A REVISION OF THE GENUS SCLERIA BERGIUS (CYPERACEAE) IN SOUTHERN AFRICA

A thesis submitted in partial fulfilment of the requirements for the degree of Doctor of Philosophy

in the

Department of Botany, Faculty of Science,
University of Natal,
PIETERMARITZBURG

Thesis (Ph.D; Botany) - University of Natal, Pietermaritzburg, 1983.

by

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The genus *Scleria* Bergius (Cyperaceae) in Southern Africa is critically examined, and the generic limits reviewed. The taxonomic position of the genus in the family is examined. Diagnosis of the tribe Sclerieae is altered to circumscribe *Scleria* as the only genus, and diagnoses of the tribes Bisboeckelereae and Sclerieae are made. Infragenetic limits are re-assessed and two subgenera, *Scleria* and *Hypoporum* recognised, the relationship of which is postulated as co-lateral, not filial. Evidence is presented that ecological specialisation in subgenus *Hypoporum* has resulted in taxa which are adapted to open, seasonally dry, temperate habitats, whereas ecological specialisation in subgenus *Scleria* has given rise to taxa which are adapted to shady, wet, tropical and subtropical habitats. Taxa in subgenus *Hypoporum* are slender, usually narrow-leaved annuals, or perennials with annual aerial parts, that is, they have evolved drought/cold escape mechanisms, the annuals by completion of the life cycle in a season, the perennials by withdrawal of food reserves into a protected, substranean perennating organ and sometimes also into enlarged culm-bases. Taxa in subgenus *Scleria* are more-or-less robust, usually broad-leaved perennials, or, less often, annuals. With few exceptions the plants are evergreen and do not manifest drought/cold escape mechanisms. The annual species occupy tropical habitats in areas where seasonal drought may be experienced and it is suggested that they have acquired
the annual habit as a drought-escape mechanism. The only perennial species in subgenus Scleria in Southern Africa which has annual aerial parts, has evolved additional storage regions in the swollen culm-bases. This species, S. transvaalensis occurs at higher, more temperate altitudes than other species in the subgenus.

The fundamental branching pattern of the inflorescence of all species examined has been shown to be the same. It is postulated that the pattern is modified in two ways, namely, by progressive contraction of all or most ramuli leading to the "glomerate-spicate" type of inflorescence characteristic of subgenus Hypoporum, in which the bracts are reduced, glumiform structures, and, by progressive contraction of some ramuli and progressive elongation of others leading to the "interrupted-paniculate" type of inflorescence characteristic of subgenus Scleria, in which the bracts are foliaceous. It is suggested that the branched glomerate-spicate type of inflorescence is less specialised than the simply glomerate-spicate type, and that in the line with interrupted-paniculate inflorescences, the greater the degree of elongation and the greater the number of elongated ramuli, the more highly specialised the inflorescence.

Evidence is put forward that the spikelet of Scleria is a monopodial, that is, racemosely-branched structure, and suggestions that it may be sympodial, refuted.
It is postulated that unisexual spikelets in *Scleria* have been derived by reduction from bisexual (androgynaeceous) spikelets. Unisexual female spikelets are unknown in subgenus *Hypoporum* which has androgynaeceous spikelets and unisexual male spikelets. It is suggested that the higher the ratio of androgynaeceous to male spikelets in the inflorescence, the less specialised the inflorescence.

Unisexual male and functionally unisexual female spikelets occur in subgenus *Scleria* and, rarely, androgynaeceous spikelets. It is suggested that species which consistently produce some androgynaeceous spikelets are more primitive than those which consistently lack them, and that species whose functionally female spikelets consistently lack any vestigial male parts are more advanced than those which have male rudiments.

The hypogynium or "disc" which is present on some achenes is considered to be a new modification of the stipe of the achene and not a vestigial structure, therefore it is postulated that the type of achene found in subgenus *Hypoporum* which has a trigonous stipe lacking any distal elaboration as an hypogynium is primitive, and that the type of achene found in subgenus *Scleria* which has an obpyramidal stipe elaborated distally as an hypogynium is derivative. It is suggested that development of the hypogynium has attained its most specialised level in one group of species in which this structure serves as a flotation device. Diagnoses of
sections in subgenus Scleria are based partly on differences in morphology of the hypogynium.

