölken 1094.

This hybrid differs from *A. decumbens* × *A. natalense* (Type B) by its shorter and barrel-shaped, rarely cylindrical segments which are glaucous green. Also 3 or 4 (-5)-flowered cymules are produced. This hybrid resembles *A. decumbens* in its glaucous segment colours, fading to bluish-red and rarely individual segments becoming yellow. It is similar to *A. natalense* in its long tapering spikes with flowers with ill-defined lateral shield and the absence of sclereids and passage cells in the palisade tissue.

7. *A. decumbens* × *A. natalense* (Type B)

CAPE.—Bredasdorp: De Hoopvlei, Tölken 517.

MOZAMBIQUE.—Lourenco Marques: Matola Bridge, Tölken 1093.

When fruiting this putative hybrid superficially resembles *A. perenne*, but the fertile segments are hardly wider than the barren segments, and 4 to 7 flowers per cymule are found. This hybrid is different from *A. decumbens* × *A. natalense* (Type A) in that it produces 4-7-flowered cymules and the flowers have a clearly defined lateral shield. This hybrid is very similar to *A. natalense* in its green, often yellow or yellowish-brown segments colours and the absence of sclereids, but occasionally passage cells occur.

Group B

8. *A. mossianum* × *A. natalense* (Type A)

CAPE.—Caledon: 10 miles west of Riviersonderend, Tölken 528.

This hybrid resembles *A. mossianum* in its woody branches and short spikes with truncate flowers, as well as having the typical sclereids in the palisade tissue. However, the uniformly thickened sclereids vary in form, 2-3 times as long as wide, angular and not branched. The stomata are sunken. The pink colour of the segments which are often shiny, the prostrate habit and the more succulent segments are characteristic of *A. natalense*.

9. *A. mossianum* × *A. natalense* (Type B)

CAPE.—Bredasdorp: Spitzkop, Tölken 522.

This hybrid is similar to *A. natalense* in producing long tapering spikes with flowers with ill-defined lateral shield and branches tough in texture. The dead leaves do not adhere to the branches, the segments are glaucous in colour and the type of sclereids in the palisade tissues is typical of *A. mossianum*. The uniformly thickened sclereids are angular and variable in form but never branched. The stomata are sunken.

10. *A. mossianum* × *A. pillansii*

CAPE.—Caledon: 10 miles west of Riviersonderend, Tölken 554.

The uniformly thickened sclereids present in the palisade tissue are not branched. This hybrid is very similar to *A. mossianum*, but the branches are flexuous and flexible, instead of producing straight erect, brittle branches. This and the many spikes clustered at the end of branches are reminiscent of *A. pillansii*. As this hybrid does not produce any stamens, it could be confused with functionally female plants of *A. mossianum*.

11. *A. decumbens* × *A. capense*

CAPE.—Caledon: Uilenkraalrivier, Tölken 502.

Although *A. decumbens* was not found in the immediate vicinity, it occurred about half a mile further up the river. The second putative parent can, however, only be *A. decumbens* because of the segment colours and the type of sclereids, which do not reach the epidermis. The frequent rooting at the nodes and the sunken stomata are characteristic of *A. capense*.

Group C

12. *A. natalense* × *A. pillansii* (Type A)

CAPE.—Peninsula: Rugby, Tölken 547.

The pink colour of the segments, the long tapering spikes with flowers with ill-defined lateral shield and spreading stigmas found in this hybrid are characteristic of those of *A. natalense*, but the shrubby habit and spirally thickened sclereids in the palisade tissue are reminiscent of *A. pillansii*.

13. *A. natalense* var. *affine* × *A. pillansii*

CAPE.—Hopefield: 8 miles west of Koperfontein, Tölken 474b.

The long prostrate main branches and long segments of this hybrid resemble those of *A. natalense* var. *affine*. However, characters such as the woody branches and spirally thickened sclereids in the palisade tissue are characteristic of *A. pillansii*.

14. *A. pillansii* × *A. terminale*

CAPE.—Namaqualand: Swart Lintjiesrivier, Pillans in BOL 18215b (BOL, STE).

On both sheets only one sprig of this hybrid is found together with the typical *A. terminale*. The spreading branches and the incomplete spiral striations of the sclereids indicate hybridity with *A. pillansii*, the other species recorded from the locality. Although no fertile material of this hybrid was available, the specimen was immediately suspected of hybridity.

15. *A. perenne* × *A. pillansii* (Type A)

CAPE.—Peninsula: Rugby, Tölken 549.

This hybrid is very similar to *A. capense* × *A. perenne* (Type A) but differs in having bulging fruiting segments as in *A. perenne*. It differs from *A. perenne* × *A. pillansii* (Type B) in having prostrate main branches, which are tough in texture and are rarely woody in old branches. The bulging fruiting segments and the brownish-red segments colour is similar to *A. perenne*, but the clustered spikes and the non-succulent segments are rather like *A. pillansii*.

16. *A. perenne* × *A. pillansii* (Type B)

CAPE.—Peninsula: Rugby, Tölken 550.

This hybrid differs from *A. perenne* × *A. pillansii* (Type A) and *A. perenne* in having brittle hardly ascending, secondary branches which become woody with age. However, the almost prostrate main branches with ascending lateral branches are very unlike the habit of *A. pillansii*.

17. *A. capense* × *A. pillansii* (Type A)

CAPE.—Peninsula: Milnerton, Adamson s.n. (CT); Rugby, Tölken 548; Paardeneiland, Tölken 147.

This hybrid resembles *A. capense* in its scarcely woody but tough branches with old leaves adhering to them and its prostrate growth, but the clustered spikes and spirally thickened sclereids are characteristic of *A. pillansii*. This hybrid is very similar to *A. perenne* × *A. pillansii* (Type A), but differs in producing barrel-shaped and cork-like dead leaves, and not bulging fruiting segments.

18. *A. capense* × *A. pillansii* (Type B)

CAPE.—Peninsula: Paardeneiland, *Tölken* 546.

This hybrid is very similar to *A. pillansii*, but can be recognized by its persistent stigmas and by the fact that the flowers are equal in size and instead of bulging, they are dented. These flowers and the sunken stomata are typical of *A. capense*. In herbarium material the cork-like segments are characteristic. It differs from *A. capense* × *A. pillansii* (Type A) in having a shrubby habit.

19. *A. capense* × *A. perenne* (Type A)

CAPE.—Peninsula: Paardeneiland, *Tölken* 551; Salt River, *Moss* 8761 (J).

This hybrid differs from *A. perenne* × *A. pillansii* (Type A) in having a different colour and smooth spikes. This hybrid resembles *A. capense* in its cylindrical spikes of which the segments do not bulge and in the cork-like dead leaves adhering to the branches, however the spirally thickened sclereids are typical of *A. perenne*.

20. *A. capense* × *A. perenne* (Type B)

CAPE.—Peninsula: Rugby, *Tölken* 549.

This hybrid is in all its characters very similar to *A. perenne* when grown under dry conditions, but the thick walls of the sclereids suggest hybridity with *A. capense*.

21. *A. decumbens* × *A. pillansii* (Type A)

CAPE.—Caledon: Mierkraal, *Tölken* 532. Port Elizabeth: Swartkopsrivier, *Archibald* 5821.

This hybrid differs from *A. decumbens* × *A. pillansii* (Type B) in its decumbent habit and its consistently 3-flowered cymules. This hybrid resembles *A. decumbens* in its decumbent habit, whereas the clustered spikes and spirally thickened sclereids in the palisade tissue indicate hybridity with *A. pillansii*.

22. *A. decumbens* × *A. pillansii* (Type B)

CAPE.—Caledon: 10 miles west of Riviersonderend, *Tölken* 531. Port Elizabeth: Swartkopsrivier, *Archibald* 5820 (BOL, GRA).

This hybrid differs from *A. decumbens* × *A. pillansii* and *A. decumbens* in its ascending habit similar to that of *A. pillansii*, but it often produces more than three flowers per cymule, a character typical of *A. decumbens*.

23. *A. decumbens* × *A. perenne* (Type A)

CAPE.—Bathurst: Kowie River, *L. Britten* 5200 (GRA).

MOZAMBIQUE.—Lourenco Marques: Lourenco Marques, *Macnae* 7.

This hybrid has straight not flexuous branches, tapering spikes when flowering and usually more than three flowers per spike in contrast with *A. decumbens* × *A. perenne* (Type B). In herbarium material it is almost indistinguishable from *A. decumbens*. In fresh material it resembles *A. perenne* in producing green segments, not glaucous as characteristic in *A. decumbens*.

24. *A. decumbens* × *A. perenne* (Type B)

CAPE.—"Albany", *Phillips* s.n.

This hybrid differs from *A. decumbens* × *A. perenne* (Type A) in having cork-like segments and the branches thin and flexuous. This hybrid resembles *A. perenne* in its prostrate habit and flexuous branching and three flowers per cymule, but the much thickened walls of the sclereids suggest hybridity with *A. decumbens*.

KEY TO THE GENERA IN SOUTHERN AFRICA

- Perennial, prostrate to ascending; not all branches ending in fruiting spikes; stigma bifid or trifid; normally protogynous..... 1. *Arthrocnemum*
 Annual shrublets; all branches ending in fruiting segments; stigma tufted; normally protandrous..... 2. *Salicornia*

1. ARTHROCNEMUM

Arthrocnemum Moq., Chenop. Monogr. Enum. 111 (1840); in DC., Prodr. 13, 2: 114 (1849); Ung.-Sternb., Vers. Syst. Salic. 36 (1866); in Atti Congr. Int. Bot. Firenze 1874: 268 (1876); Benth. & Hook.f., Gen. Pl. 3, 1: 65 (1880); Moss in Adamson in J. S. Afr. Bot. 20: 4 (1954); Brenan in Fl. Trop. E. Afr. Chenopodiaceae: 18 (1954). Type species: *A. fruticosum* (L.) Moq.

Perennial plants, prostrate, decumbent or ascending. *Branches* often rooting at the nodes and not all branches terminating in flowering spikes. *Cymules* often three flowered but also up to nine-flowered. *Flowers* equal in size, or nearly so, normally distinctly protogynous or protandrous (*A. mossianum*), rarely flowering simultaneously. *Stigma* bifid or trifid, minutely papillose to plumose, up to 4 mm long, distinctly visible in fresh material. *Seeds* with membranous testa, glabrous, papillose or covered with hairs, with no endosperm and a conduplicate embryo or with hard pericarp, endosperm present and a straight embryo.

The genus has a world wide distribution and occurs mainly in saline marshes.

KEY TO THE SPECIES OF ARTHROCNEMUM BASED ON FLOWERING MATERIAL

Hybrids are not included in this key: they are dealt with separately (see pp. 268). Hybrids can be recognized by no embryo developing in the seeds; the pollen grains not round but often dented; and much smaller grains occurring together with normal ones. Indications of hybrid material are:—

- (1) Branches often tortuous.
 - (2) Prominent stigmas persisting for a long time.
 - (3) Flowering spikes produced outside the normal flowering period.
- 1a. Flowers covered by the bract below, or nearly so; perianth tube dorsiventrally flattened, opening at the apex of the flower:
 - 2a. Flowers deeply embedded in and fused to upper segment; fruit with glabrous, hard pericarp; endosperm present; fruit released only with the decay of the spike..... 1. *A. indicum*
 - 2b. Flowers scarcely embedded in and not fused to the segments; seeds with papillose, membranous testa; endosperm absent; fruit falling out easily..... 2. *A. natalense*
 - 1b. Flowers scarcely covered by the bract below; perianth tube obpyramidal, opening in the centre of the lateral shield:
 - 4a. Branches (not including the succulent leaf sheath) 5–30 mm in diam., not swollen at the nodes, often laterally compressed: plants ascending:
 - 5a. Spikes terminal, solitary, rarely more than one per branch; secondary branches erect, fastigiate; fleshy perianth becoming cork-like, not shrivelling when fruiting:
 - 6a. Growing in inland salt marshes; spikes less than 25 mm long; vegetative segments 8–15 mm long, 2–3 mm wide..... 4. *A. terminale*
 - 6b. Growing on gravelly beaches; spikes 20–30 (–100) mm long; vegetative segments 5–8 mm long, 3–5 mm..... 7. *A. littoreum*
 - 5b. Spikes clustered at the end of branches; secondary branches spreading; fleshy perianth shrivelling when fruiting (if not, then segments shorter than 5 mm):
 - 7a. Segments rarely up to 4 mm in length, distinctly keeled; leaf apex very much spreading, at right angles to stem when dried; uniformly thickened sclereids present in the palisade tissue..... 3. *A. mossianum*

- 7b. Segments usually longer than 4 mm, faintly keeled, leaf apex hardly spreading when dried; spirally thickened sclereids present in the palisade tissue:
- 8a. Succulent leaf sheaths shrinking considerably when dried, exposing the bare stem between them..... 6. *A. xerophilum*
- 8b. Succulent leaf sheaths hardly shrinking when dried..... 5. *A. pillansii*
- 4b. Branches (not including the succulent leaf sheath, if present) up to 5 mm in diam., rarely thicker, but then conspicuously swollen at the nodes, not laterally compressed; plants prostrate, decumbent:
- 9a. Seeds glabrous or irregularly papillose; spikes clustered at the end of the branches; branches not rooting at the nodes..... 5. *A. pillansii*
- 9b. Seeds uniformly papillose or covered with hairs; spikes usually terminal, solitary on the branches; branches often rooting at the nodes:
- 10a. Seeds papillose; 5-7 (-10) flowers per cymule; stems decumbent, rarely rooting at the nodes..... 10. *A. decumbens*
- 10b. Seeds covered with hairs; 3 rarely 4 or 5 flowers per cymule; stems prostrate, usually rooting at the nodes:
- 11a. Flowers always 3 per cymule; barren segments 10-16 mm long, 2-3 mm in diam.; uniformly thickened sclereids present in the palisade tissue..... 9. *A. capense*
- 11b. Flowers 3-5 per cymule; barren segments 5-15 mm long, 3-5 mm in diam.; spirally thickened sclereids present in the palisade tissue..... 8. *A. perenne*

KEY TO THE SOUTH AFRICAN SPECIES AND VARIETIES OF ARTHROCNEUM AND SALICORNIA
BASED ON ANATOMICAL AND VEGETATIVE CHARACTERS

As there are numerous specimens without flowers in herbaria, a second key based on anatomical and vegetative characters has been constructed. In the identification of herbarium material, even flowering specimens of doubtful nature can be checked by means of their anatomical characters. Hybrids are not included in the key, but are dealt with separately (see p. 268).

All the anatomical characters used are based on transverse sections of the segments, but it is advisable to cut longitudinal sections in case branched sclereids are present.

When dealing with herbarium material, a whole old segment or the top half of an old segment, preferably one that is not completely flattened by the drying process, is detached. It is soaked in tap water for one or two days. (The addition of a little salt was found helpful). Only in the case of very cork-like segments is it advisable to heat the material to boiling point in order to hasten the process of softening. Otherwise, boiling normally softens the tissue too much and, apart from the treated material being difficult to cut, it never regains its shape satisfactorily. Ordinary hand-sections are cut just below the membranous leaf apex, preferably several sections through the lateral ridges and several sections below that.

In assessing the anatomical features, it should be noted that the cells of the water tissue touching the epidermis in the lateral ridges are not regarded here as passage cells.

