

Tendencies in the geographical distribution of the genus *Mariscus* (Cyperaceae) in southern Africa*

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ABSTRACT

The genus *Mariscus* occurs over practically the whole of the Flora of Southern Africa (FSA) region, with the exception of the west coast and the Karoo region of the Cape Province. Practically no species occur under conditions of less than 250 mm of rain per annum, whereas the highest concentrations of subgenera/sections and species occur where the annual rainfall is more than 500 mm. All the species in the region are summer rainfall plants, or if they occur in the winter rainfall area they behave like summer rainfall plants. The different subgenera/sections recognized within the genus differ widely in respect of their water requirements, yet there is a general concentration of taxa in the eastern part of the country where the rainfall is higher than in the west. Nevertheless, the highest concentrations of taxa are not in the areas of highest rainfall, which suggests that topographical diversity is probably the most important factor determining concentrations of taxa.

The geographical distribution of each subgenus/section in the FSA region is explained in relation to the total distribution of the subgenus/section. The possible climatic or environmental conditions which may determine the distribution of each subgenus/section are mentioned, and the concentration of species within each subgenus/section is demonstrated by means of maps.

RÉSUMÉ

TENDANCES DANS LA DISTRIBUTION GÉOGRAPHIQUE DU GENRE MARISCUS (CYPERACEAE) EN AFRIQUE AUSTRALE

Le genre *Mariscus* se rencontre pratiquement dans l'entièreté de la flore d'Afrique australe, à l'exception de la région côtière de l'Ouest et de la région du Karoo dans la province du Cap. Pratiquement aucune espèce ne se trouve sous des conditions de moins de 250 mm de pluie par an, tandis que les concentrations les plus élevées de sous-genres/sections et espèces se rencontrent là où les précipitations annuelles sont de plus de 500 mm. Toutes les espèces dans la région sont des plantes de régime pluvial estival, ou, si elles surviennent dans la région à pluies d'hiver, elles se comportent comme des plantes de régime pluvial estival. Les différentes sous genres/sections reconnus dans le genre diffèrent largement en ce qui concerne leur nécessité en eau, et pourtant il y a une concentration générale des taxa dans la partie orientale du pays où les chutes de pluies sont plus élevées qu'à l'Ouest. Néanmoins, les concentrations de taxa les plus élevées ne sont pas dans les régions où la densité de pluies est la plus élevée; ce qui suggère que la diversité topographique est probablement le facteur le plus important qui détermine la concentration des taxa.

La distribution géographique de chaque section/sous genre dans la région floristique de l'Afrique du Sud est expliquée en relation avec la distribution totale de la section/sous genre. Les conditions climatiques et de milieu éventuelles qui peuvent déterminer la distribution de chaque section/sous genre sont mentionnées et les concentrations des espèces dans chaque section/sous genre sont démontrées à l'aide de cartes.

The aim of the present paper is to describe the geographical distribution of the genus *Mariscus* in the Flora of Southern Africa region, and to correlate this distribution pattern with environmental conditions and the taxonomic interrelationships within the genus.

The genus *Mariscus* has, at various times in the past, been recognized as a separate genus, or as a section or subgenus of the genus *Cyperus*. It is characterized by bisexual florets, three stamens, three style branches, no hypogynous scales or bristles, and spikelets which are shed in their entirety. The latter characteristic distinguishes it from *Cyperus*, where the florets and glumes are shed but the rachillae of the spikelets remain attached to the plant. Taking into account the large size and heterogeneity of *Cyperus*, the present tendency to

subdivide genera in the family Cyperaceae, and the general distinctiveness of *Mariscus*, the latter is here recognized as a separate genus.

The species which are at present placed in the genus *Mariscus* occur over practically the whole of the Flora of Southern Africa region (Fig. 1), but are absent from the west coast and the semi-desert Karoo area of the Cape Province. This wide distribution is a manifestation of the adaptation of groups within the genus to widely differing habitat types. Once this adaptation had been accomplished to some degree, it resulted in spatial separation of the taxa, and this geographical separation together with the evolutionary pressure exerted by the different habitat types, must rapidly have resulted in the different groups of species which can be recognized today. Definite evolutionary lines can be distinguished, which are correlated with habitat preference.