It has been demonstrated that the cell-walls of the pericarp are silicified, that the process of silicification is progressive proceeding from the apex towards the base of the fruit, and that abscission of the fruit takes place when silicification is complete and the vascular supply is severed. The achenes of subgenus Hypoporum have all cells silicified; those of subgenus Scleria have all cells except those of the free flange(s) of the hypogynium silicified.

Scanning electron microscopy has revealed details of surface ornamentation of the achenes not previously known, which provide additional diagnostic characters at species level.

Attempts to germinate achenes of Scleria have been unsuccessful: the conditions required, physical and physiological, are not understood.

Analysis of anatomical evidence, in particular those characters seen in transverse sections of laminas and culms, confirms that there has been specialisation along two divergent pathways; one which has led to successful occupation of relatively dry, temperate habitats (subgenus Hypoporum), and the other to successful occupation of shaded damp, and open aquatic, subtropical
and tropical habitats (subgenus Scleria).

One section, Hypoporum, is recognised in subgenus Hypoporum, pending survey of the subgenus on a world basis.

Four sections are recognised in subgenus Scleria, namely, Scleria, Acriulus, Schizolepis and Ophryoscleria. Section Scleria may comprise several natural groups, the delimitations of which can not be attempted until a world survey has been made.

A map showing world distribution of the genus, and regional distribution maps of Southern African species are provided, also a Table showing the total distribution range of species recorded from Southern Africa.

Generic, subgeneric, sectional and species descriptions are provided. Two new species are described. Keys to the Southern African species for use in the herbarium, in the field, and one based on anatomical characters of the laminas are presented. Original descriptions and photographs of type specimens of taxa represented in Southern Africa are included as appendices.
Acknowledgements

To Dr T.D. Steinke, Professor of Botany in the University of Durban-Westville I express my thanks for the use of the facilities in his Department and for his personal interest in this project. I am grateful to my colleague Mr C.J. Ward for the many gatherings of Scleria spp. which he has made which have contributed to our knowledge of the distribution of the genus in Southern Africa and for his generosity in sharing his knowledge of the genus in the field with me. To Dr F.M. Getliffe (Mrs R. Norris) who accompanied me on several field trips and who unstintingly shared her knowledge of Cyperaceae I am most grateful.

I thank Dr J.H. Ross, Dr T.H. Arnold and Dr H.F. Glen, all of whom during their tenure of office as South African Liaison officers at the Royal Botanic Gardens, Kew, assisted me by obtaining type specimens, copies of old documents and photographs and I thank their wives, who kindly extended hospitality to me on my several visits to the United Kingdom. To Miss S.S. Hooper, Curator of Cyperaceae in the Herbarium of the Royal Botanic Gardens, Kew, I extend my thanks for her help, advice, criticism and hospitality.
I am grateful to the Directors, Keepers and Curators of various herbaria in South Africa, the United Kingdom and Europe for the use of their facilities, for the loan of specimens and for photographs of types, in particular to Dr H. Baijnath of the University of Durban-Westville for his assistance in obtaining material on loan.

I am indebted to Dr J.R. Lawton for her encouragement and for advice in the techniques of electron-microscopy, and to Dr N.R. Comins of the National Physical Research Laboratory of the Council for Scientific and Industrial Research, Pretoria for energy-dispersive X-ray analyses.

To the staff of the Interlibrary loan Department of the University of Durban-Westville I offer my thanks for their courtesy and their helpfulness in locating and obtaining facsimile copies of essential references on my behalf.

For technical assistance I am grateful to Miss A. Munz, Mrs J. Evers, Mrs Y. Naidoo, Mr S. Kasavan and Mr H. Ramkisson and for her invaluable help in the preparation of photographs to Mrs E.L. Lawes. To Mrs R. Bunsee who typed the manuscript and to Miss P. Govender who assisted with the typing of preliminary drafts I express my thanks.
For their willingness to act as "guinea-pigs" by testing keys and checking observations I thank several successive generations of undergraduate students in the Department of Botany of the University of Durban-Westville.