Furthermore the author is well aware that sunken stomata do not constitute a very constant character (Esau, 1960, Baumgärtel, 1917). However, for the identification of herbarium material which is normally collected in the field and not cultivated, the position of the stomata was found to be consistent.

- 1a. Palisade tissue a single cell thick; palisade cells of equal size, surrounding a single layer of isodiametric, lignified cells, in contact with the vascular bundles..... 1. *A. indicum*
- 1b. Palisade tissue 2-3 (-4) cells thick; palisade cells not of equal size, continuing into the parenchymatous water tissue, lignified cell layer absent; vascular bundles not in contact with the palisade tissue:
- 2a. Sclereids absent in the palisade tissue:
- 3a. Passage cells absent; palisade tissue with all cells containing chloroplasts 2. *A. natalense*
- 4a. Segments 5-15 mm long, 2-4 mm in diam.; main branches herbaceous, with lateral branches often longer than half their length..... var. *natalense*

- 4b. Segments 15–35 mm long, 4–6 mm in diam.; main branches hard, with lateral branches never longer than half their length..... var. *affine*
- 3b. Passage cells or other non-chlorophyllose cells present in the palisade tissue:
- 5a. Palisade tissue with many passage cells present; main branches usually tortuous, thin (2–4 mm in diam.)..... 10. *A. decumbens*
- 5b. Palisade tissue with very few passage cells present; main branches usually straight, thick (4–10 mm in diam.)..... 8(b). *A. perenne* var. *lignosum*
- 2b. Sclereids present in the palisade tissue:
- 6a. Uniformly thickened sclereids present:
- 7a. Sclereids branched and narrower than the palisade cells:
- 8a. Sclereids longer than the layer of the palisade tissue, reaching the epidermis
3. *A. mossianum*
- 8b. Sclereids shorter than the layer of palisade tissue, not reaching the epidermis
4. *A. terminale*
- 7b. Sclereids long, rectangular, as wide as, or wider than, the palisade cells:
- 9a. Sclereids rectangular but normally narrower in the middle, reaching the epidermis
9. *A. capense*
- 9b. Sclereids rectangular, not reaching the epidermis..... 10. *A. decumbens*
- 6b. Spirally thickened sclereids present:
- 10a. Sclereids about 8 times as long as wide..... 6. *A. xerophilum*
- 11b. Sclereids 2–4 (–6) times as long as wide:
- 11a. Old segments not becoming cork-like; erect annual shrublets; (usually the whole plant with tap root is collected):
- 12a. Occurring in Northern Natal and Mozambique, secondary cortex 5–8 cells thick
S. pachystachya
- 12b. Occurring in South Africa except northern Natal and Mozambique; secondary cortex 2–3 (–4) cells thick:
- 13a. Lateral branches spreading; shrublets up to 30 cm high; stomata protruding
S. meyerana
- 13b. Lateral branches erect, fastigiate; shrublets up to 15 cm high; stomata sunken
S. uniflora
- 11b. Old segments often becoming cork-like; perennials, erect bushes or prostrate herbs; (normally only a branch, often with adventitious roots, is collected):
- 14a. Branches usually without succulent leaf sheath, 5–30 mm in diam. (excluding leaf sheath), often laterally compressed; segments normally becoming light brown, seldom greyish when dried; plants frutescent or shrubby:
- 15a. Chloroplasts absent in the secondary cortex of branches that have lost their leaf sheath..... 8 (b). *A. perenne* var. *lignosum*
- 15b. Chloroplasts present in the secondary cortex of branches that have lost their succulent leaf sheath:
- 16a. Spiral striations of the spirally thickened sclereids normally faint, perpendicular or nearly so to the lateral walls; stomata at the same level as the epidermis:
- 17a. Branches erect, fastigiate; growing on gravelly beaches.... 7. *A. littoreum*
- 17b. Branches spreading; growing in inland salt marshes..... 5. *A. pillansii*
- 16b. Spiral striations of spirally thickened sclereids normally strongly lignified, oblique to the lateral walls; stomata sunken:
- 18a. Segments 2 (3) mm in diam.; western Cape Province..... 5. *A. pillansii*
- 18b. Segments (3–) 4–6 mm in diam.; Lüderitz Bay, S.W.A. 5 (b) *A. pillansii* var. *dunense*
- 14b. Branches usually with succulent leaf sheath but, if not, then up to 5 mm in diam., not laterally compressed; segments normally becoming dark coloured when dried; plants prostrate:
- 19a. Adventitious roots absent; spiral striations of spirally thickened sclereids perpendicular, or nearly so, to the lateral walls..... 5. *A. pillansii*
- 19b. Adventitious roots often present; spiral striations of spirally thickened sclereids oblique to the lateral walls:
- 20a. Branches without succulent leaf sheath, rarely exceeding 2 mm in diam.
8 (a) *A. perenne* var. *perenne*
- 20b. Branches without succulent leaf sheath 2–5 mm in diam. 8 (b) *A. perenne* var. *lignosum*

1. *A. indicum* (Willd.) Moq., Chenop. Monogr. Enum. 113 (1840); in DC., Prodr. 13, 2: 151 (1849); Ung.-Sternb., Vers. Syst. Salic. 69 (1866); in Atti Congr. Int. Bot. Firenze 1874: 274 (1876); Hook.f., Fl. Brit. India 5, 1: 12 (1886); Bak. & C.B.Cl. in Fl. Trop. Afr. 6, 1: 86 (1909), quoad descr., excl. specim. cit.; Moss in Adamson in J. S. Afr. Bot. 20: 5 (1954); Brenan in Fl. Trop. E. Afr. Chenopodiaceae: 18 (1954). Type: India, Madras Presidency, Tranquebar, Klein in Herb Willdenow 54 (B, holo.; PRE, photo!).

Salicornia indica Willd. in Ges. Naturf. Fr. Neue Schriften 2: 111–112, pl. 4, fig. 2 (1799); Vahl, enum. 1: 10 (1804); Wight, Icon. 3, 1, fig. 737 (1844).

Woody or scarcely woody perennial, prostrate or decumbent up to 25 cm high, forming mats about 60 cm in diameter. *Barren segments* 5–9 mm long, 4–6 mm in diameter, obconical to barrel-shaped, with keeled leaf apex and lateral ridge, glaucous green fading to bluish-red; leaf apex of young leaves spreading when dried, cylindrical and cork-like in older leaves; dead leaves adhering to the branches. *Sclereids* uniformly thickened and in shape similar to the palisade cells; palisade tissue in a single layer, each cell about twice as long as wide, surrounding a single layer of isodiametric cells which become lignified. *Spikes* terminal, 10–30 mm long, rarely longer, tapering when flowering, often cylindrical when fruiting; flowering segments wider than the barren segments below; fruiting spikes becoming hard and cork-like, and fruit released by its decay. *Cymules* 3-flowered; flowers completely embedded in lower and upper segments. *Perianth tube* 3-dentate, not truncate but dorsiventrally flattened, opening at the apex, fused to the upper segments. *Anther* 1 or 0. *Stigmas* bifid, papillose, spreading. *Fruits* triangular, much flattened laterally with hard pericarp, glabrous, light yellow to brown; endosperm starchy, anterior; embryo straight, posterior. FIG. 3: 3.

A. indicum occurs in salt marshes in all tropical regions around the Indian Ocean and occasionally on the west coast of Africa. No specimen of this species from South Africa has been seen by the present author, and the Galpin collection reputedly from Eshowe, cited by Moss as the southernmost locality, could not be traced. Flowering and fruiting period from July to March.

MOZAMBIQUE.—Lourenco Marques: Maputo, Hornby 2591; Lourenco Marques, Moss 3135 (GRA, J); St. Georges Island, Gomes e Sousa 4166; Matola Road, Moss & Otley 11740 (J); Porto Amelia, Macnae in J 37543 (J).

Brenan (1954) mentions that he was unable to find stamens in the material investigated. However, in fresh material from Lourenco Marques an anterior stamen was observed, but it does not develop to its full size in all flowers and, in addition, the staminode is sometimes fused to the anterior wall of the perianth tube. A second posterior stamen was never seen.

Although Moquin effected the combination for this species under *Arthrocnemum*, there is some doubt whether he referred to the same species. “Semen . . . hispidulum. Albumen parcissimum. Radicula exerta . . .” suggests seeds very unlike those of *A. indicum*.

According to Moss (1954) the greater part of *A. macrostachyum* sensu Hiern, Cat. Afr. Pl. Welw. 1, 4: 899 (1900), non Moris et Delport, must be referred to *A. indicum*. This can also be deduced from the descriptions of the specimens by Hiern. The same specimens are cited by Baker & C. B. Clark (1909) under *A. macrostachyum* and *A. fruticosum* and not under *A. indicum*, though mentioned as a different species.

When Chevalier (1922) transferred *Salicornia pachystachya* to the genus *Arthrocnemum*, he based his decision on the collection, Perville 661, a specimen of *A. indicum* from Madagascar (see *S. pachystachya*, p. 298).

2. *A. natalense* (Bunge ex Ung.-Sternb.) Moss in Adamson in J. S. Afr. Bot. 20: 15 (1954). Type: "Port Natal", Drege s.n. (LE, lecto.; PRE, photo.!).

Scarcely woody perennial, prostrate or decumbent, forming dense mats or solitary in irregular rosettes 20–80 cm in diameter, not higher than 30 cm; main branches flat on the ground, often rooting at the nodes. *Barren segments* 5–35 mm long, 2–6 mm in diameter, obconical or cylindrical, slightly keeled, with or without a lateral ridge, shining to dull grey-green or light yellowish-green, fading to brownish-yellow or pinkish-red; leaf apex spreading when dried; dead leaves adhering to the branches. *Sclereids* absent in the palisade tissue. *Spikes* terminal, rarely lateral, (10–) 20–30 (–80) mm long, tapering when flowering and fruiting; flowering segments not wider than barren segments below. *Cymules* 3-flowered; flowers hidden by the bract below in fresh material, in dried material flowers often exposed, protogynous. *Perianth tube* with three dentate lobes, seldom with a fourth anterior lobe, not truncate but dorsiventrally flattened, adhering to the seeds. *Anthers* 1 or 2. *Stigmas* bifid, papillose, spreading. *Seeds* compressed, oblong to ovate with membranous testa, rough or papillose; endosperm absent; embryo conduplicate.

A. natalense is the most common of all the species occurring in South Africa and is found from Angola to Mozambique, mainly along the coast, but also as far inland as Calvinia, Worcester and Riversdale. It has also been recorded from Madagascar (Bossier 15431). It does not thrive when submerged by sea water, even temporarily.

Moss and others remarked on the similarity of *A. natalense* and *A. indicum* but the resemblance is merely superficial. If the flowers, seeds and the anatomy are investigated, significant differences are found.

Two varieties are recognized in South Africa:

Barren segments 5–15 mm long, 1–4 mm in diameter; main branches softly herbaceous, with lateral branches often longer than half their length..... (a) var. *natalense*

Barren segments 15–35 mm long, 4–6 mm in diameter; main branches hard, with lateral branches never longer than half their length..... (b) var. *affine*

(a) var. *natalense*

Salicornia natalensis Bunge ex Ung.-Sternb., Vers. Syst. Salic. 62 (1866); in Atti Congr. Int. Firenze 1874: 292, fig. 11 (1876); Wright in Fl. Cap. 5, 1: 450 (1911). *Salicornia fruticosa* var. *capensis* Ung.-Sternb., Vers. Syst. Salic. 59 (1866), non Wright. Type: "Cap. ('Salicornia indica, W. Ecklon und Zeyher pl. Cap. 26n. oder '62, 11'?)".

Arthrocnemum natalense (Bunge ex Ung.-Sternb.) Moss in Adamson in J. S. Afr. Bot. 20: 15 (1954). *A. africanum* Moss ex Fourcade, Mem. Bot. Surv. S. Afr. 20: 19 (1941), nomen nudum. *A. africanum* Moss in Adamson in J. S. Afr. Bot. 14: 37 (1948); J. S. Afr. Bot. 20: 7 (1954); Adamson in Fl. Cape Penins. 357 (1950). Type: Peninsula, Fishhoek, Moss in BOL 14243 (BOL, holo.!).

Herbaceous perennial, prostrate, forming dense mats, seldom higher than 15 cm; much branched with inconspicuous main branches and secondary branches irregularly branched and longer than half the main branches, often tortuous, soft and flexible. *Barren segments* 5–15 mm long, 2–4 mm in diameter, usually obconical, shining to glaucous green. *Seeds* compressed, oblong to obovate. FIG. 3: 1.

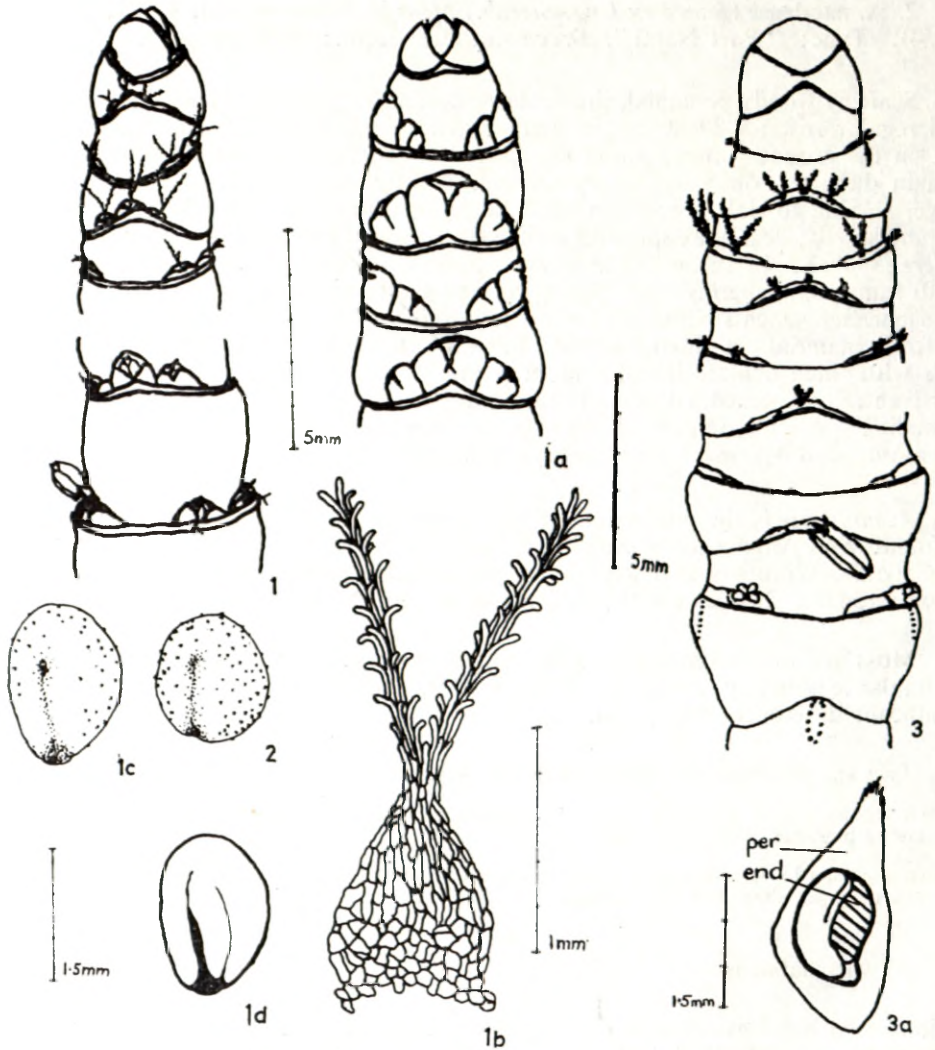


FIG. 3.—1, *Arthrocnemum natalense* var. *natalense*, flowering spike; 1a, fruiting spike; 1b, gynoecium; 1c, seed in surface view; 1d, seed in longitudinal section. 2, *A. natalense* var. *affine*, seed in surface view. 3, *A. indicum*, flowering spike; 3a fruit in longitudinal section. end.—endosperm; per.—pericarp.