The supraspecific groups within the genus *Mariscus* were given the rank of subgenus or section, and each is characterized by the morphology of the basal parts and inflorescence. The morphology of the basal parts are considered to be of great

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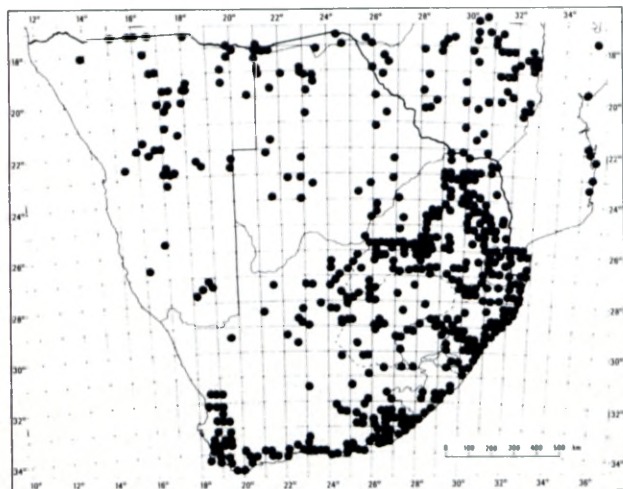


FIG. 1.—Genus *Mariscus*: map showing known geographical distribution in FSA area.

taxonomic importance, because this is the factor which enables the plants to live under specific conditions of soil moisture. The anatomical distinctiveness of the subgenera and sections indicates that these taxa are natural, and not merely the result of morphological convergence caused by similar environmental pressures on the different species within each of the presently recognised groups.

In the course of my revisionary work on the South African species of *Mariscus*, the species were grouped into the subgenera and sections listed below. As the recognition of some of these subgenera and sections in the genus *Mariscus* requires nomenclatural changes, this matter is treated elsewhere. For the purpose of the present paper those names which have not yet been validated, are printed between quotation marks. The following supraspecific taxa are recognized:

1. Subgenus '*Decidui*'
2. Subgenus '*Thunbergiani*'
3. Subgenus '*Umbellati*'
 - a. Section '*Umbellati*'
 - b. Section '*Latespica*'
 - c. Section '*Laxigluma*'
4. Subgenus '*Bulbocaulis*'
5. Subgenus '*Tunicati*'

From the distribution records given for species by Kükenthal (1936), *Mariscus* is clearly a genus of tropical and subtropical regions, with the number of species rapidly diminishing further than 30° from the equator. This global situation also holds good for southern Africa, where the largest concentrations of species and individuals are found in the warm, moist eastern third of the country (Fig. 3). Its absence from the west coast and the Karoo region can be correlated to an annual rainfall of less than 250 mm. It is also absent from a large area where the borders of the Cape Province, South West Africa/Namibia and Botswana meet. The latter area constitutes deep sandy soil and semi-desert conditions, and it is uncertain whether the lack of records should be attributed to poor collecting or to low rainfall.

As far as subgenera and sections are concerned, the higher concentrations of these taxa occur in the eastern part of the country (Fig. 2). The highest concentrations of subgenera and sections have not been recorded right at the coast in the areas getting the highest rainfall, but rather some distance inland. These concentrations are found along the escarpment, where a wide variety of habitats are available over a short distance. Therefore the highest concentration of subgenera and sections has been recorded in the area around Pretoria, which does not have a particularly lush vegetation and receives a mere 700 mm of rain per annum compared with up to twice as much along parts of the east coast and the eastern escarpment. Yet the Pretoria area offers over a short distance places receiving severe winter frost as well as virtually frost-free niches, marshy streamside situations to deep, dry sand or shallow humus-rich soil over flat rock slabs under intense insolation, and exposed sites to dense ravine forest. Moreover, this area is centrally situated in relation to the distribution areas of the individual subgenera and sections, so that the colonization of the different habitats would not require any great problem of migration.