I am deeply grateful to my brother-in-law, Captain G.H. Hennessy R.M. and his wife, Della, for their hospitality during my visits to the United Kingdom and to my husband, Lieutenant Commander B.J. Hennessy R.N. and my son, Timothy for their support and encouragement.

Finally, I wish to express my thanks to my supervisor, Dr K.D. Gordon-Gray, formerly Associate Professor of Botany in the University of Natal, Pietermaritzburg, for her guidance, for her continued interest in this project, and for engendering my interest in Scleria in the first place.
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Fig. 1. Geographical distribution of the genus *Scleria* Bergius, modified from Piérart, 1953.
1. Introduction

Evidence from all available sources, including chemical, anatomical and morphological data, has led to wide acceptance that the allied families Cyperaceae and Poaceae constitute a single order, Cyperales G.T. Burnett (1835) of the subclass Commelinidae Takhtajan (1966) of the class Liliopsida Cronquist; Takhtajan and Zimmerman (1966). Fossil pollen of a type characteristic of members of Commelinidae has been found which ante-dates fossil pollen of members of Liliidae (Cronquist, 1981) and this, together with evidence from other sources, refutes the theory (Hutchinson, 1959) that Cyperales have been derived from Liliaceous ancestors.

Within the Commelinidae the most archaic order, Commelinales, has perfect flowers which lack nectaries and are pollinated by pollen-gathering insects. The flowers of the other six orders (Eriocaulales, Restionales, Juncales, Cyperales, Hydatelales and Typhales) show different degrees of reduction associated with wind pollination, with some exceptions among Eriocaulales which have developed petal nectaries and are pollinated by nectar-gathering insects.

Whereas in the recent past the Cyperaceae were considered to have been derived from the Juncaceae and
the Poaceae from the Restionaceae, Cronquist (1968, 1981) has presented cogent reasoning in support of the view that the relationships are more nearly collateral than filial, with the three orders, Juncales, Restionales and Cyperales originating from the Commelinales. The two families of Cyperales, Cyperaceae and Poaceae, are considered by Cronquist to represent closely related lines diverging at an angle from a common source.

Classification within Cyperaceae lacks uniformity. While there is no consensus of opinion it is generally agreed that there are several main spikelet and flower forms represented and therefore genera have been grouped in taxonomic assemblages to which the rank of tribe has been accorded. The number and delimitations of tribes varies. Of post Darwinian workers, Bentham (1887) recognised six tribal units, Clarke (1908) seven, Holttum (1948) five, Hutchinson (1959) seven, Koyama (1961) six, Hooper (in Metcalfe, 1971) eight and Eiten (1976) nine with two genera (Scleria and Dulichium) not assigned to tribes because of uncertainty with regard to their taxonomic position.

The main lines of evolutionary development have been suggested by the grouping of tribes in categories of higher hierarchical level within which the positioning of the tribes indicates putative phylogenetic relationships. Bentham (l.c.) grouped his six tribes
into two series, Monoclines and Diclines. Clarke (l.c.) placed his seven tribes in four sub-families. Holttum (l.c.) accepted Bentham's arrangement but switched the position of two tribes in Monoclines. Hutchinson (l.c.) failed to recognise sub-familial rank thereby indicating his seven tribes as representing separate evolutionary lines. Koyama (l.c.) placed his six tribes in four sub-families; Hooper (l.c.) recognised five sub-families and Eiten (l.c.) three sub-families.

In most of these systems of classification the genus Scleria has, on the basis of its having unisexual flowers, been placed among the more advanced members of the family, since it has been widely accepted that unisexual cyperaceous flowers are specialised and derived by reduction from bisexual flowers such as occur in Scirpus of the tribe Scirpeae through an intermediate stage such as that found in Cladium (Rhynchosporeae). It has been suggested (Mattfeld, 1938; Holttum, 1948; Kern, 1962; Schultze – Motel, 1959, 1964) that bisexual flowers such as those of Scirpus may possibly have been derived from unisexual ones such as those of Hypolytreae (Mapanieae). Such a view implies that the tropical Hypolytreae are more primitive than Scirpeae, a concept which is not upheld by Eiten (1976), who considers the Mapanieae with their unisexual flowers aggregated in pseudanthia to belong to the most advanced subfamily, Mapaniodeae. In
Eiten's scheme, *Scleria* is assigned to the second of her three subfamilies, Caricoideae. Scirpeae and Rhynchosporoeae are placed in the most primitive subfamily, Cyperoideae (= Rhynchosporoidae). This accords with the view that unisexual flowers are derived from bisexual ones in Cyperaceae and, in turn, that reduced, anemophilous flowers are derived from perfect, entomophilous flowers.