This variety is recorded from Lambert's Bay and the Vanrhynsdorp district along the South African coast to Mozambique. It grows normally in soils of lesser salinity and not along the sea unless it has a supply of fresh water. It occupies the lowest zone in inland salt marshes. In the Cape it is often submerged in temporary vleis for up to three months. The old leaves rot off and only small terminal and lateral buds on the apparently dead branches remain dormant until the branches re-appear above the surface of the water. This has led to the frequently expressed view that this species is an annual. The flowering and fruiting period is usually from January to May. In Natal it begins to flower again in June–July indicating that it has two main flowering seasons there.

CAPE.—Bathurst: Kowie River, *L. Britten* 2118 (GRA, J, K); Great Fish River, *Tölken* 396. Bredasdorp: Elim, *Tölken* 505; De Hoop Vlei, *Barker* 8729 (NBG); Spitzkop, *Tölken* 519. Caledon: Botrivier, *Tölken* 488; Hermanus, *L. Guthrie* in BOL 1700 (BOL); Riviersonderend, *Tölken* 530. Calvinia: *Leighton* 2440. Clanwilliam: Lambert's Bay, *Pole Evans* 27; *Tölken* 142 (BOL). East London: Buffalo River, *Ottley* 2568 (J); Nahoon River, *Galpin* 5673. Elliotdale: Bashee River, *Macnae* in J 33177 (J). George: Wilderness, *Stephens* in BOL 18839 (BOL). Hopefield: 2 miles west of Hopefield, *Tölken* 417. Humansdorp: Gamtoos River, *Tölken* 376. Knysna: Swartvlei, *Martin* 4521; Keurboomsrivier, *Tölken* 409. Malmesbury: Ysterfontein, *Tölken* 484a. Mossel Bay: Great Brak River, *Moss* 4342 (J). Peddie: Great Fish River, *Tölken* 396; Keiskama River, *Tölken* 401. Peninsula: Rugby, *Tölken* 347; 348; Salt River, *Burchell* 667 (K); Black River, *H. Bolus* 3708 (BOL); Uitvlugt, *Wolley Dod* 2691 (BOL); Mowbray Flats, *Marloth* 8145; Noordhoek, *Barnard* in SAM 44148 (SAM); Fishhoek, *Moss* in BOL 14243 (BOL). Port Elizabeth: Swartkopsrivier, *Archibald* 5814 (BOL, GRA); *Moss* 17041 (J). Port St. Johns: Second Beach, *Tölken* 405. Riversdale: *Muir* 4645 (J); Gouritz River, *Tölken* 350. Stellenbosch: Kuilsrivier, *Tölken* 300. Somerset West: Strand, *Parker* 4732 (BOL, K, NBG). Vánrhynsdorp: Salt River, *Acocks* 14187. Vredendal: near Heerenlogement, *Tölken* 539. Worcester: Over Hex Station, *Tölken* 491.

NATAL.—Durban: Isipingo, *Forbes & Obermeyer* 32; *Strey* 4566; Durban Bay, *Pillans* 6277. Hlabisa: St. Lucia Estuary, *Ward* 4375; False Bay Park, *Ward* 4216. Ingwavuma: Kosi Estuary, *Tinley & Ward* 3. Lower Umfolozi: Richard's Bay, *Lawn* 1608 (NH). Mtunzini: Umlalazi, *Ward* 4228. Umlazi: Umgababa River, *Tölken* 407.

MOZAMBIQUE.—Lourenco Marques: Maputoland, *Wager* s.n. (GRA); Costa da Sol, *Macnae* s.n. (BOL, J); Inhaca Island, *M. Moss* 27423; *Mogg* 27145.

The type of *S. natalensis* is cited as being in the Bunge Herbarium and in the type description both flowers and adventitious roots are mentioned. Also the type is given as being a collection made by Drege at Port Natal (Durban).

The only sheet from Herb. Bunge containing a specimen collected by Drege at Port Natal, that could be found by Prof. Rycroft during his visit to Leningrad, was one on which were three specimens bearing characteristic Drege collecting labels. These specimens are annotated as "*Salicornia indica* Willd. a Cap. b. sp. Drege; *Salicornia herbacea procumbens* Cap. b. sp. Drege; 80. 20 Cap. b. sp. Drege". Judging from the citation in Drege, *Zwei pflanzengeographische Documente*, the only collection made by Drege at Port Natal was that distributed under the name *S. indica*. This specimen bears both adventitious roots and flowers and appears to be the main element from which Ungern Sternberg prepared his description, as it is the only specimen with flowering spikes. It seems that this specimen on the bottom left hand corner must be taken as the lectotype despite the fact that the specimen at the bottom right hand corner, without flowers, is accompanied by a label, in an unknown hand, reading "*S. natalensis* Bunge sp. nov. teste Bunge". It is possible that this label was intended to refer to all three specimens.

The ovate seeds and the mention of the similarity of the flowers to *A. indicum* by Ungern Sternberg (1866) can apply only to *A. natalense* as defined here and not to *A. perenne*, the only other species occurring in the vicinity of Durban. In the Cape the seeds of this variety are oblong in contrast to the ovate seeds of the var. *affine*. In Natal, however, they are more ovate. It is curious to find that Moss regarded the rooting at the nodes, mentioned in the type description, as a major obstacle in accepting that *A. natalense* is the same species as what he called *A. africanum*. This character can be seen in numerous specimens. Moss's suggestion that the Drege specimen is a hybrid does not seem likely, as Ungern Sternberg gave such detailed descriptions of the seeds. The present author has never found seeds in specimens regarded as being hybrids. Eventually Moss distinguished between *A. africanum* and *A. natalense* on the presence or absence of endosperm, respectively. In specimens identified and cited by Moss as *A. africanum* no endosperm could be found and this material could not be separated from *A. natalense*. The type specimen of *A. africanum* is in the flowering stage and does not bear any seeds. Therefore, *A. africanum* is treated as a synonym of *A. natalense*.

It is not possible to decide finally whether *S. fruticosa* var. *capensis* is also synonymous with *A. natalense*, but the obconical segments combined with prostrate growth strongly suggest that this is the case.

Two specimens of *A. natalense* (Tölken 142a, 417) were found which show peculiarities in their anatomy, in exhibiting dumb-bell shaped sclereids, in longitudinal sections of the secondary cortex. Superficially this form is indistinguishable from the typical form of *A. natalense*, which lacks these sclereids.

In *A. natalense*, terminal proliferation, i.e. vegetative growth above the spike, can often be observed (cf. Tölken 147b). This might be repeated up to three times.

The following putative hybrids are recorded (for key see p. 268):—

<i>A. mossianum</i> × <i>A. natalense</i>	<i>A. capense</i> × <i>A. natalense</i>
<i>A. natalense</i> × <i>A. terminale</i>	<i>A. decumbens</i> × <i>A. natalense</i>
<i>A. natalense</i> × <i>A. pillansii</i>	

(b) var. *affine* (Moss) Toelken, stat. nov.

A. affine Moss in Adamson in J. S. Afr. Bot. 20: 8 (1954). Type: Swakopmund, Moss 18122a (PRE, lecto.!: J!).

Scarcely woody perennial, prostrate or decumbent, forming rosettes or mats up to 30 cm high; main branches long, straight; lateral branches arising in pairs at each node, shorter than half the length of the main branches, usually not branched. *Barren segments* 15–35 mm long, 4–6 mm in diameter, usually cylindrical or nearly so, light greyish-green or bluish-green. *Seeds* ovate. FIG. 3: 2.

The var. *affine* is recorded from Angola, southwards along the coast to Ysterfontein. It occurs in similar habitats to the var. *natalense*, except that it is also found around lagoons with sea water. The main flowering and fruiting period is from November to April, but it appears that in the Namib, if water is plentiful, continuous flowering throughout the year is possible.

CAPE.—Hopefield: 8 miles east of Koperfontein, Tölken 475b. Malmesbury: Ysterfontein, Tölken 484. Namaqualand: Orange River, Pillans 5577 (BOL); Wallekraal, Pillans in BOL 18218; 18219 (BOL, STE). Vanrhynsdorp: Salt River, Tölken 538.

SOUTH WEST AFRICA.—Kaokofeld: Unjab River, Giess 3927. Swakopmund: 11 miles north of Swakopmund, Hardy & De Winter 1454; Swakopmund, Moss 18122; Merxmüller & Giess 1740; Bradfield 590; Dinter in SAM 71408 (SAM); Galpin & Pearson 7586; Sandwich Harbour, Giess 5049 (Windhoek).

In its typical form *A. affine* has stouter and longer segments, but intermediates occur. The collection Merxmüller & Giess 1740 consists of branches of the typical form and of a much less vigorous plant, both found at the same locality. These two forms are similar in habit. In typical *A. affine* a few conspicuous main branches with much shorter lateral branches are found, arising regularly in pairs at each node. In contrast, the branching in the typical *A. natalense* is irregular and if long main branches are produced, such as in shade forms of this species, these do not branch as regularly as in the typical *A. affine*. This difference in branching is the only distinguishing character. The two forms are not geographically isolated and consequently *A. affine* is regarded as a variety of *A. natalense*.

The type is a mixed collection. On the sheet of the type in PRE there is a specimen of *A. perenne* var. *lignosum* probably from Lüderitz Bay. *A. perenne* has never been recorded to the north of Lüderitz Bay. As recommended by the International Code of Nomenclature (1961), Article 9, a lectotype is designated.

The following putative hybrid is recorded (for key see p. 268):—

A. natalense var. *affine* × *A. pillansii*

3. *A. mossianum* Toelken, sp. nov., ab *A. pillansii* segmentis obonicis ad 4 mm longis differt.

A. hottentoticum sensu Moss in Adamson in J. S. Afr. Bot. 20: 10 (1954), partly, excl. lectotype.

Arbuscula erecta, lignea ad 50 cm alta, ad 80 cm lata; rami primarii 8–30 cm lati, saepe compressi, asperi, raro leves; rami secundarii, ramis lateralibus multis plerumque 1–2 cm longis sed nonnunquam gracilioribus. *Articuli* obconici, clare carinati, costis lateralibus, 2–3 mm longi, raro 4 mm longiores, 2–4 mm lati, obscure virides raro glauci vel rubescentes; foliorum siccorum apices extensissimi; folia mortua ramis non inhaerentia. *Spicae* terminales et laterales, 8–20 mm longae, ad apicem fastigiatae flore, cylindricae fructu, ad fines ramorum dispositae. *Cymae* triflorae, flore medio floribus lateralibus paulo longiori, floribus protandris. *Perianthii tubus* lobis 4, truncatus, scutulo laterali, semini inhaerens. *Antherae* 2 vel 0. *Stigmata* 2 vel 3, undique papillosa. *Semina* oblonga, atra, c. 2 mm longa, testa coriacea, glabra, saepe nitida; endospermum nullum; embryo conduplicatus. PLATE 1. F. G. 4: 1.

Type: Cape, Caledon District, 10 miles west of Riviersonderend, *Tölken* 552 (PRE, holo.).

Erect woody shrubs forming bushes up to 50 cm high, 80 cm in diameter; main branches 8–30 mm thick often laterally flattened, with a rough bark, seldom smooth; secondary branches with many short and thin lateral branches. *Barren segments* obconical, distinctly keeled with a lateral ridge, 2–3 mm long (rarely up to 4 mm), 2–4 mm in diameter, dull green or seldom glaucous, fading to brownish-red; leaf apex much spreading when dried; dead leaves not adhering to the branches. *Sclereids* in the palisade tissue branched, uniformly thickened, reaching from the water tissue to the epidermis. *Spikes* terminal and lateral, 8–20 mm long, tapering when young, cylindrical when fruiting, clustered at the end of branches; flowering segments scarcely wider than barren segments below. *Cymules* 3-flowered; central flower scarcely longer than the lateral ones; flowers protandrous. *Perianth tube* with 4 crenate segments, truncate with lateral shield, cork-like when mature and adhering to the seed. *Anthers* 2 or 0. *Stigmas* bifid or trifid, plumose, erect. *Seeds* compressed oblong, very dark, about 2 mm long with membranous testa, glabrous, often shining; endosperm absent; embryo conduplicate.

A. mossianum is recorded only from the area between Caledon and Riversdale, always away from the coast. It occupies the highest zone in salt marshes or often on river banks. Flowering and fruiting period from March to May.

CAPE.—Bredasdorp: Vogelvlei, *Galpin* 11345a; Spitskop, *Tölken* 520. Caledon: Rietkuil, *Henrici* 3676 (BOL); 10 miles west of Riviersonderend, *Tölken* 525; 526; 552; 553. Montagu: Montagu, *Michell* in BOL 15659 (BOL); *Rogers* in BOL 15498 (BOL); *Tölken* 555. Riversdale: *Marloth* 3587; Doornkraal, *Muir* 3079 (BOL). Swellendam: *Tölken* 412b.

The type collection of *A. hottentoticum* Moss consists of a mixture; the portion which answers to the description must be referred to *A. pillansii*, while the remaining portion represents an undescribed species (see *A. pillansii*, p. 285). It is now described as *A. mossianum* in honour of the late Prof. C. E. Moss for his pioneer work done on the South African species of *Arthrocnemum* and *Salicornia*.

Two barren specimens, *Rogers* in BOL 15498 and *Michell* in BOL 15659, from Montagu, are in all respects bigger than the typical *A. mossianum*. However, from fruiting specimens collected at the same locality (*Tölken* 555) it is concluded that these specimens represent a slightly different but localized population.

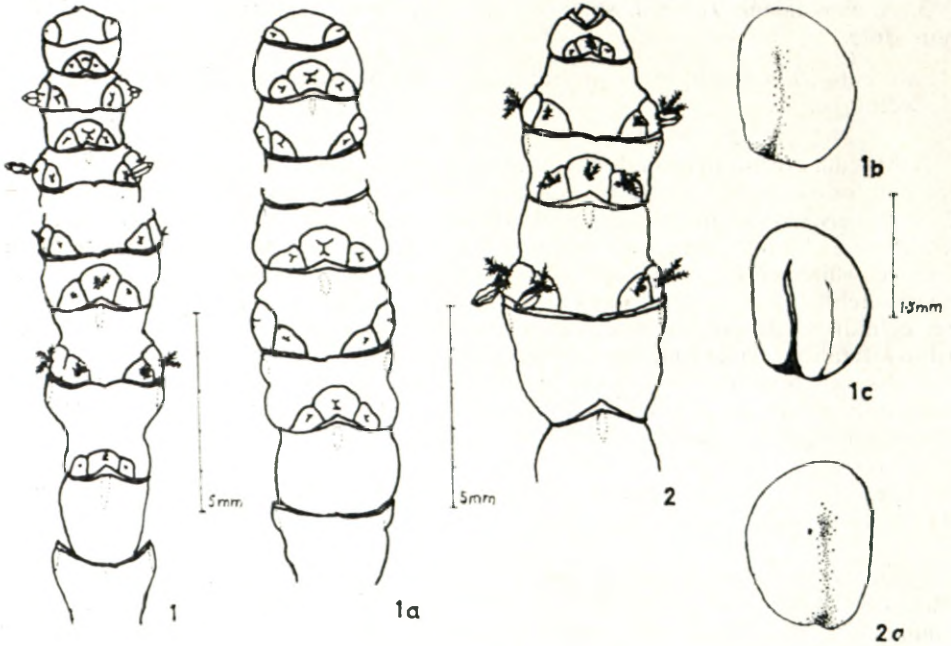


FIG. 4.—1, *Arthrocnemum mossianum*, flowering spike: 1a, fruiting spike; 1b, seed in surface view; 1c, seed in longitudinal section. 2, *A. terminale*, flowering spike: 2a, seed in surface view.