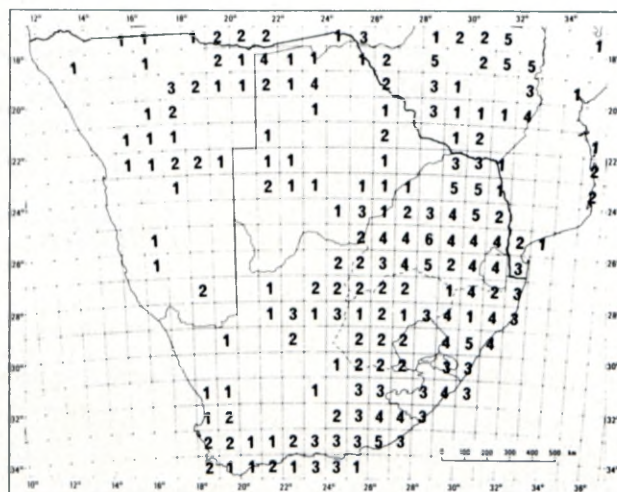


FIG. 2.—Genus *Mariscus*: map showing known concentration of subgenera/sections in FSA area.

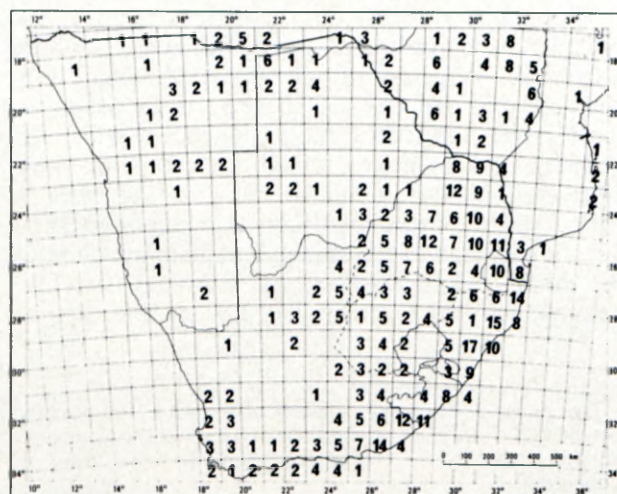


FIG. 3.—Genus *Mariscus*: map showing known concentration of species in FSA area.

In general terms, winter temperatures are probably not particularly restrictive in the geographical distribution of the genus, as all the southern African species (except two inhabitants of evergreen forest) die back to their basal parts during winter. Nevertheless it is conspicuous that certain species are restricted to areas receiving little or no frost during winter, and no species have been recorded from areas which receive snow during winter, such as the high Drakensberg escarpment between Lesotho and Natal. Most species seem to thrive under high summer temperatures as befits an essentially tropical genus, but a number of species show a definite preference for temperate or cool summer conditions. Not surprisingly, these species are mostly endemic in the region under discussion. The concentration of subgenera/sections as well as species in the moister eastern part of the country and their absence where the annual rainfall is less than 250 mm, leaves the impression that *Mariscus* is a hygrophylous genus in general. It is, however, noteworthy that there is wide individual variety in this respect, with some species growing only in wet soil, whereas others are pronounced xerophytes and grow only in the driest, best-drained places, even within areas of high rainfall.

The genus is a typical summer-rainfall one, and the presence of three species in the south-western Cape fynbos which receives its rain mostly during winter, must be ascribed to migration from the summer rainfall area. It is noteworthy that all three species which occur under winter rainfall conditions also occur in the adjacent summer rainfall area, and that they behave like summer rainfall plants in the sense that they grow actively during summer but die back during winter. These species are, however, independent of rainfall for their water supply, as they occupy riverside habitats which are wet throughout the year.