To the tribe Sclerieae have been assigned those genera with unisexual flowers aggregated in spikelets some of which have both male and female flowers, some with a solitary female flower and some with only male flowers. The spikelet of Cariceae differs from that of Sclerieae in that the female flower is enclosed in an utricle which is not present in Sclerieae.

Spikelet structure has been interpreted in two ways. The classical view is that the bisexual spikelet of Sclerieae is a monopodial structure with an indeterminate axis bearing bracts (glumes) with a single flower in the axil of each glume. Another interpretation is that the bisexual spikelet of Sclerieae is a double axis system, with the female flower terminal on an axis from which a lateral axis bearing the male flowers arises (Pax, 1886; Core, 1936; Kern, 1961; Napper, 1963; Schutze-Motel, 1964 and Koyama, 1967; 1969). Eiten (1976) supports the view that the bisexual spikelet is monopodial.
Whereas most systems of classification include the genera *Bisboeckelera* (= *Hoppia*), *Becquerela*, *Calyptrocarya*, *Diplacrum* (including *Pteroscleria*) and *Scleria* (including *Acriulus*) in the tribe *Sclerieae*, Eiten excludes *Scleria* from the group, placing *Bisboeckelera*, *Becquerela*, *Calyptrocarya* and *Diplacrum* in a single tribe, *Bisboeckelereae* Mattfeld in Diels (1936) and not assigning *Scleria* to any tribe. *Scleria* is excluded from the assemblage on the grounds that whereas the other genera have inflorescences in which axes which terminate in male spikelets arise from axes which apparently terminate in pistils, in *Scleria* this pattern of branching in the inflorescence never occurs. The branching pattern of the bisexual spikelet of *Scleria* is similar to that of *Rhynchospora* (*Rhynchosporaeae*), *Schoenoxiphium* and *Kobresia* (*Cariceae*). *Scleria* in Eiten's view cannot be assigned to *Rhynchosporaeae* since it has unisexual flowers and those of *Rhynchosporaeae* are bisexual, nor to *Cariceae* because the female flower of *Scleria* is not inside an utricle or semiutricular prophyll.

Uncertainty about the tribal affiliation of *Scleria* is likely to persist until all species of the genus and those of other genera assigned by various workers either to *Sclerieae* or *Bisboeckelereae* are adequately known morphologically and agreement is reached with regard to interpretation of spikelet structure.
Generic limits within the tribe Sclerieae (Clarke, 1908) are still not clearly defined. Acceptance of the evolutionary outlook in the latter part of the nineteenth century resulted in scrutiny of established generic limits in order to determine their phylogenetic significance and as a result fifteen small genera, most of them established by Nees von Esenbeck, were reduced by Bentham (1883) to congenerity in Scleria, among them the genus Diplacrum R. Br. Most subsequent workers have excluded Diplacrum from Scleria with the exception of Kern (1961), Koyama (1961) and Raymond (1966). Similarly the genus Acriulus Ridl. (1884) has been variously upheld or reduced to congenerity in Scleria. Evidence obtained from the present study supports the inclusion of Acriulus in Scleria.

Uniformity is also lacking in classification within the genus. Species have been grouped in infra-generic taxa variously designated as subgenera, sections and series, the delimitations of which vary. Criteria used to separate infra-generic, supraspecific taxa include morphology of the inflorescence, the spikelet and the fruit, as well as the habit of the plants. Comparison of the systems of classification of the genus is made difficult by the fact that all (except those of Boeckeler (1874) & Clarke (1908) ) have been based on work undertaken on a regional basis. The most comprehensive accounts published since Clarke's day have been those of Core (the Americas, 1936), Chermezon
(Madagascar, 1936), Pierart (Belgian Congo and Ruanda Urundi, 1951), Hutchinson (West Tropical Africa, 1936), Nelmes and Baldwin (Liberia, 1952), Nelmes (Africa, 1955, 1956), Kern (Malaysia, 1961), Koyama (Japan, 1951) and Robinson (Flora Zambesiaca area, 1966). There has been no revision of Southern African species since Clarke's account in Flora Capensis (1898).