Although the flowers of *A. mossianum* are usually hermaphrodite, some plants have been found in which only female flowers are produced (cf. *Tölken* 525 and 526 in flowering stage; *Tölken* 552 and 553 in fruiting stage). In these plants the anthers are represented only as staminodes (cf. *A. pillansii*). As *A. mossianum* is protandrous, these female plants might be mistaken as protogynous, but in fact the anthers never develop. Since only a proportion of the flowers in these female plants set seed, it is thought that they are fertilized by pollen from hermaphrodite plants in the vicinity.

The following hybrids are recorded (for key, see p. 268):—

A. mossianum × *A. natalense*

A. mossianum × *A. pillansii*

4. *A. terminale* *Toelken*, sp. nov., ab *A. mossiano* articulis cylindricis longioribus 5–12 mm longis, spicis terminalibus differt.

Arbuscula lignea ad 1 m alta; rami primarii ad 3 cm lati, leves, ascendentes vel decumbentes, ramis lateralibus erectis, fastigiatis. *Articuli* cylindrici, obscure carinati, costis lateralibus, 5–12 mm longi, 2–3 mm lati, obscure virides raro glauci, vel flavovirentes et testacei; folia sicca ut videtur sulcata et foliorum siccarum apices extensi; folia mortua ramis non inhaerentia. *Spicae* solum terminales, 8–20 mm longae, non longiores, cylindricae flore et fructu. *Cymae* triflorae, flore medio floribus lateralibus paulo longiori, floribus protogynis. *Perianthii tubus* lobis 4, truncatus, scutulo laterali, semini inhaerens. *Antherae* 2. *Stigmata* 2 vel plures, undique papillosa, saepe ut videtur cristata. *Semina* oblonga, atra, c. 2 mm longa, testa coriacea, glabra, saepe nitida; endospermum nullum; embryo conduplicatus. PLATE 2. FIG. 4: 2.

Type: Cape, Vanrhynsdorp District, Salt River, *Tölken* 536 (PRE, holo.).

Woody shrub forming bushes up to 1 m high with main branches smooth, ascending or decumbent, with erect, fastigiate lateral branches. *Barren segments* cylindrical, with faintly keeled leaf apex and lateral ridge, 5–12 mm long, 2–3 mm in diameter, dull green to glaucous, fading to yellowish-green and brownish-red; the segments shrinking regularly so as to appear grooved; leaf apex spreading when dried; dead leaves not adhering to the branches. *Sclereids* in the palisade tissue uniformly thickened, branched or often star-shaped, next to the water tissue, not reaching the epidermis. *Spikes* terminal, 8–20 mm long, not longer, cylindrical when flowering and fruiting; flowering segments not wider than barren segments below. *Cymules* 3-flowered; flowers about equal in size, protogynous. *Perianth tube* with four crenate segments, truncate with lateral shield, adhering to seeds. *Anthers* 2. *Stigmas* with 2 or more branches, plumose, often appearing tufted. *Seeds* compressed oblong, very dark, about 2 mm long with membranous testa, glabrous, often shining; endosperm absent; embryo conduplicate.

This species is found along rivers in Namaqualand, growing at a higher level on the banks than *A. pillansii*. The type plant was flowering and fruiting from February to April.

CAPE.—Namaqualand: Swart Lintjiesrivier, *Pillans* in BOL 18215a (BOL, STE). Vanrhynsdorp: Salt River, *Tölken* 536; 8 miles north of Vanrhynsdorp, *Moss* 18043 (J).

A. terminale is very similar to *A. mossianum* but differs from that species in its long narrow segments and consistently terminal spikes, hence the choice of the name.

Flowering in *A. terminale* is protogynous, but the anthers soon appear in rapid succession while the stigmas are maintained in apparently receptive condition even after the pollen is shed in the individual flowers. Furthermore, the stigma is often not only bifid or trifid, but with many branches, which gives it an appearance similar to that of the tufted stigma of the species of *Salicornia*.

The following hybrids are recorded (for key, see p. 268):—

A. natalense × *A. terminale*

A. pillansii × *A. terminale*

5. ***A. pillansii*** *Moss* in Adamson in J. S. Afr. Bot. 14: 38 (1948). Type: Cape, Milnerton, *Moss* 8764 (PRE, holo!).

Woody shrub, either ascending or decumbent, up to 70 cm high; main branches up to 30 mm thick, often laterally compressed. *Barren segments* cylindrical or slightly obconical, faintly keeled with lateral ridge, 4–20 mm long, 2–6 mm in diameter, green to glaucous fading to bluish-red; leaf apex scarcely spreading when dried; dead leaves adhering to the branches, but older branches bare. *Sclereids* in the palisade tissue spirally thickened, with faint spiral striations almost perpendicular to the lateral walls. *Spikes* terminal and lateral, (15–) 20–30 (–70) mm long, tapering when flowering and fruiting, rarely cylindrical, clustered at the end of branches; flowering segments hardly wider than barren segments below. *Cymules* 3-flowered; central flower often one-third larger than the lateral ones, or more or less equal in size; flowers protogynous. *Perianth tube* with three or four crenate teeth, truncate with lateral shield, shrivelling when mature, adhering to the seeds. *Anthers* 1 or 2, rarely 0. *Stigmas* bifid or rarely trifid, plumose, usually erect, branches often tangled with one another, sometimes reflexed. *Seeds* compressed oblong, light brown, about 1–1.5 mm long, with membranous testa, glabrous or slightly rough; endosperm absent; embryo conduplicate.

A. pillansii occurs along the South African coast from Lüderitz Bay to Mozambique. Usually it is found in inland marshes and occasionally also near the sea, but then always at a higher level than the flooded zone. The flowering and fruiting period is from January to June.

This species is not only very variable in form and habit but has apparently also hybridized freely with a wide range of other species, thus forming the most diverse complex encountered in this genus in Southern Africa. The species can vary in habit from ascending to decumbent. Sometimes it has short spreading, almost spinescent lateral branches with spikes up to 25 mm long, or it produces long slender branches with long spikes up to 70 mm long.

In typical *A. pillansii*, specimens with very prominent stigmas, which persist for a long time, have been observed (*Levy* 3535; *Archibald* 4900/4b; *Tölken* 543). This form does not produce any anthers and not even staminodes were found (cf. *A. mossianum*). When the spikes were covered with polythene bags, no seeds had been set after a month, which leads one to conclude that these plants are functionally female. This behaviour was observed in one individual plant in two successive years. It should be noted that functionally female plants are also found in *A. pillansii* var. *dunense* (*Tölken* 461).

Two varieties are recognized in South Africa:

- Old barren segments 8–20 mm long, 2–4 mm in diameter, rarely cork-like; stigmas 1–2 mm long; southern Africa except Lüderitz Bay..... (a) var. *pillansii*
 Old barren segments 4–8 mm long, 4–6 mm in diameter, becoming cork-like; stigmas 3 or 4 mm long; Lüderitz Bay..... (b) var. *dunense*

(a) var. *pillansii*

Salicornia fruticosa var. *densiflora* Ung.-Sternb., Vers. Syst. Salic. 59 (1866); in Atti Congr. Int. Bot. Firenze (1874) 301 (1876); Wright in Fl. Cap. 5, 1: 449 (1912). Type: Cape, Paardeneiland, “*Drege* Sammlung (‘ III, B), b ’” (LE, holo.).

Arthrocnemum pillansii Moss ex Fourcade, Mem. Bot. Surv. S. Afr. 20: 20 (1940); nomen nudum; Moss in Adamson in J. S. Afr. Bot. 14: 38 (1948); J. S. Afr. Bot. 20: 13 (1954); Adamson in Fl. Cape Penins. 358 (1950). Type: Cape, Milnerton, Moss 8764 (PRE, holo.). *A. hottentoticum* Moss in Adamson in J. S. Afr. Bot. 20: 10 (1954), partly, as to lectotype & descr. Type: Cape, Milnerton, Moss 8874 (sheet in PRE, lecto.). *A. namaquense* Moss in Adamson in J. S. Afr. Bot. 20: 15 (1954). Type: Vanrhynsdorp, Salt River, Moss 17908 (J, holo!; BOL!).

Woody shrubs, decumbent or ascending with main branches up to 30 mm in diameter, often laterally compressed. *Barren segments* cylindrical, 8–20 mm long, 2–4 mm in diameter, seldom becoming cork-like when old. *Sclereids* in the palisade tissue usually only a few, spirally thickened with faint spiral striations perpendicular to the lateral walls. *Stigmas* short, erect, branches often tangled with one another, hardly visible in dried material. FIG. 5: 1.

Var. *pillansii* is recorded from the Orange River along the South African coast to Mozambique. It forms a zone well above the high water level, lying between *A. decumbens* and *A. mossianum*.

CAPE.—Alexandria: Bushmans River, *Archibald* 5010 (BOL); Kariega River, *Tölken* 384. Bathurst: Kowie River, *Acocks* 13276; *L. Britten* 5198 (GRA, J). Bredasdorp: Vogelvllei, *Galpin* 11345b; near Struisbaai, *Levy* 3535 (CT). Caledon: 10 miles west of Riviersenderend, *Tölken* 529. Clanwilliam: Lambert’s Bay, *Tölken* 342; Leipoldtville, *Tölken* 332. Hopefield: Langebaan, *Tölken* 478; 8 miles west of Koperfontein, *Tölken* 473; 474. Humansdorp: Gamtoos River, *Tölken* 375. Kirkwood: Addo Bush, *Cohen* in J 37948 (J). Knysna: *Duthie* 885a (BOL, STE); *Duthie* 5198 (J). Malmesbury: Ysterfontein, *Tölken* 482; Skrywershoek, *Walgate* 1065 (BOL). Mossel Bay: Great Brak River, *Bolus* in BOL 18835; 18836 (BOL). Namaqualand: Orange River, *Pillans* 5585 (BOL); Okiep, *Pillans* 6247 (BOL); Konfontein Gorge, *Giffen* 34 (CT); Hondeklipbaai, *Pillans* in BOL 18221 (BOL, STE); Wallekraal, *Pillans* s.n. Peddie: Keiskama River, *Tölken* 400. Peninsula: Milnerton, Moss 8874; Rugby, *Levy* s.n. (CT); Salt River, Moss 3141 (J); 17908 (J, BOL): Lakeside, *Weintraub* in J 18367 (J). Piketberg: Elandsbaai, *Tölken* 540. Port Elizabeth: Swartkops River, *Archibald* 4900/4a & b (GRA); *Rodin* 1212; *Troughton* (J 36913). Riversdale: Stilbaai, *Tölken* 358; Gouritz River, *Tölken* 351. Swellendam: *Tölken* 524. Vanrhynsdorp: Salt River, Moss 17863 (J); 17908 (J, BOL); *Acocks* 14186. Vredenburg: St. Helenabaai, *Tölken* 431; Danger Bay, *Tölken* 423. Worcester: Chervonnes, *Van Breda* 219; Over Hex Station, *Tölken* 492.

NATAL.—Mtunzini: Umlalazi River, *Macnae* s.n.

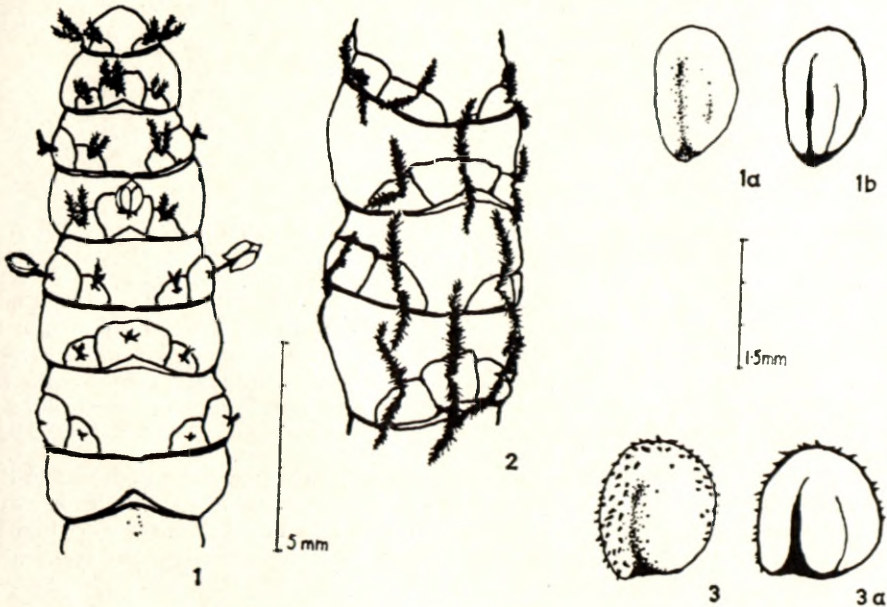


FIG. 5.—1, *Arthrocnemum pillansii* var. *pillansii*, flowering spike; 1a, seed in surface view; 1b, seed in longitudinal section. 2, *A. pillansii* var. *dunense*, flowering spike. 3, *A. xerophilum*, seed in surface view; 3a, seed in longitudinal section.

The typification of *A. hottentoticum* Moss is referred to briefly under *A. mossianum* (p. 281). *A. hottentoticum* is described as a plant about 70 cm high, 1.3 m in diameter, the segments 5–6 mm long, the seeds covered with curved hairs and with spirally thickened sclereids recorded from the palisade tissue. These characters do not apply to *A. mossianum*. The type of *A. hottentoticum* is cited as Moss 8874 from Milnerton. Three sheets with this number have been seen (in PRE, J and K) and it is apparent that a mixture is involved. Of these three, the PRE sheet agrees with the description and is, therefore, nominated as the lectotype. However, this specimen proves to be conspecific with the type of *A. pillansii* (Moss 8764) and so *A. hottentoticum* is relegated to synonymy. The remaining two sheets in J and K represent a previously undescribed species, now described as *A. mossianum* (p. 281), typified by Tölken 552. Another point of interest is that I have not been able to find *A. mossianum* at Milnerton, nor at any locality west of Caledon. This throws doubt on the locality cited on the J and K sheets.

A. namaquense, typified by Moss 17908, cannot be distinguished from *A. pillansii*. There are, however, indications that Moss intended the name *A. namaquense* for the species now described as *A. xerophilum* (see p. 287).

A. fruticosum var. *densiflora* Ung.-Sternb. based on a Drege specimen from Paarden-eiland can only refer to *A. pillansii*, because Ungern Sternberg described it as a woody, frutescent plant.