The subgenus '*Decidui*' (*Cyperus* sect. *Decidui* Kükenth.) has a horizontal sub-underground rhizome, 2–3 mm in diameter, consisting of spherical nodes connected to each other by thinner runners. This is a common base type amongst hydrophyllous Cyperaceae, and the sole species, *Mariscus deciduus* (Boeck.) C.B. Cl., is indeed confined to stream banks and similar wet habitats where it occurs between other grassy vegetation. As a low heliophyte (about 500 mm high) it is restricted to short grassland on cool highlands. It is known from ca. 10½°S in Zaïre to 29°S in Natal, wherever there is short grassland on streambanks. This area is probably temperate in summer, and winter frost is light or absent. (Fig. 4).

The subgenus '*Thunbergiani*' (*Mariscus* sect. *Thunbergiani* C.B. Cl.) has rather massive and hard rhizomes with nodes crowded together and covered with old leaf bases. The plants are medium-sized to large (up to 2 m high), and are usually found in streamside habitats on rather wet soil. In all the species the glumes contain a brown to reddish-brown pigment. Kükenthal (l.c. 430) amplified Clarke's original circumscription of the erstwhile section by including species from North, Central and South America, the West Indies, Ascension Island,

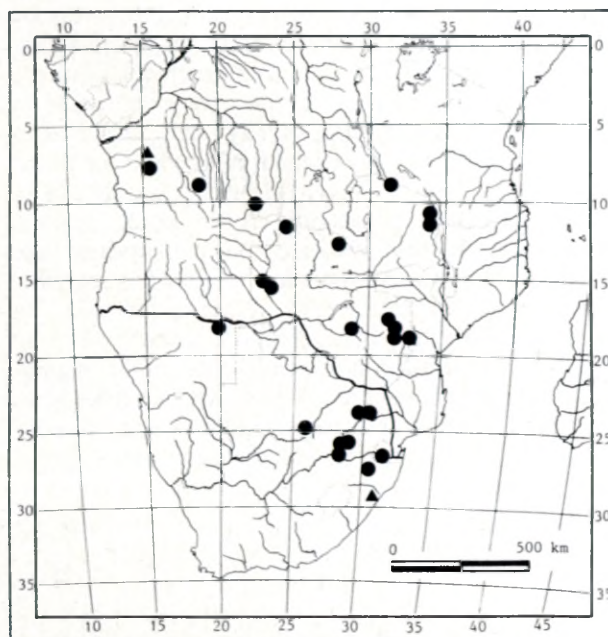


FIG. 4.—*Mariscus* subgen. '*Decidui*': map showing total known geographical distribution of the sole species, *M. deciduus* (Boeck.) C.B. Cl.

Madagascar and Australasia. I have not seen any authentically named material of these species, and as Kükenthal erroneously (in my opinion) included *M. congestus* (Vahl) C.B. Cl. in this section, it may indicate that the non-southern African addition to the section is anomalous. I have neither seen any material which could be placed in this subgenus from any of the areas mentioned above. In southern Africa this subgenus is represented by 7 species, which are all endemic. Four of these have rather restricted distribution areas, whereas the other three occupy larger areas, one of which includes nearly the total distribution area of the subgenus in southern Africa. The plants all occur in temperate to subtropical streambank situations in areas which are frost free or getting only very light frost. As a result of their streamside habitats, the distribution of these species is probably independent from rainfall, and it is not impossible that low winter temperatures is the restrictive factor in their distribution. In southern Africa the suitable habitats coincide with a narrow zone along the entire eastern and southern coast and extending northwards along the escarpment parallel to the coast to as far north as 17½°S. It occurs further inland along the eastern and northern Transvaal escarpment and the highlands of eastern and northern Zimbabwe. One species, *M. thunbergii* (Vahl) Schrad., is very common in the winter rainfall area of the south-western Cape Province, extending eastwards along the south coast into the summer rainfall region where its place is taken by another species. Still another species, *M. tabularis* (Schrad.) C.B. Cl., occurs in one enclave in the winter rainfall area of the south-western Cape and in another enclave in the eastern Cape, separated by a gap of some 400 km; yet the plants of the two areas are virtually identical. Two types of basal morphology are found in this subgenus. In the first group of four species the rhizome is horizontal, and the plants tend to form extensive clones of more or less spaced

individual aerial plants which are linked together by their rhizomes. These species all occur in grassland, in direct sunlight. In the second group of three species the rhizomes are vertical and the plants form dense tufts. Two of these species occur in glades in evergreen montane or coastal forest, while the third, known from only a single gathering, was found in short montane grassland under cool climatic conditions. If the southern African species are considered to constitute an endemic subgenus, which is strongly suspected of being the case, an analysis of species concentration reveals that the largest concentration of species occurs in the vicinity of Grahamstown, where 5 of the 7 species have been recorded. It would not be unreasonable to consider this area to be the subgeneric centre of distribution. (Fig. 5).