Clarke (1908) recognised seven subgenera, two of which were further subdivided into sections; Core (1.c.) basing his classification on that of Pax (1887) recognised five sections in the Americas; Nelmes (1.c.) four in Africa; Koyama (1.c.) two subgenera in Japan, Scleria and Diplacrum, of which Scleria was divided into three sections based on Clarke's circumscriptions; Kern (1.c.) eight sections including Diplacrum in Malaysia, of which three were new, and Robinson (1.c.) two subgenera in the Flora Zambesiaca area, one of which, Scleria, included four of Clarke's subgenera plus Acriulus and the other, Ophryoscleria, being maintained unaltered. In most of the earlier treatments the subgenus/section Hypoporum was diagnosed as having bisexual (androgynaeceous) spikelets aggregated in "glomerules" in unbranched or sparingly branched "glomerate-spicate" inflorescences with greatly-reduced bracts ("bracteoles"), as opposed to the lax or compact paniculate inflorescences with foliaceous bracts of most
species of other sections all of which have functionally unisexual spikelets.

In addition, the absence of an hypogynous disc in Hypoporum or its presence and morphology in other sections has provided a character used to distinguish infrageneric taxa.

The presence of subandrogyneceous spikelets in many species assigned to taxa other than Hypoporum led Robinson (1966) to question the validity of separating Hypoporum from other subgenera on the basis of gender of the spikelets. The subgenus Ophryoscleria was maintained on the grounds of its members having "highly specialised development of the hypogynium and a persistent and highly differentiated style-base".

There is also disagreement with regard to interpretation of phylogenetic trends within the genus. One school, exemplified by Nelmes (1955) considers that section Hypoporum is advanced by virtue of its members having slender, smooth culms, glumiform bracteoles, glomerate-spicate inflorescences, hypogynia reduced to absence and a large number of annual species. The opposite view is that section Hypoporum is primitive (Robinson, 1962) in having fully androgynaeceous spikelets, in having among its members species with the least-modified panicles in the genus, a simultaneous inflorescence and no hypogynium developed, that is,
Because of the extended geographical range of some taxa there may be considerable morphological diversity over their distribution range. This has not always been appreciated with the result that considerable nomenclatural confusion at the species level still exists, mainly because much of the earlier descriptive work was undertaken on a purely regional basis.

Whereas some Southern African species of *Scleria* are endemic to the region, the majority have wide distribution in Africa north of our boundaries and some also in Malagasy, India, Malaysia, Australia, the East Indies, South and Central America and the West Indies. Many of the Southern African species of *Scleria* are inconspicuous in the field, therefore distribution records are poor and are often a better indication of distribution of collectors in whom an awareness of Cyperaceae has been engendered than they are of distribution of species of *Scleria*. It is noteworthy in this regard that the Herbarium of the University of Orange Free State has not a single specimen of *Scleria* in its collection. This situation is at least partly due to the lack of a comprehensive key to the twenty-one species recorded to date in Southern Africa, the only key in existence being that of Clarke in *Flora Capensis* (1898) in which eleven species were listed, some of which have since been placed in synonymy.
Although it is known that anatomical data aid in the elucidation of phylogenetic relationships in Cyperaceae, little information on the anatomical structure of Southern African species of *Scleria* is available. Descriptions have been published of leaf anatomy of four locally represented species, *S. foliosa* Hochst. ex A. Rich., *S. unguiculata* E.A. Robinson, *S. welwitschii* (Ridl.) C.B.Cl. and *S. greigiifolia* (Ridl.) C.B.Cl. (as *Acriulus greigiifolius* Ridl.), and of culm anatomy of the same four species and of *S. rehmannii* C.B.Cl. by Metcalfe (1971) and of leaf and culm anatomy of *S. poaeformis* Retz. by Govindarajalu (1975), but none of the specimens examined was of Southern African origin. Critical studies of anatomical structures of all species represented in the region are necessary in order to aid in the elucidation of infra-generic relationships.