A form of var. *pillansii* exhibiting shorter spikes and more cylindrical segments occurs in the drier areas in the Cape and can easily be confused with *A. mossianum* (see Pillans 5585, Levyns 4102, Giffen 34). Although this form, unlike typical *A. pillansii*, exhibits many heavily lignified spirally thickened sclereids with spiral striations, strongly oblique to the lateral walls, no other distinction could be found.

The following putative hybrids are recorded (for key, see p. 268):—

- | | |
|---|--|
| <i>A. natalense</i> × <i>A. pillansii</i> , | <i>A. natalense</i> var. <i>affine</i> × <i>A. pillansii</i> , |
| <i>A. mossianum</i> × <i>A. pillansii</i> , | <i>A. perenne</i> × <i>A. pillansii</i> , |
| <i>A. capense</i> × <i>A. pillansii</i> , | <i>A. debumbens</i> × <i>A. pillansii</i> , |
| <i>A. pillansii</i> × <i>A. terminale</i> . | |

(b) var. *dunense* (Moss) Toelken, stat. nov.

A. dunense Moss in Adamson in J. S. Afr. Bot. 20: 14 (1954). Type: S.W. Africa, Lüderitz Bay, Moss 18048 (PRE, holo.!; J!).

Scarcely woody or woody perennial, normally decumbent, rarely with ascending branches. *Barren segments* barrel-shaped, rarely cylindrical, normally 4–8 mm long, 4–6 mm in diameter (rarely 5–15 mm long, 3–4 mm in diameter), becoming cork-like when old. *Sclereids* in the palisade tissue numerous, spirally thickened with spiral striations oblique to the lateral walls. *Stigmas* up to 5 mm long, spreading or reflexed, usually visible in herbarium material. F.G. 5: 2.

Var. *dunense* is recorded from Lüderitz Bay and, possibly, from the Orange River. It grows on very brackish soil near the sea and is often almost completely covered by drifting sand. The main flowering period seems to be in January and February, but flowering specimens are also recorded at various times throughout the year.

CAPE.—Namaqualand: Orange River, *Pillans* 5587 (BOL, K).

SOUTH WEST AFRICA.—Lüderitz Bay: *Marloth* 1163; *Moss* 18048; 11707 (J); Radford Bay, *Dinter* 6012 (BOL, STE); Lagoon, *Range* 1668 (SAM); *Tölken* 461; 466; Grosse Bucht, *Tölken* 464; Diaz Point, *Tölken* 469; Halifax Bay, *Tölken* 471.

Typical var. *dunense* differs from var. *pillansii* in its shorter and stouter segments, becoming cork-like with age. However, the specimens *Dinter* 6012, *Tölken* 461, 466, 469, 471 show a complete range merging into typical var. *pillansii*. On a few branches of *Tölken* 466 the segments are short and thick below, then suddenly become narrower and much longer on the same axis. This could be due to the unusually heavy rainfall for the area recorded the previous year. The long stigmas of var. *dunense*, visible even in herbarium material, provide the only constant character separating the two varieties.

6. *A. xerophilum* Toelken, sp. nov., ab *A. pillansii* spicis brevioribus, seminibus denticulatis, habitatis aridis differt.

Arbuscula erecta, lignea ad 50 cm alta, ramis primariis ad 1.5 cm latis, raro compressis, asperis. *Articuli* succulenti, ad fines constricti vel cylindrici, obscure carinati, costis lateralibus, 5–7 mm longi, 4–6 mm lati, glauci vel purpurascens; folia sicca atra et magnopere contraerentia ita adeo caulus nudus inter articulos apparens; foliorum apices non extensi: folia mortua ramis non inhaerentia. *Spicae* terminales, et laterales, 10–25 mm longae, non longiores, cylindricae, nodis, ad fines ramorum dispositae. *Cymae* triflorae, flore medio floribus lateralibus paulo longiori. *Perianthii tubus* lobis 3, truncatus, scutulo laterali, fructu rugescens, semini inhaerens. *Antherae* 2. *Stigmata* 2, papillosa. *Semina* obovata, fusca, testa coriacea, denticulata praecique in radicula; endospermum nullum; embryo conduplicatus. FIG. 5: 3. PLATE 3.

Type: Cape, Vanrhynsdorp District, *Compton* 20874 (NBG, holo.; BOL).

Stunted woody shrubs up to 50 cm high with several woody branches 5–15 mm thick, rarely laterally compressed, rough. *Barren segments* barrel-shaped or cylindrical, faintly keeled with a lateral ridge, 5–7 mm long, 4–6 mm in diameter glaucous or greyish-green fading to bluish-red, becoming dark coloured and shrinking considerably when dried, so that the bare stem between them becomes visible; leaf apex not spreading; dead leaves not adhering to the branches. *Sclereids* in the palisade tissue spirally

thickened, about eight times as long as wide. *Spikes* terminal and lateral, 10–25 mm long, not longer, cylindrical, bulging, often clustered at the end of branches; flowering segments hardly wider than barren segments below. *Cymules* 3-flowered; flowers about equal in height, protogynous. *Perianth tube* with three crenate segments, truncate with lateral shield, shrivelling when mature, adhering to the seeds. *Anthers* 2. *Stigmas* bifid, spreading, plumose. *Seeds* compressed obovate, light brown with membranous testa, denticulate mainly on the radicle; endosperm absent; embryo conduplicate.

A. xerophilum is known only from the dry mountain slopes in the Knersvlakte, Namaqualand. It is the only species in the whole genus in South Africa which grows away from the moister marshy areas. The flowering and fruiting period is from September to December.

CAPE.—Namaqualand: Garies, *Marloth* 5620. Vanrhynsdorp: *Pillans* in BOL 18786 (BOL); Knersvlakte, *Compton* 20874 (BOL, NBG); *Acocks* 14788; *Hutchinson* 812.

From a personal letter (in Bolus Herbarium) from Professor Moss to N. S. Pillans it is known that Moss originally recognized this new species, as he gave a recognizable description of it in his letter when referring to the specimens *Pillans* in BOL 18786 and *Marloth* 5620. However, *A. namaquense*, as published, falls, both as regards type and description, within the range of variability of *A. pillansii*. The two specimens mentioned above were not cited by Moss (1954).

A remarkable characteristic of this species is the early flowering in September and October. Even under cultivation in Worcester Karoo Gardens, the plants adhered to their early flowering period.

7. *A. littoreum* Moss in Adamson in J. S. Afr. Bot. 14: 38 (1948); J. S. Afr. Bot. 20: 9 (1954); Adamson in Fl. Cape Penins. 358 (1950). Type: Cape, Camps Bay, Moss 8775 (PRE, holo.!, J!).

Salicornia fruticosa sensu Harv., Gen. Pl. ed. 1: 285 (1838), nomen nudum, non L.; H. Bol. & Wolley-Dod in Trans. S. Afr. Phil. Soc. 14: 311 (1903), nomen nudum; Wright in Fl. Cap. 5, 1: 449 (1911), pro majore parte.

Arthrocnemum fruticosum sensu Harv., Gen. Pl. ed. 2: 314 (1868), non Moq.

Erect woody shrub up to 1 m high with several erect stems 3–8 cm thick at the base, seldom laterally compressed; secondary branches erect, fastigiate. *Barren segments* cylindrical, with slightly keeled leaf apex, with lateral ridge, 5–8 mm long, 3–5 mm in diameter, glaucous or green fading to yellow, rarely to reddish-brown; leaf apex spreading when dried; dead leaves not adhering to the branches. *Sclereids* in the palisade tissue spirally thickened. *Spikes* terminal, 20–30 (–100) mm long, tapering when flowering, cylindrical when fruiting; flowering segments wider than barren segments below. *Cymules* 3-flowered; flowers about equal in size, protogynous. *Perianth tube* with three crenate segments, truncate with lateral shield, becoming cork-like when mature, adhering to the seeds. *Anthers* 2. *Stigmas* bifid, plumose, erect, branches normally tangled with one another. *Seeds* compressed oblong, light brown, with membranous testa with recurved hairs, seldom coiled at the apex; endosperm absent; embryo conduplicate. FIG. 6.

This species occurs in the Cape on rocky beaches below or at spring-tide mark, often much battered by the sea. The flowering and fruiting period is from September to May, and often spikes are found releasing ripe seeds below and continuing to flower above.

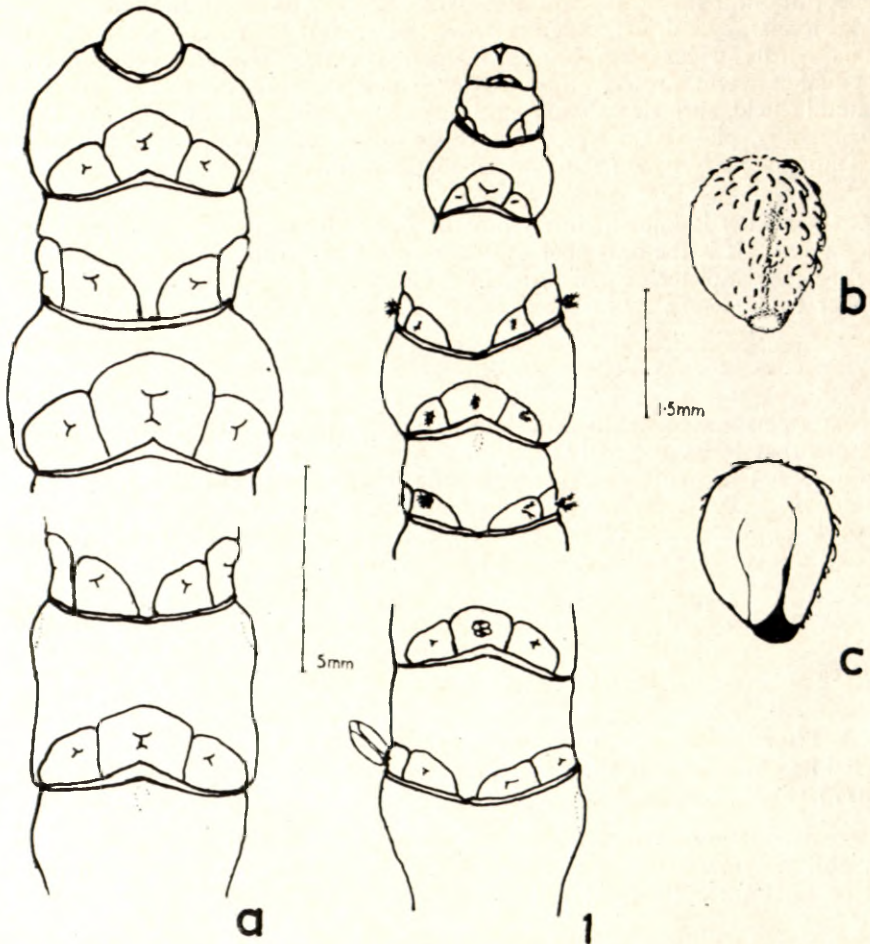


FIG. 6.—1, *Arthrocnemum littoreum*, flowering spike; a, fruiting spike; b, seed in surface view; c, seed in longitudinal section.

CAPE.—Alexandria: Kariega River, *L. Britten* 5237 (GRA). Bredasdorp: Cape Agulhas, *Salter* 4128 (BOL); *Pillans* 8101 (BOL). Caledon: Pringle Bay, *Tölken* 487; Hermanus, *L. Guthrie* s.n. (BOL); Danger Point, *Pillans* 3539 (BOL); *Compton* 10212 (NBG). Hopefield: Langebaan, *Tölken* 477. Knysna: *Moss* 8763 (J); Plettenberg Bay, *Smart* s.n. Malmesbury: Ysterfontein, *Tölken* 481. Mossel Bay: *Moss* 4341; *Burt Davy* s.n. (BOL). Namaqualand: Hondeklipbaai, *Pillans* s.n. (BOL, STE). Peninsula: Robben Island, *Walgate* 489 (NBG); Camps Bay, *Wolley-Dod* 3056 (BOL); *Moss* 8775; Kommetjie, *Simons* 88; Schusters Bay, *Tölken* 205; Olifantsbosch, *Tölken* 165 (BOL); Buffels Bay, *Tölken* 159 (BOL); below Paulsberg, *Wolley-Dod* 3012 (BOL); Kalkbaai, *Pillans* 3242; *Guthrie* 1395 (CT). Port Elizabeth: *Lurie* in *J* 18181 (J); Skoenmakerskop, *Smith* D.107; Bird Island *Schonland* 5128 (BOL). Riversdale: Stilbaai, *Muir* 3149; 166. Vredenburg: Danger Bay, *Tölken* 428.

A. littoreum is the only species occurring along unsheltered, rocky beaches. Thus the woody specimen referred to by Harvey can only be this species. Only once, as Langebaan, were plants of *A. littoreum* found growing next to those of *A. pillansii*.

8. *A. perenne* (Mill.) *Moss ex Fourcade*, Mem. Bot. Surv. S. Afr. 20: 20 (1941). Type: from England.

Woody and scarcely woody perennial, prostrate or decumbent, forming mats up to 25 cm high; main branches prostrate and often rooting at the nodes. *Barren segments* barrel-shaped to cylindrical, with faintly keeled leaf apex and lateral ridge, 6–12 mm long, 3–5 mm in diameter, dull green to shiny green, fading to yellow or reddish-brown; leaf apex seldom spreading and the whole specimen becoming dark grey when dried; dead leaves adhering to the branches but disintegrating on old bushes. *Sclereids* in the palisade tissue spirally thickened with striations oblique to the lateral walls. *Spikes* terminal, 15–35 (–50) mm long, tapering when flowering, cylindrical when fruiting; fruiting segments wider than barren segments below, and bulging about the middle. *Cymules* 3-flowered, rarely 4- or 5-flowered; central flower slightly higher than the lateral ones; flowers protogynous. *Perianth tube* with three crenate segments, truncate with lateral shield, often becoming cork-like when mature, adhering to the seeds. *Seeds* compressed, oblong or obovate, brown, with membranous testa with hairs recurved or coiled at the apex; endosperm absent; embryo conduplicate,

A. perenne, as construed here, occurs along the coast of South Africa, western north Africa and south-western Europe. It usually forms a separate zone from below the high-water mark and just above it. In South Africa the flowering and fruiting period is from January to June.

Two varieties are recognized in South Africa:

Branches (not including the succulent leaf sheath) rarely exceeding 3 mm in diameter, often rooting at the nodes; succulent segments green fading to reddish-brown..... (a) var. *perenne*

Branches (not including the succulent leaf sheath) up to 8 mm in diameter, rarely rooting at the nodes; succulent segments green, fading to yellow..... (b) var. *lignosum*

(a) var. *perenne*.

Salicornia perennis Mill., Gard. Dict. ed. 8 (1768); Moss in J. Bot. Lond. 49: 179 (1911). *S. radicans* Smith, Eng. Bot. t.1691 (1807). *S. fruticosa* var. *radicans* (Smith) Gr. & Godr., Fl. Fr. 3: 28 (1855). ———var. *paardeneilandica* Ung.-Sternb., Vers. Syst. Salic. 59 (1866); Wright in Fl. Cap. 5, 1: 449 (1912). Type: Cape, Paardeneiland, "Drege Sammlung, n. 221" (LE, holo.). *S. perennis* var. *radicans* (Smith) Moss in New Phytol. 11: 408 (1912); Moss & Salisbury in Camb. Brit. Fl. 2: 188, fig. 195 (1914). *S. arabica* var. *paardeneilandica* (Ung.-Sternb.) Chev. in Rev. Bot. appl. 2: 33, (1922).