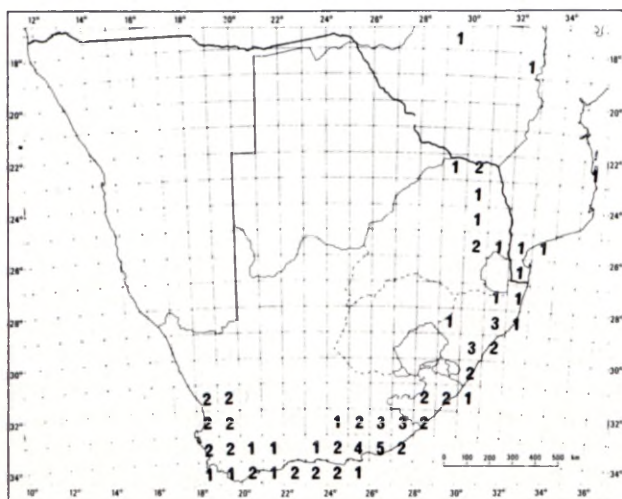


FIG. 5.—*Mariscus* subgen. 'Thunbergiani': map showing known geographical distribution, and concentration of species, in FSA area.

The subgenus 'Umbellati' has spherical or tear-shaped basal parts, 5–10 mm in diameter and clad in leaf bases. Vegetative propagation is by means of lateral innovations which are formed outside the enveloping sheath of leaf bases around the older base. The plants are medium-sized and the inflorescence is a simple or compound umbel. This concept consists of three clearly separate entities, yet they are united by their common base type and the general architecture of the inflorescence to such an extent that I have placed them in the same subgenus, albeit in three separate sections. On account of their identical basal parts one would expect the three sections to have similar water requirements, but in fact they differ considerably.

The first section, *Umbellati* C.B. Cl., consists of small to medium-sized plants, normally 200–500 mm high. The inflorescence is a simple umbel which is extended or may be contracted to varying degrees. The spikelets are terete and one- to few-flowered, and the glumes are green to yellowish-green. Kükenthal (*l.c.* 506 *et seq.*) listed 27 species in this section from the more tropical parts of Africa, the Mascarenes, Asia, Australia, North, Central and

South America and the West Indies. This section is decidedly tropical in its requirements, and in southern Africa the species all occur in more or less frost free areas with an annual rainfall of at least 800 mm. This corresponds with the lowlands of Natal and the eastern Cape Province, as well as the Transvaal lowveld and foot of the escarpment (Fig. 6). One species, *M. macer* Kunth, extends into central Transvaal, but is confined to frost-free niches in the hills, where it occurs more or less sheltered in dry ravine forest. These species are all dry land plants, being dependent on rain for their moisture supply, so that their distribution is strictly governed by rainfall patterns. Of the six species recorded in the FSA region, *M. sumatrensis* (Retz.) J. Raynal has the widest distribution, namely throughout the moister parts of tropical Africa and tropical Asia. *M. sublimis* C.B. Cl. and *M. cylindristachyus* Steud. are widespread tropical African endemics, whereas *M. macer*, *M. macrocarpus* Kunth and an undescribed species have restricted distribution areas. The impression was gained that *M. sumatrensis* may be an introduced weed, and the same may hold true for *M. sublimis* and *M. cylindristachyus* which are known from only a few collections in the FSA region.