The purpose of this investigation has been to obtain a clearer understanding of taxonomic relationships of and within the genus *Scleria* through critical analysis of morphological and anatomical evidence, ecological preferences and distribution of the species represented in Southern Africa. Particular attention has been given to interpretation of floral morphology and spikelet structure, for until such time as all species are adequately known morphologically, interpretations may well be doubtful and opinions with regard to tribal affiliation are thus likely to remain divided.
During the course of this investigation three visits have been made to the Herbarium of the Royal Botanic Gardens, Kew, in order to examine gatherings of Scleria from the whole range of its distribution. Type material of every species represented in Southern Africa has been examined and literature relating to Cyperaceae from all areas of the world where the genus is known has been consulted. Complete descriptions of the genus and of all the species previously recorded from our area have been made. Two new species have been described (Franklin, 1983) and keys for use in the field and the laboratory have been prepared.

1.1. **Historical review of the family Cyperaceae**

One of the hundred "Ordines Naturales" established by Antoine Laurent de Jussieu in 1789 was the Cyperoideae (de Jussieu, 1789).

Several accounts of the family followed, among them those of A.P. de Candolle (1805) who was the first to use the name "Cyperaceae", now conserved, Robert Brown (1810), T.G. Lestiboudois (1819) John Lindley (1830), and J.H.F. Link (1833), but it was not until 1834 that subdivision of the family into tribes took place. In that year C.G.D. Nees ab Esenbeck (1834) divided the family into nine tribes, namely, Cypereae, Hypolytreae,
Chrysitricheae, Scirpeae, Rhynchosporeae, Cladieae, Sclerieae, Elyneae and Cariceae. By the addition of Fuireneae (Endlicher, 1836) the number was raised to ten. Endlicher (1836) followed Nees' treatment of the family and incorporated additional information obtained from an unpublished account by Fenzl (Fenzl mss. cited in Endlicher, 1836). In Endlicher's account the tribe Rhynchosporeae was divided into two sub-tribes, Rhynchosporeae Verae and Schoenoideae and the tribe Fuireneae was proposed with three sub-tribes, Melanacrideae, Hemichlaeneae and Ficineae. Nees (1842) raised Ficineae to tribal rank bringing the number of tribes to eleven.

In his "Enumeratio Plantarum", C.S. Kunth (1837) combined Ficineae, Fuireneae and Scirpeae in a single tribe, Scirpeae, and combined Cladieae with Rhynchosporeae in Rhynchosporeae. Boeckeler (1869) adopted Kunth's treatment of the family.

Bentham (in Bentham and Hooker, 1883) reviewed the classification of Cyperaceae, according tribal rank to six units which in turn he grouped into two categories of higher hierarchical level. Possible phylogenetic relationships were suggested by the positioning of the six tribes in the two series. In Monoclines (with hermaphrodite flowers) were placed the tribes Scirpeae, Hypolytreae and
Rhynchosporaeae and in Diclines (with unisexual flowers) the tribes Cryptangieae, Sclerieae and Cariceae.

Pax (1866, 1887) also divided the family into two sub-families; Scirpoideae (spikelet without a terminal flower) and Caricoideae (spikelet with a terminal flower), in which Sclerieae was included. Some of his observations were faulty and his system has been strongly criticised, especially by Holtttum (1948);