Arthrocnemum perenne (Mill.) Moss ex Fourcade Mem. Bot. Surv. S. Afr. 20 : 20 (1941). Type: from England. ———var. *radicans* (Smith) Moss ex Fourcade, Mem. Bot. Surv. S. Afr. 20 : 20 (1941); Moss in Adamson in J. S. Afr. Bot. 14 : 40 (1948); J. S. Afr. Bot. 20 : 11 (1954); Adamson in Fl. Cape Penins. 358 (1950). *A. fruticosum* var. *radicans* (Smith) Moq., Chenop. Monogr. Enum. 112 (1840); in DC., Prodr. 13, 2 : 151 (1849). *A. variiflorum* Moss in Adamson in J. S. Afr. Bot. 14 : 39 (1948); J. S. Afr. Bot. 20 : 17 (1954); Adamson in Fl. Cape Penins. 358 (1958). Type: Cape, Milnerton, Moss 8765 (PRE, holo.!).

Scarcely woody perennial, with bare main branches seldom thicker than 3 mm, not conspicuously swollen at the nodes, often rooting at the nodes. *Barren segments* dull to shiny green often with a pinkish tinge between the segments, fading to reddish-brown. *Seeds* oblong (1–2 mm long) densely hairy; hairs usually coiled at the apex FIG. 7 : 1.

This variety grows in the lowest zone of muddy maritime salt marshes, and has been mainly recorded from the eastern coast of South Africa.

CAPE.—Alexandria: Bushmans River, *Dyer* 3368; *Archibald* 5009 (BOL). Bathurst: Kowie River, *L. Britten* 5202 (GRA, J, K); 5206 (GRA, J). East London: Nahoon River, *Tölken* 403. Elliotdale: Bashee River, *Tölken* 404. Hopefield: Langebaan, *Isaac* in BOL 23472 (BOL, PRE). Humansdorp: Gamtoos River, *Tölken* 377. Kentani: *Pegler* 648. Knysna: *Moss* 9937 (J); 8770 (J); *Duthie* 894 (BOL, J); 893 (BOL, STE); *Fourcade* 1997b (BOL); Bitou River, *Tölken* 368. Komga: Great Kei River, *Flanagan* 1119; *M. Moss* in J 27425 (J). Mossel Bay: Great Brak River, *Bolus* in BOL 18837 (BOL); *Tölken* 361. Peddie: Keiskama River, *Comins* 1612; *Wager* in PRE 29115. Peninsula: Milnerton, *Moss* 8756 (J); 11330 (J); Rugby, *Moss* 8776 (GRA, J); Salt River, *Moss* 3130 (GRA); 5259 (J). Port Elizabeth: Swartkopsrivier, *Rodin* 1213 (BOL, K); *Archibald* 4927 (BOL); 5815 (BOL, GRA). Riversdale: Stilbaai, *Muir* 3209 (J); 46456 (J); Gouritz River, *Tölken* 352. Umtata: Umtata River, *West* 3171.

NATAL.—Durban: *Medley Wood* 418 (SAM); Umbilo, *Moss* 3139; 4335 (J); Salisbury Island, *Forbes* 62 (NH); 324; *Moss* 18397 (J); *Galpin* 12132. Mtunzini: Umlalazi Estuary, *Macnae* s.n. (PRE).

SOUTH WEST AFRICA.—Lüderitz Bay: Orange River, *Merxmüller & Giess* 2290.

According to the International Code of Botanical Nomenclature (1961), Article 24, the var. *radicans*, having been described as the typical form, has been changed to var. *perenne*.

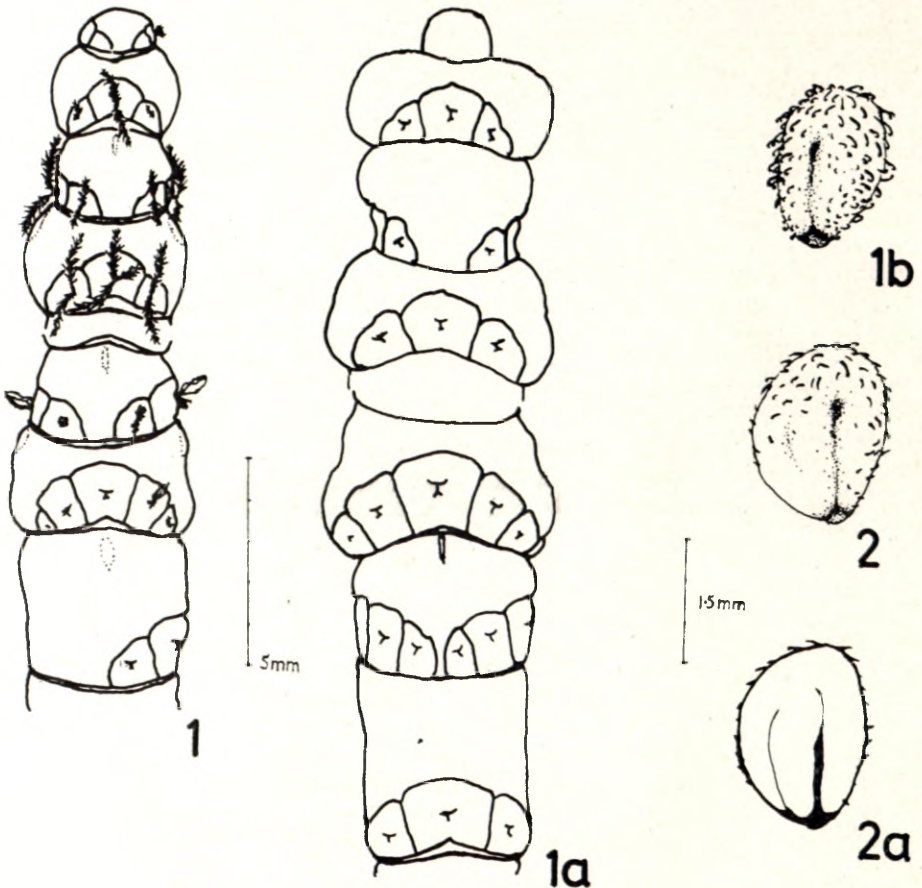


FIG. 7.—1, *Arthrocnemum perenne* var. *perenne*, flowering spike; 1a, fruiting spike; 1b, seed in surface view. 2, var. *lignosum*, seed in surface view; 2a, seed in longitudinal section.

From field observation it appears that *A. variiflorum* is merely a vigorous form of *A. perenne*. Furthermore, the type seems to be an unfortunate choice, as it exhibits spikes hardly longer than 2 cm instead of 3–3.5 cm long, and not a single cymule with more than three flowers could be found. The growth and pollen suggest that the specimen is a hybrid. *A. variiflorum* is regarded as a synonym of *A. perenne* var. *perenne*.

The following putative hybrids are recorded (for key, see p. 268):—

A. natalense × *A. perenne*, *A. capense* × *A. perenne*,
A. perenne × *A. pillansii*, *A. decumbens* × *A. perenne*.

(b) var. **lignosum** (Woods) Moss in New Phytol. 11 : 409 (1912); Moss & Salisbury in Camb. Brit. Fl. 2 : 189 (1914); Moss in Adamson in J. S. Afr. Bot. 14 : 40 (1948). Type: from England.

Salicornia lignosa Woods in Bot. Gaz. (London) 3 : 31 (1851). *S. natalensis* sensu Marloth, Fl. S. Afr. 1 : 184, fig. 84b (1913), non Bunge ex Ung.-Sternb.

Woody perennial, prostrate or decumbent, rarely rooting at the nodes, with bare main branches 3–5 (–10) mm thick, often conspicuously swollen at the nodes. *Barren segments* dull or shiny green, fading to yellow, never reddish-brown. *Seeds* compressed obovate, 2–3 mm long, up to twice the size of those of var. *perenne*, sparsely hairy with hairs not coiled at the apex. FIG. 7 : 2.

The var. *lignosum* has so far been found only at Knysna and at Lüderitz Bay in Southern Africa. It grows in the lowest zone in gravelly maritime salt marshes, preferably in sheltered localities.

CAPE.—Knysna: Moss 8875 (J); Tölken 365.

SOUTH WEST AFRICA.—Lüderitz: Moss 1175 (J); 18123 (J); De Winter & Hardy 7936; Lagoon, Kinges 2034; Range 1750 (SAM); Diaz Point, Tölken 470; Halifax Bay, Tölken 472.

This variety is very similar to *A. littoreum* in its colour and habitat, but differs from that species in its decumbent or prostrate habit.

Seeds collected at Lüderitz Bay indicated that the seed characters used by Moss to differentiate the two varieties are not completely reliable. The two entities are kept separate because the var. *lignosum* never produces the red segment colour. All plants of *A. perenne* at Lüderitz Bay must be referred to the var. *lignosum*, although most of the specimens grow on a sandy substrate and not on gravel. Also specimens of both varieties were grown under similar conditions at the Botanical Research Institute, Pretoria, but they never changed their respective colours.

Marloth's *S. natalensis* is referred to this variety in view of its recorded occurrence at lower levels at Lüderitz Bay.

9. ***A. capense*** Moss in Adamson in J. S. Afr. Bot. 14 : 38 (1948); J. S. Afr. Bot. 20 : 13 (1954); Adamson in Fl. Cape Penins. 358 (1950). Type: Cape, Milnerton, Moss 11621 (PRE, holo.).

Scarcely woody or woody perennial, decumbent or prostrate, forming dense mats or irregular rosettes 40–80 cm in diameter and up to 25 cm high; main branches prostrate, often rooting at the nodes, with terminal and lateral branches erect, but young branches often prostrate. *Barren segments* cylindrical, with keeled leaf apex and pronounced lateral ridge, 10–16 mm long, 2 (–3) mm in diameter, glaucous or dull green fading to reddish-brown; leaf apex of only young leaves spreading when dried; dead leaves adhering to the branches. *Sclereids* in the palisade tissue uniformly thickened, reaching from the water tissue to the epidermis. *Spikes* terminal and lateral,

15–35 mm long, seldom longer, tapering when flowering, cylindrical when fruiting, usually solitary but also clustered at the end of branches; flowering segments not wider than the barren segments below. *Cymules* 3-flowered; central flower hardly larger than the lateral ones; flowers protogynous. *Perianth tube* with three crenate segments truncate with lateral shield, shrinking when dried, adhering to the spike and the seeds. *Anthers* 2. *Stigmas* bifid or trifid, plumose, reflexed. *Seeds* compressed oblong, light brown, with membranous testa with few hairs recurved not coiled at the apex; endosperm absent; embryo conduplicate. FIG. 8.

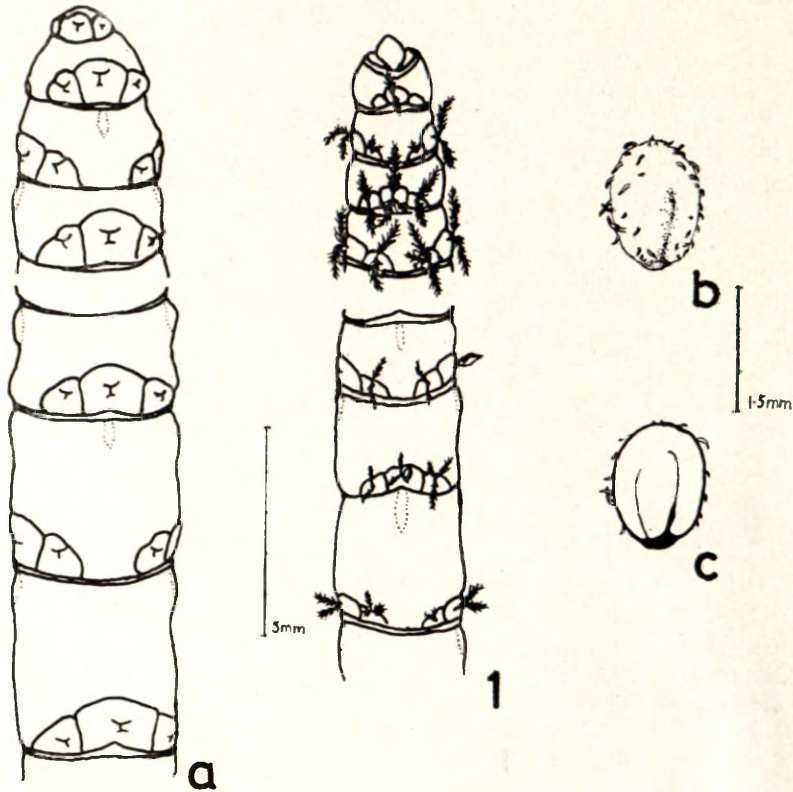


FIG. 8.—1, *Arthrocnemum capense*, flowering spike: a, fruiting spike; b, seed in surface view; c, seed in longitudinal section.

This species was previously recorded from the vicinity of Cape Town only, but has since also been found at isolated localities at Hermanus and Port Elizabeth. It grows usually in sandy, hardly saline soils, forming a zone above the *A. pillansii* zone. The flowering and fruiting period is from October to April.

CAPE.—Caledon: Mosselrivier, *L. Guthrie* s.n. (BOL); Uilenkraalrivier, *Tölken* 500; 503. Malmesbury: Mamre Road, *Compton* 9812 (NBG). Peninsula: Milnerton, *Moss* 11621; Rugby, *Tölken* 326; Uityvlugt, *Wolley-Dod* 1480 (BOL); Raapenburgvlei, *Wolley-Dod* 2690 (BOL); Isoetesvlei, *Tölken* 304; Rondevlei, *Andraea* 237 (STE); Noordhoek, *Moss* 3144; *Pillans* 3222 (BOL); Kommetjie, *Moss* 8883a. Port Elizabeth: Blue Hole, *Archibald* 5818 (GRA). Stellenbosch: Kuilsrivier, *Tölken* 301.

Although this species produces few or no flowering spikes in dry seasons, it can be easily recognized by its thin, but tough branches with marked lateral ridge on the segments.

The following putative hybrids are recorded (for key, see p. 268):—

A. capense × *A. natalense*, *A. capense* × *A. pillansii*,
A. capense × *A. decumbens*, *A. capense* × *A. perenne*.

10. *A. decumbens* Toelken, sp. nov., ab *Salicornia blackiana* floribus cymae omnibus in linea transversa dispositis, spicis saepe longioribus 3 cm; ab *Salicornia australis* seminibus obovatis, denticulatis, differt.

A. heptiflorum sensu Moss in Adamson in J. S. Afr. Bot. 20 : 18 (1954), partly, excl. type. *A. australasicum* sensu Moss in Adamson in J. S. Afr. Bot. 20 : 19 (1954), non (Moq.) Moss.

Suffrutex decumbens, vix ligneus, ad 40 cm altus; rami primarii ad 15 mm lati, non compressi; rami secundarii erecti, ramis lateralibus paulo. *Articuli* plerumque cylindrici, carinati, costis lateralibus, 5–15 mm longi, 3–6 mm lati, glauci vel purpurascens; foliorum siccorum apices, novellorum extensi; folia mortua saepe cortica, ramis inhaerentia. *Spicae* 15–40 (–50) mm longae raro ad apices fastigiatæ, plerumque cylindricæ, sub articulis latissimæ. *Cymae* (4–) 5–7 (–9)-floribus flore medio prope instar florum lateralium. *Perianthii tubus* lobis, 4, 3, 2, saepe rima, truncatus scutulo laterali, semini non inhaerens. *Antherae* 2. *Stigmata* 2, raro 3, undique papillosa, reflexa. *Semina* obovata, raro oblonga, fusca testa coriacea, papillosa; endospermum nullum; embryo conduplicatus. PLATE 4. FIG. 9.