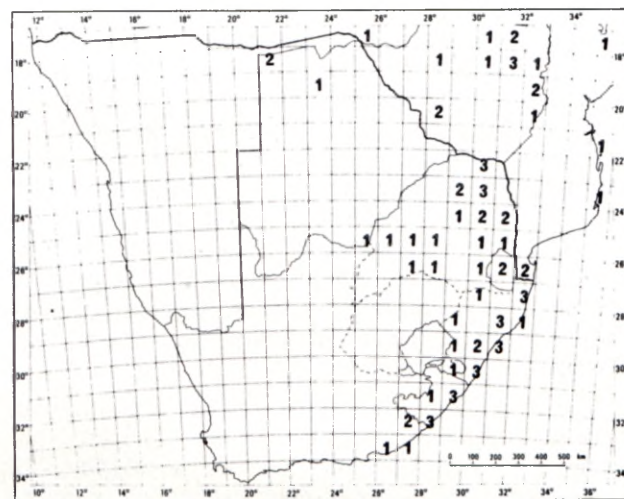


FIG. 6.—*Mariscus* sect. *Umbellati*: map showing known geographical distribution, and concentration of species, in FSA area.

The second section, 'Latespica,' consists of two medium-sized hydrophytic species, one endemic and one probably an introduced weed. The inflorescence is a compound umbel, the spikelets are laterally compressed and many-flowered, and the glumes are tightly imbricate and have a purple-black pigmentation. Both are generally confined to cool areas or cool niches, where they occur on stream banks or in bogs. The endemic species, *M. congestus*, (Vahl) C.B. Cl., is very common wherever there are suitable habitats in the eastern third of South Africa. Its occurrence in the south-western Cape, South West Africa and Zimbabwe may be the result of its having been introduced into these areas. Its endemism is indeed somewhat surprising, considering the ease with which it established itself in recent times in Europe and Australia. The second species, *M. keniensis* (Kükenth.) S. Hooper, is known from the east African escarpment, from the

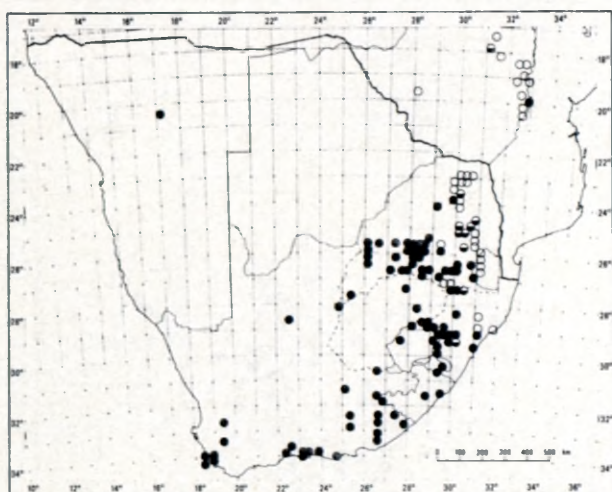


FIG. 7.—*Mariscus* sect. 'Latespica': map showing known geographical distribution in FSA area. ●: *M. congestus*; ○: *M. keniensis*.

equator southwards to Natal. In southern Africa I have only seen it in association with commercial timber plantations, and it has almost certainly been introduced into this region. Its distribution suggests a requirement for somewhat more tropical conditions than *M. congestus* (Fig. 7).

The third, section, '*Laxigluma*' (*Mariscus* subsect. *Laxiglumae* C.B. Cl.), is represented by a single medium-sized xerophytic species, *M. laxiflorus* Turrill, in the FSA region. Its inflorescence is a compound umbel, the spikelets are laterally compressed and many-flowered, and the straw-coloured glumes are set at an obtuse angle relative to the rachilla. Kükenthal (*l.c.* 458) recognized 23 species in this section, mostly from the dry areas of Central and South America, but also from North America (five species), Sikkim (one species) and Africa (three species). It is tempting to speculate on the