In "Flora Capensis" C.B. Clarke (1897) published a system of classification which was re-published, unaltered, four years later in "Flora of Tropical Africa" (1902) and again, with some modifications, in his posthumously published monograph (Clarke, 1908). He originally recognised five (1897, 1902) and later seven (1908) tribes which were grouped into four sub-families, namely Scirpo-Schoeneae which included the tribes Cypereae, Scirpeae and Schoeneae with Rhynchosporaeae added later; and Mapanieae, Sclerieae and Cariceae each with a single tribe. Clarke's separation of the Mapanieae as a separate sub-family resulted in a more natural system than that proposed by Bentham.
Holttum (1948) recognised six tribes, of which he considered the most primitive to be the tribe Hypolytreæ (of Bentham, not of Pax) with the tribes Scirpeæ and Rhynchosporææ, Scleriaæ, Cryptangiææ and Cariceææ representing higher levels of specialisation. He considered the tribes of the Diclines (of Bentham), namely, Scleriaæ, Cryptangiææ and Cariceææ, to be less closely related to each other than to the Monoclines from which he believed them to have diverged from different origins. Hutchinson (1959) recognised seven tribes, but indicated them as representing separate evolutionary lines by his failure to recognise sub-familial rank.

Koyama (1961) recognised six tribes in four sub-families. Whereas separation of sub-families in earlier systems had been based primarily on the sex of the flowers and the number of fruit-bearing flowers within a spikelet, with less importance attached to the presence or absence of a terminal flower, Koyama considered the last character to be the most important. He also attached great importance to the morphology and position of the prophyll as a means to delimit larger groups. The sub-families and tribes recognised by Koyama (1961) were Mapanioideææ with
one tribe, Hypolytreae; Scirpoideae with two tribes, Scirpeae and Cypereae; Rhynchosporoideae with the tribe Rhynchosporeae divided into three sub-tribes, Cladiinae, Gahniinae and Rhynchosporinae, and the tribe Sclerieae; and Caricoideae with one tribe, Cariceae.

The system which has found greatest favour among English-speaking cyperologists is that of Clarke, (1908), albeit with some modifications. Hooper (in Metcalfe, 1971) proposed the acceptance of the seven tribes used by Hutchinson with the addition of an eighth tribe for Dulichium, arranged, with slight modification in the sequence of some genera, in the framework proposed by Clarke. In sub-family Scirpoideae were placed the tribes Cypereae, Scirpeae, Rhynchosporeae (= Rynchosporeae and Schoeneae of Clarke) and Dulichieae (Schultze-Motel, 1959); in Mapanieae the tribe Hypolytreae; in Caricoideae the tribes Sclerieae (= Sclerieae part 1 of Clarke), Cryptangieae (= Sclerieae part 2 of Clarke) and Cariceae.

Eiten (1976) proposed a system of classification based upon analysis of the branching patterns of the ultimate branch orders of the inflorescence and the sex of the flowers. She recognized three sub-families, nine tribes
and two genera whose tribal position was considered to be uncertain. The arrangement of the three sub-families differs from that of earlier systems in their sequence, the placing of the Mapanioideae last, indicating Eiten's opinion that this is the most specialised group in the family. An outline of her proposed system is given below.

Sub-family 1. Cyperoideae (= Rhynchosporoideae) having true bisexual flowers arranged in true, racemosely-branched spikelets.

Tribes Scirpeae, Cypereae, Rhynchosporeae and the genus Dulichium.

Sub-family 2. Caricoideae having true, always unisexual flowers arranged in true, racemosely-branched spikelets.

Tribes Lagenocarpeae, Bisboeckelerae, Cariceae and the genus Scleria.

Sub-family 3. Mapanioideae having an inflorescence of one or more pseudospikelets, each pseudospikelet made up of pseudanthia of unisexual flowers borne racemosely on a rhachilla.

Tribes Mapanieae, Syntrinemeae, Micropapyreae.
By its placement in the tribe Sclerieae (Nees, 1834) the distinctiveness of *Scleria* within Cyperaceae was early recognised. Its unisexuality was also soon brought to attention (Bentham, 1883). Both Pax (1886, 1887) and Eiten (1976) placed the genus in sub-family Caricoideae but, according to the former author the sub-family was diagnosed by "spikelet with a terminal flower"; according to the latter author the "true, always unisexual flowers are arranged in true, racemosely-branched spikelets". This reflects both the changing diagnoses of categories with time and increasing understanding and knowledge and, for *Scleria*, the on-going conflict in interpretation of the position of the female flower in the androgynaeceous spikelet.