Type: Cape: Mossel Bay District, Great Brak River, Tölken 362 (PRE, holo.).

Scarcely woody to sometimes woody perennial, decumbent, up to 50 cm high with main branches up to 15 mm thick not laterally compressed; secondary branches usually straight erect and with few lateral branches. *Barren segments* cylindrical to barrel-shaped, keeled with lateral ridge, 5–15 mm long, 3–6 mm in diameter, glaucous fading bluish-red, leaf apex of only young leaves spreading when dried; dead leaves often becoming cork-like, adhering to the branches. *Sclereids* in the palisade tissue uniformly thickened next to the water tissue, not reaching to the epidermis. *Spikes* 15–30 (–50) mm long, rarely tapering, normally cylindrical; flowering segments usually much wider than barren segments below. *Cymules* (4–) 5–7 (–9)-flowered; flowers about equal in size, protogynous. *Perianth tube* with 4, 3 or 2 crenate segments, often only a slit, truncate with lateral shield, becoming cork-like when mature, not adhering to the seeds. *Anthers* 2. *Stigmas* bifid, seldom trifid, plumose, reflexed. *Seeds* compressed obovate or ovate, light brown with membranous testa with pointed or blunt papillae; endosperm absent; embryo conduplicate.

A. decumbens occurs along the east coast of South Africa from Bredasdorp to Lourenco Marques. The gap in the distribution from the Kei River to Lourenco Marques is significant, and is attributed to the higher rainfall which does not provide extensive, seldom flooded salt marches. The species usually occupies a separate zone below the zone of *A. pillansii*, with which it appears to be in strong competition. The flowering and fruiting period is from January to June.

CAPE.—Bathurst: Kowie River, L. Britten 5199 (GRA); 5025 (GRA, J); M. Moss in J 20844 (J); Bredasdorp: De Mond, Taylor 105 (BOL); Seekoeivlei, Tölken 511; De Hoopvlei, Tölken 518; Caledon: 10 miles west of Riviersonderend, Tölken 416; 527. East London: Gulu River, Galpin 9590. Humansdorp: Gamtoos River, Tölken 378. Komga: Great Kei River, M. Moss in J 27425 (J). Mossel Bay: Great Brak River, Moss 4344; 4345 (J); Bolus in BOL 18805 (BOL); Tölken 362. Peddie: Keiskama River, Tölken 399. Port Elizabeth: Swartkopsrivier, Archibald 4891 (GRA, BOL); 5819 (BOL); Zeyher 3615 (GRA); Paterson 497 (GRA); Cape Recief II, Zeyher (BOL, GRA, K, SAM, STE). Swellendam: Tölken 413; 523.

MOZAMBIQUE.—Lourenco Marques: Moss 3136 (J); 4335 (J); Inhaca Island Moss 16996 (J); M. Moss in J 27630; in J 27632 (BOL).

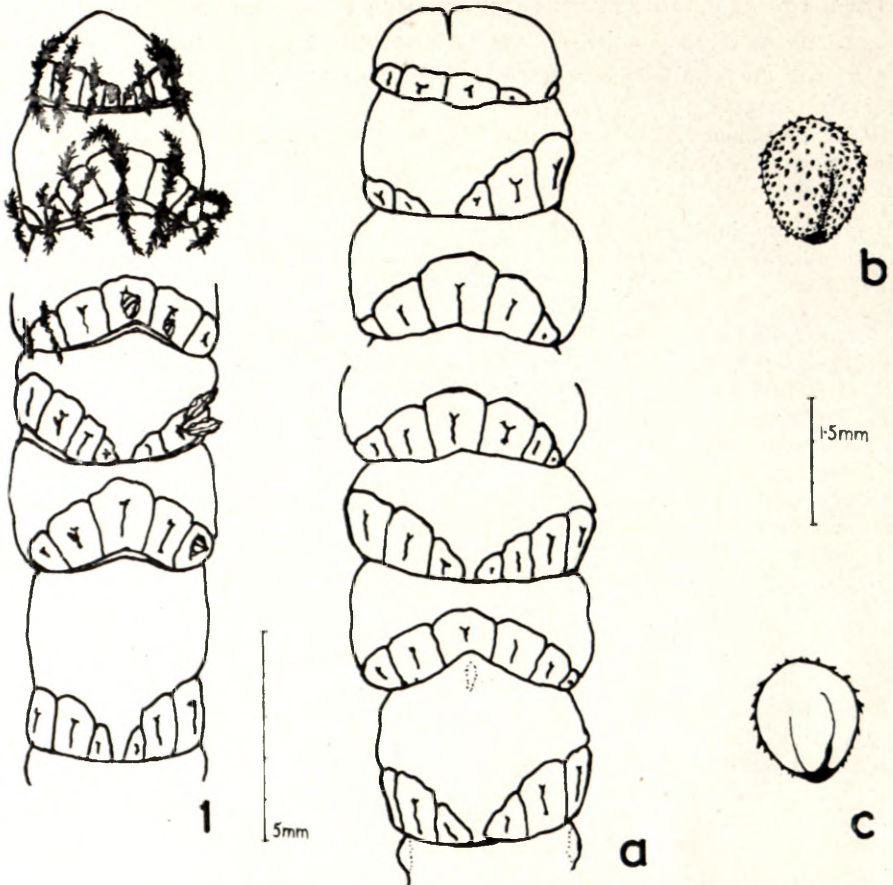


FIG. 9.—1, *Arthrocnemum decumbens*, flowering spike; a, fruiting spike; b, seed in surface view; c, seed in longitudinal section.

Although the new species here described was linked by Moss with various Australian species, it seems to be distinct. Moss applied the following two names to the South African plants which I now regard as belonging to one species, *A. decumbens*.

1. *A. heptiflorum* Moss, based on one of the syntypes of *Salicornia australis* Soland. ex Benth. (see discussion below) and under which he included *Salicornia pachystachya* Black (1921), non Ung.-Sternb.

2. *A. australasicum* (Moq.) Moss, based on *Halocnemum australasicum*, an Australian species.

Solander's *S. australis* was a manuscript name, and Forster, *Florulae Insularum Australium Prodrum* (1786), also published just the name. The first description of this species appears to be that of Bentham in 1870. This name is antedated by *S. quinqueflora* Ung.-Sternb. (1866). Moss (1954) seems to have been unaware of Bentham's description as he treated *S. australis* as a *nomen nudum*, and described *A. heptiflorum* based on one of the syntypes of *S. australis* (Forster, New Zealand). Thus Moss incorrectly included the South African specimens under *A. heptiflorum*, a synonym of *S. quinqueflora*.

The following table, drawn up from herbarium and preserved material investigated, indicates the characteristics of the taxa, probably species, as seen by the present author.

	<i>A. perenne</i>	<i>S. quinqueflora</i> (= <i>S. australis</i>)	<i>S. blackiana</i>	<i>A. decumbens</i>
Old segments	barrel-shaped, cylindrical with pointed leaf apex	cylindrical distinctly keeled with very pointed leaf apex	barrel-shaped with blunt leaf apex	barrel-shaped, rarely cylindrical with blunt leaf apex
Segments length	6-12 mm	5-8 (10) mm	3-6 (8) mm	5-15 mm
Segment diameter	3-5 mm	2-4 mm	3-5 mm	3-6 mm
Spikes.....	15-40 (50) mm	20-40 (50) mm	15-25 (30) mm	15-40 (50) mm
Fruiting segments	bulging, wider than barren segments	bulging, hardly wider than barren segments	cylindrical, wider than barren segments	cylindrical, wider than barren segments
Number of flowers per cymule	3 (4, 5)	7, 8 (-12)	5-7 (-8) +1, 2(3) in sec. row	(4-) 5-7 (-9)
Sclereids.....	spirally thickened	spirally thickened, rare	many spirally thickened	uniformly thickened
Seeds.....	with hairs coiled at the apex	with hooked hairs	with rounded papillae	with short or long stout papillae
Flowering Period	Jan.-March	Nov.-March	Aug.-Nov.	Jan.-March
Distribution...	S.W. Europe, South Africa	New Zealand, Australia	Australia	South Africa

Black (1921) described *S. pachystachya*, non Ung.-Sternb. (1866), for which Ulbrich (1934) then proposed the new name *S. blackiana*. This species is very similar to *A. decumbens*, but differs from the latter in often producing additional flowers in a second row below the central flower, and having spirally thickened sclereids in the palisade tissue.

From Moquin's (1840) description of *Halocnemum australasicum* it is not clear to which species he referred. In his more detailed description (Moquin, 1849), where he still refers to the reputed R. Brown specimen only, it can be recognized that he refers to the more recent *A. lylei* as already pointed out by Black (1921). The phrase "sepala ovata, tenuia, membranacea" gives the impression of a three-lobed perianth, membranous at the apex, as it is found in *A. lylei* (Black, 1919; plate 34). It also

reflects Moquin's motive for putting his species into the genus *Halocnemum*, the flowers of which he described as "calyx 3-sepalus; sepalis squamaeformibus, adpressis", in contrast with the perianth of *Arthrocnemum* described as "calyx ventricosus . . . apice truncatus vel 3, 4, 5 dentatus". The subsequent misunderstanding by Moquin and Betham regarding the identity of *H. australasicum* and the R. Brown specimen seems to be based on different specimens seen by the different authors. According to Stearn (1960) it is unlikely that Moquin had seen a Brown specimen in Herb. Paris, as duplicates of Brown's collections were distributed only after his death in 1851. This is much later than Moquin's publications. Perhaps this might explain the query after Moquin's (1849) citation of the Brown specimen.

A. australasicum sensu Moss seems to refer to a mixture consisting of specimens (a) of a form of *A. decumbens* and (b) the putative hybrid *A. decumbens* × *A. perenne*. In Moss's description of *A. australasicum*, the mention of "green shoots" and the lesser number of flowers per cymule applies to both these elements, whereas "few large spirally thickened cells" indicate the hybrid, which in herbarium material is almost indistinguishable from this form of *A. decumbens*. This form of *A. decumbens*, where the sclereids do not normally develop but in which the typical uniformly thickened sclereids are sometimes formed, combined with the stomata being in line with the epidermis, exhibits all transitional forms between it and the typical *A. decumbens*. It is thus regarded as an ecological form of *A. decumbens*, as it exhibits all the symptoms of specimens grown under humid conditions.

In *A. decumbens*, papillose seeds are usually found, though occasionally seeds with stout, straight hairs may occur, but these hairs are never hooked at the apex.

It is remarkable that the several flowers below the central flower of a cymule of *S. blackiana* have never been described before. This is unique in the genus *Arthrocnemum*.

The following putative hybrids are recorded (for key, see p. 268):—

A. decumbens × *A. natalense*, *A. decumbens* × *A. pillansii*,
A. decumbens × *A. perenne*, *A. capense* × *A. decumbens*.

2. SALICORNIA

Salicornia L. Sp. Pl. 3 (1753); Moq., Chenop. Monogr. Enum. 113 (1840); Adamson in Fl. Cape Penins. 358 (1950); Moss in Adamson in J. S. Afr. Bot. 20 : 20 (1954). Type species: *S. europaea* L. *S.* subgen. *Eusalicornia* Gr. & Godr., Fl. Fr. 3 : 27 (1855); *S.* subgen. *Vulgata* Ung.-Sternb., Vers. Syst. Salic. 43 (1866); *S.* sect. *Annuae* Duval-Jouve in Bull. Soc. Bot. Fr. 15 : 170 (1866); Moss in J. Bot. Lond. 49 : 178 (1911); Ulbrich in Pflanzenfam. ed. 2, 16c : 550 (1934). *S.* sect. *Salicorniella* Moss & Salisbury in Camb. Brit. Fl. 2 : 187 (1914).

Annual shrublets, erect, rarely decumbent; branches not rooting at the nodes and all branches ending in spikes. *Barren segments* usually drying out at anthesis or just before maturity of the seeds. *Cymules* 3-flowered; lateral flowers not completely separated by the central flower, or only a central flower with rarely 1 or 2 much smaller lateral flowers present. *Flowers* protandrous, sometimes overlapping. *Stigma* tufted, hardly visible. *Seeds* with membranous testa covered with slender hairs, coiled at the tip; endosperm absent; embryo conduplicate.

Species of this genus occur in salt marches throughout the world, except in Australia.

KEY TO THE SPECIES OF SALICORNIA

Flowers 1, rarely 2 or 3 per cymule..... 3. *S. uniflora*

Flowers consistently 3 per cymule:

Spikes becoming thicker, up to 8 mm wide when fruiting; perianth cork-like when mature; apex of central flower strongly obtuse..... 1. *S. pachystachya*

Spikes not becoming thicker, 2-3 mm wide when fruiting; perianth shrivelling when mature; apex of central flower acute, rarely becoming obtuse when fruiting..... 2. *S. meyerana*

1. *S. pachystachya* Bunge ex Ung.-Sternb., Vers. Syst. Salic. 51 (1866); in Atti Congr. Int. Bot. Firenze 1874 : 278, fig. 18A, B (1876); Brenan in Fl. Trop. E. Afr. Chenopodiaceae : 21 (1954). Type: Madagascar, Bay of Suarez, *Boivin* 2370 (LE, holo., P!).

S. perrieri Chev. in Rev. Bot. appl. 2 : 748 (1922); Moss in Adamson in J. S. Afr. Bot. 20 : 22 (1954); Cavaco in Fl. Madagascar, Chenopodiaceae : 9 (1954). Type: Madagascar, Ambongo Province: *Soalala, De la Bathie* 1580 (P, holo.!).

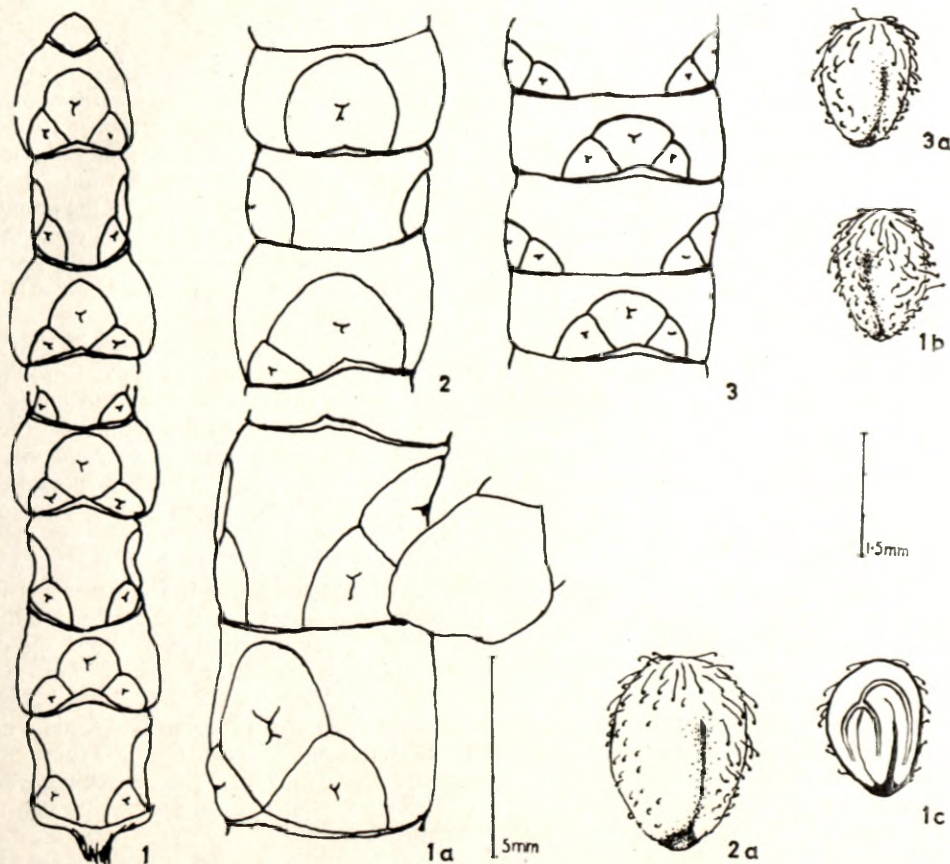


FIG. 10.—1, *Salicornia meyerana*, fruiting spike; 1a, fruiting spike with lateral proliferation; 1b, seed in surface view; 1c, seed in longitudinal section showing a clearly differentiated stele. 2, *S. uniflora*, fruiting spike; 2a, seed in surface view. 3, *S. pachystachya*, fruiting spike; 3a, seed in surface view.