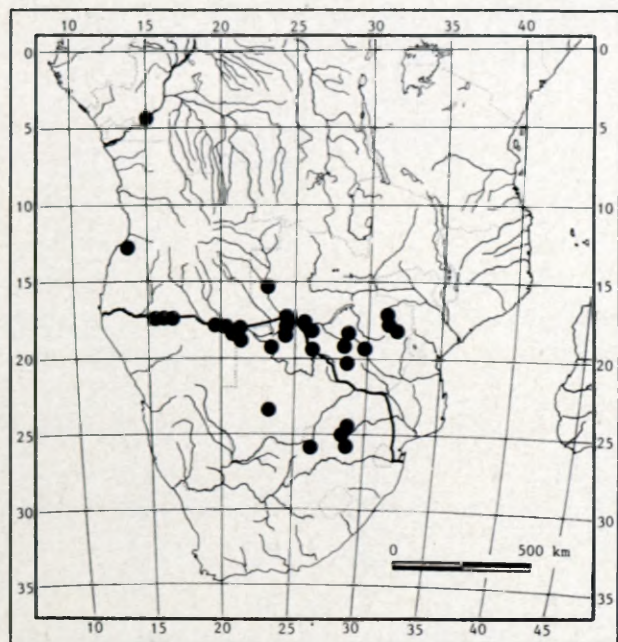


FIG. 8.—*Mariscus* sect. '*Laxigluma*': map showing total known geographical distribution of the species represented in the FSA area, *M. laxiflorus* Turrill.

representation of this essentially *American* section in Africa. That the species on the two continents are closely related, leaves no doubt, as Kükenthal's illustration of *Cyperus spectabilis* Link from Central America (*l.c.* 460) shows a plant remarkably similar to *M. laxiflorus*. *M. laxiflorus* occurs from about 4°S in Zaïre to about 26°S in the Transvaal (Fig. 8), usually in dry, tall, open woodland in partial shade, and usually on deep, loose sand. This area becomes hot in summer and is more or less frost free. It receives 500 to 750 mm of rain per annum, concentrated within two or three very hot summer months.

The subgenus *Bulbocaulis* C.B. Cl. is characterized by narrowly ovate basal pseudobulbs, which comprise somewhat thickened stem bases covered by numerous layers of non-fleshy leaf bases. Unlike the subgenus '*Umbellati*,' vegetative propagation is by means of lateral innovations which are formed within the enveloping sheath of old leaf bases. The plants are small to medium-sized, with a variety of inflorescence types ranging from a compound umbel to a single head-like spike. The glumes have a variety of colours. This is essentially an African subgenus, and practically all 38 species recognized by Kükenthal (*l.c.* 538 *et seq.*) occur in the dry tropical savanna of Africa and Madagascar. Only *M. dubius* (Rottb.) Kükenth. ex G.E.C. Fischer and possibly *M. dregeanus* Kunth extend as far as Asia, the former occurring as far east as the Tonkin province of China, whereas one species (*M. maritimus* Miq.) is endemic to the Philippines. Both *M. dubius* and *M. dregeanus* are confined to tropical regions with an annual rainfall in excess of 700 mm. *M. dubius* especially is often found associated with *M. sumatrensis* of the section *Umbellati*, and it is noteworthy that these two species have a similar distribution pattern in Africa and Asia. The remaining species are all xerophytes to varying degrees, occurring more or less in the open on bare ground or wedged into cracks in rocks, often under extreme insolation in very well-drained niches. Fifteen species are recognized in the FSA area. They occur throughout the summer rainfall region wherever the annual rainfall exceeds 250 mm but, in spite of their xerophytic nature, the highest concentrations of species are along the east coast and eastern escarpment (Fig. 9).

The subgenus '*Tunicati*' (*Cyperus* subsect. *Tunicatae* C.B. Cl. (p.p.??)) is represented in the FSA region by two xerophytic species. Kükenthal (*l.c.* 121) included 8 species in this section, all from Africa but with one species extending through Asia to Australia. The plants are characterized by having a series of underground true bulbs which are interconnected by filiform scale-clad rhizomes. The aerial plants are strictly annual and regeneration in spring takes place from the underground bulbs. The two southern African species have a wide distribution in southern and eastern Africa, where they occur under dry conditions of 260 to 600 mm of rain per annum (Fig. 10). These plants favour more or less open, sunny sites where they occur on loose sandy soil to very hard, stony soil. '*M. fulgens*' (*Cyperus fulgens* C.B. Cl.) shows a tendency to