Erect woody shrublets up to 40 cm high; main branches up to 10 mm in diameter, erect with shorter lateral branches; apices of lateral branches not higher than the apex of the main stem. *Barren segments* cylindrical, faintly keeled with lateral ridge, 5–10 mm long, 2–4 mm in diameter, glaucous or green fading to brownish-red; leaf apex hardly spreading when dried. *Sclereids* in the palisade tissue spirally thickened. *Spikes* terminal and lateral, 10–25 (–80) mm long, becoming longer and thicker when fruiting, up to 8 mm thick, tapering when flowering and fruiting or sometimes cylindrical when fruiting. *Cymules* 3-flowered; apex of the central flower strongly obtuse; flowers protandrous. *Perianth tube* with three crenate segments, truncate with lateral shield, becoming cork-like when fruiting. *Anthers* 2, 0.5–1 mm long. *Stigma* tufted often bifid or trifid. *Seeds* compressed oblong, brown with membranous testa with few long hairs coiled at the apex; endosperm absent; embryo conduplicate. FIG. 10 : 3.

This species occurs in tropical East Africa and Madagascar. In South Africa it is found only in northern Natal. The flowering period is insufficiently known, but the few specimens seen indicate a flowering time from June to October and fruiting from December to January.

NATAL.—Hlabisa: False Bay Park, *Ward* 4220. Ingwavuma: Nyamiti Pan, *Tinley* 521, Sheet I and II.

MOZAMBIQUE.—Lourenco Marques: *Roger & Moss* in J 4340 (J); *Moss* 3137 (J); Inhaca Island, *M. Moss* in J 27633; J 28245; Matola, *Macnae* 2; *Moss* 11742 (J); Costa da Sol, *Macnae* 3.

Two forms of this species were observed in the field and these are clearly shown in Sheet I and II of *Tinley* 521. The one form which grows apparently always on drier soils, has an erect growth with the apex of the lateral branches not higher than the apex of the main branches. All branches end in spikes, which are 20–30 (–50) mm long. The second form is much more branched, almost decumbent and the apex of the lateral branches are often higher than the apex of the main branch. A few branches at the end of the main branch begin flowering in June while the lower branches still grow vegetatively. Flowers are born on the latter type of branches later or not at all. The length of the spikes of this second form are 20–50 (–80) mm long.

The specimen *Ward* 3267 from Lake St. Lucia, which shows the typical growth of the second form, is thought to be a hybrid because no seeds develop and anthers are often aborted. Unfortunately no anthers with mature pollen were found in order to establish whether pollen of two sizes is found in putative hybrids of *Salicornia*, as is the case with *Arthrocnemum*. The problem is, however, that no other species of *Salicornia* has been recorded from that area and no indications of any species of *Arthrocnemum* being involved, could be found.

The typical spikes of *S. pachystachya* can be recognized from the illustrations in Ungern Sternberg (1876), t.18, fig. A, B. *S. brachiata* Roxb., a species from India and the East Indies, is very similar to *S. pachystachya*, the differences in the shape of the perianth, as described by Ungern Sternberg, seem to be rather insignificant.

Chevalier's (1922) claim that the type specimen of *S. pachystachya* has seeds with endosperm is thought to be based on a specimen of *A. indicum* (Perville 661!). I therefore agree with Moss (1954) that *A. pachystachyum* sensu Chevalier is conspecific with *A. indicum*, while *S. perrieri* Chev., being described as the second species occurring in Madagascar, is a synonym of *S. pachystachya*.

2. *S. meyerana* Moss in Adamson in J. S. Afr. Bot. 14 : 36 (1948); J. S. Afr. Bot. 20 : 20 (1954); Adamson in Fl. Cape Penins. 357 (1950). Type: Cape, Paarden-eiland, *Levy* in J 16969 (PRE, holo.!, J!).

Scarcely woody shrublet, erect rarely decumbent, up to 40 cm high; erect main branches up to 10 mm in diameter at the base, often twisted; secondary branches spreading and longer than the central stem. *Barren segments* cylindrical, faintly keeled or not keeled at the leaf apex, with lateral ridge, 5–15 mm long 2–3 mm in diameter, glaucous or green fading to deep bluish-red, then often shiny; leaf apex of young leaves slightly spreading when dried. *Sclereids* in the palisade tissue spirally thickened. *Spikes* terminal and lateral, (5–) 10–30 (–120) mm long, tapering when flowering, cylindrical when fruiting. *Cymules* 3-flowered; central flower acute or nearly so at its posterior apex; flowers protandrous. *Perianth tube* with three crenate segments, truncate with lateral shield. *Anthers* 2, 0.5–1 mm long. *Stigmas* tufted. *Seeds* compressed, oblong, 1–2 mm long, brown, with membranous testa covered with long seed hairs coiled at the apex; endosperm absent; embryo conduplicate. FIG. 10 : 1.

This species is recorded from all along the South African coast from Vanrhynsdorp to Durban. It is a pioneer plant mainly in maritime salt marshes, rarely in inland salt marshes, and rarely occurs in the lowest zone. The flowering and fruiting period is from February to May.

CAPE.—Bathurst: Kowie River, *L. Britten* 2096 (GRA); 2862 (GRA); Great Fish River, *Tölken* 397. Bredasdorp: Vogelvei, *Tölken* 507; near Struisbaai, *Levyns* 3536 (CT). Caledon: Hermanus Lagoon, *Jordaan* s.n. (STE); *Tölken* 499; Uilenkraalrivier, *Tölken* 504. Clanwilliam: Lambert's Bay, *Tölken* 340. Humansdorp: Kabeljourivier, *Tölken* 273a & b. Knysna: *Duthie* 884 (BOL); 902 (BOL, STE); *Duthie* sub Moss 8771 (J). Malmesbury: Ysterfontein, *Tölken* 485a & b. Mossel Bay: Little Brak River, *Moss* 4346 (J); Great Brak River, *Bolus* in BOL 18807 (BOL). Peninsula: Milnerton, *Moss* 3131 (J); 8826 (J); Rugby, *Tölken* 329; 330; Paardeneiland, *Levyns* in J 16969; Salt River, *Schlechter* 254 (GRA); *Moss* 8755 (GRA, J); 8758 (J). Port Elizabeth: Swartkopsrivier, *L. Britten* 3016 (GRA); *Troughton* in J 36909 (J). Vanrhynsdorp: Salt River, *Tölken* 535. Vredenburg: Danger Bay, *Tölken* 424; 480.

NATAL.—Durban: Congella, *Moss* 4336 (J); 5252.

This complex species is insufficiently known and some specimens differ very little from the European species but never entirely agree with the descriptions of Ball (1964). A form which is different from the typical *S. meyerana* has been observed in the field, often near disturbed areas. This form has very long spikes, 4–10 cm long, with wider flowering segments, more than two branches at the node and the central flower more acute and bigger in comparison with the lateral flowers. Usually only single specimens are seen, but at Danger Bay (Vredenburg district) a whole population was found. The following specimens are referred to this form: *Moss* 5252; *Tölken* 273; 424; 480; 485a. *Tölken* 485a shows somewhat intermediate characters. When plants of this form were grown from seeds collected at Danger Bay, together with those of the typical form under uniform conditions, they were indistinguishable from one another. This form is very similar to the European species, *S. dolichostachya*, but differs in always producing spirally thickened sclereids in the palisade tissue.

3. *S. uniflora* Toelken, sp. nov., ab *S. meyerana* cymis unifloris, raro bifloris, seminis ad 2 mm longis differt.

Suffrutex erecta ad 20 cm alta, ad 15 cm lata. *Articuli* cylindrici carinati, costis lateralibus, 4–8 mm longi, 2–3 (–4) mm lati, obscure virides vel purpurascetes; folia sicca vix extensi: folia mortua ramis inhaerentia. *Spicae* terminales et laterales, (8–) 10–20 (–30) mm longae, ad apices fastigiatae flore et fructu. *Cymae* uniflorae, raro biflorae, flore medio laterali longissimo. *Perianthii tubus* lobis 3, truncatus scutulo laterali, semini nonnunquam inhaerens. *Antherae* 2. *Stigma* cristata. *Semina* oblonga, fusca 2 mm longa, testa coriacea, pilosa, pilis adpressis apice circinatus; endospermum nullum; embryo conduplicatus. PLATE 5. FIG. 10 : 2.

Type: South West Africa, Lüderitz Bay, *Tölken* 460 (PRE, holo.).

Herbaceous annual, erect, up to 20 cm high and 15 cm in diameter; lateral branches fastigiate but not arising at an acute angle to the main branch. *Barren segments* cylindrical to barrel-shaped with keeled leaf apices and lateral ridge, 4–8 mm long, 2–3 (4) mm in diameter, glaucous green fading to bluish-red; leaf apices scarcely spreading when dried. *Sclereids* in the palisade tissue spirally thickened. *Spikes* terminal and lateral, (8–) 10–20 (–30) mm long, tapering when flowering and fruiting. *Cymules* 1-flowered, rarely 2, 3-flowered; central flower much larger than the lateral flowers and rounded at the apex; flowers protandrous. *Perianth tube* with three crenate segments, truncate with lateral shield, sometimes adhering to seeds. *Anthers* 2, 0.5–0.8 mm long. *Stigma* tufted. *Seeds* compressed oblong, brown, 2–3 mm long, with membranous testa covered with long hairs, adpressed, coiled at the apex; endosperm absent: embryo conduplicate.

This species is so far recorded only from Lüderitz Bay and Malmesbury district. It grows at Lüderitz Bay in maritime salt marshes in open spaces above the *A. perenne* zone. *S. uniflora*, judging from observations *in situ* at Lüderitz Bay, flowers in December and January and fruits in February and March.

CAPE.—Malmesbury: near Darling, *Walgate* 1070 (BOL).

SOUTH WEST AFRICA.—Lüderitz Bay: *Dinter* 6016 (BOL, STE); Lagoon, *Tölken* 460; 467.

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PLATE 1.—*Arthrocnemum mossianum* Toelken (*Tolken* 552, holotype, PRE).



PLATE 2.—*Arthrocnemum terminale* Toelken (Tölken 536, holotype, PRE).



PLATE 3.—*Arthrocnemum xerophilum* Toelken (*Compton 20874*, holotype, NBG).

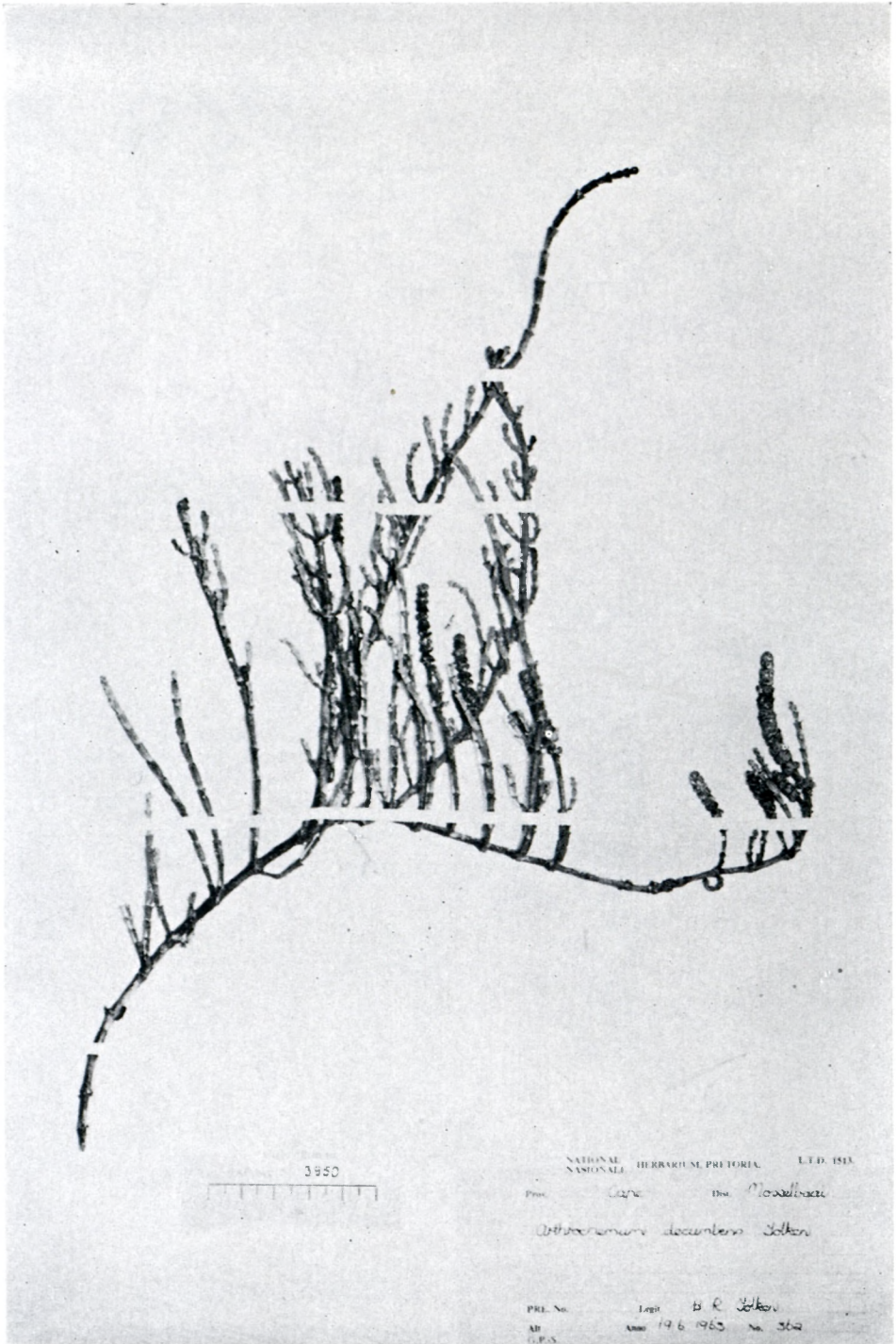


PLATE 4.—*Arthrocnemum decumbens* Tolken (Tolken 362, holotype, PRE).