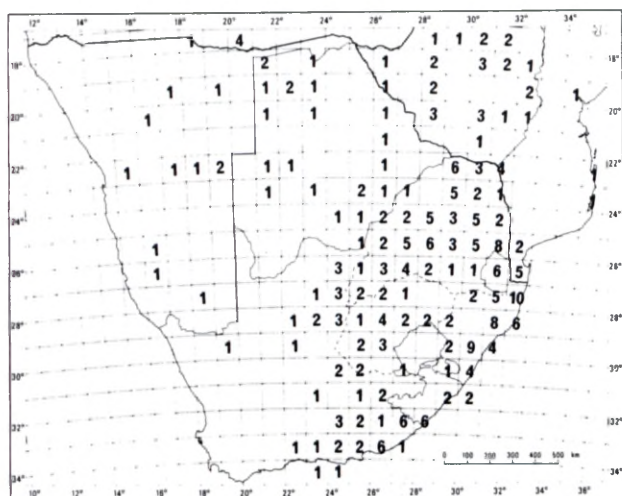


FIG. 9.—*Mariscus* subgen. *Bulbocaulis*: map showing known geographical distribution, and concentration of species, in FSA area.

become a weed in cultivated lands. The wide distribution of both species suggests a considerable degree of adaptability in respect of environmental requirements. The underground bulbs are almost certainly a mechanism for surviving drought, and the distribution of the southern African species in relation to rainfall patterns suggests that a rainfall of more than about 600 mm per year is a limiting factor in their distribution. This is borne out by observations on cultivated plants. As both species die back completely during winter, it is difficult to envisage winter frost as a limiting factor in their distribution, yet '*M. usitatus*' (*Cyperus usitatus* Burch.) occurs almost five degrees longitude further south than '*M. fulgens*.' and this can only be explained in terms of increased cold resistance.

It will be realized that, whereas it is possible to indicate trends in the distribution, pinpoint concentrations, and suggest reasons for the observed distribution patterns of subgenera/sections and species, it would be unwise to speculate on areas of origin of the taxa or past migrations. Clearly the

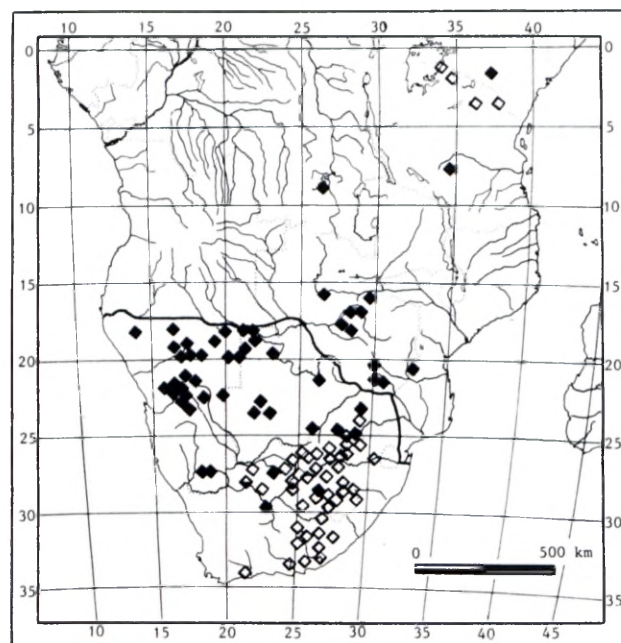


FIG. 10.—*Mariscus* subgen. '*Tunicati*': map showing total known geographical distribution of the two species represented in the FSA area. ◆ : *M. 'fulgens'*; ◇ : *M. 'usitatus'*.

southern African subgenera and sections, if not species, exhibit a low degree of endemism and must be seen as a mere extension of the large pantropical distribution of the genus. It will only be possible to see the southern African taxa in true perspective once the whole genus has been studied, which is unfortunately outside our mandate.

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