Eiten's recent work on South American plants has brought yet further authority to the opinion favouring a lateral positioning of the female flower. It will be of interest and importance to find whether subsequent studies by workers, considering and re-considering species from parts of the world other than South America, with Eiten's conclusions before them, support or refute her findings.
1.2. History of the genus Scleria

The genus Scleria was founded by Peter Jonas Bergius in 1765. The generic name is derived from the Greek word meaning hardness and refers to the hard achenes, the pericarp of which is now known to be silicified. Prior to 1765 several members of the genus had been described as members of other genera. The first of these (Core, 1936) was a Jamaican plant described and illustrated by Hans Sloane (1707) which he called Gramen cyperoides silvaticum maximum geniculatum, asperius, semine mili folis. Linnaeus (1759) described Sloane's plant and named it Schoenus secans. Subsequently C.B. Clarke (1900) transferred it to Scleria. Scleria secans (L.) C.B. Cl. was not the first species of the genus to receive a binomial for Linnaeus (1753) had described and named the plant now known as Scleria lithosperma as Scirpus lithospermus which he transferred to Schoenus in 1762, and which was later placed in Scleria by Olof Swartz (1788).

Bergius (1765) described two species S. flagellum-nigrororum and S. mitis, both American. With S. flagellum-nigrororum Bergius included Schoenus lithospermus L. (1753), "Carex tenuior altissime scandens" of Patrick Browne (1756, which is believed to be Scleria secans) and Schoenus
secans L. (1759), thereby initiating a welter of confusion which was aggravated by later authors and persisted until Britton (1915) having examined the type of *S. secans* (L.) C.B.Cl at BM was able to state "that it was the same as *Scleria reflexa* HBK., and not the same as *Scleria flagellum-nigrorum* Berg.". The identity of *S. flagellum-nigrorum* as a separate taxon was confirmed by Core (1936) who established that *S. flagellum-nigrorum* Berg., *S. secans* (L.) C.B.Cl. and *S. lithosperma* (L.) Sw. are distinct taxa and provided full synonymy for these three species. Writing of *S. flagellum-nigrorum* and *S. secans* he stated:-

"The two species are quite distinct and it is difficult to see how the confusion arose. *Scleria secans* has white fruits and a long membranaceous appendage to the ligule, while in *Scleria flagellum-nigrorum* the fruits are variegated with purple and the ligule is short and unappendaged. The latter species is also much more scabrous than the former."

It is even more difficult to see how *Scleria lithosperma* whose achenes lack hypogynia, could have been confused with *S. flagellum-nigrorum* whose achenes have well-developed hypogynia with three rounded lobes, or *S. secans* with its subentire, suborbicular hypogynia.
Although Swartz (1788) and Clarke (in Urban, 1901) recognised *Scleria lithosperma* as a distinct taxon, both authors cited *Schoenus lithospermus* L. (1762) and *Carex lithosperma* L. (1767) as partial synonymms of *Scleria flagellum* Sw., and both cited *Scirpus lithospermus* L. (1753) as a synonymn of *Scleria lithosperma* Sw. Clarke (l.c.) also cited *Schoenus lithospermus* L. as a synonymn of *Scleria lithosperma* Sw. "pro parva parte".

The confusion over the identity of *Scleria flagellum-nigrorum* was particularly unfortunate since Bergius intended it as the type species of the genus.

Swartz (1788) published a comprehensive account of the genus which by then included six species, three of them new. The species enumerated were *S. flagellum* Berg. (sic), *S. mitis* Berg., *S. lithosperma* (L.) Sw., *S. latifolia* Sw., *S. filiformis* Sw. and *S. hirtella* Sw. He perpetuated the confusion created by Bergius with regard to synonymy and compounded it by omitting half the specific epithet of the type species.

In 1834 C.G.D. Nees ab Esenbeck segregated the species which lacked hypogynia under the genus *Hypoporum* and proposed the genus *Cylindropus* based
on the species now known as *S. junciformis* Thwaites. In 1842 he segregated all but a few of the remaining species under the new genera *Chondrolomia*, *Hymenolytrum* *Trachylomia*, *Mastigoscleria*, *Omoscleria*, *Macrolomia*, *Ophryoscleria* and *Schizolepis*. The genus *Diploschyphus* was proposed by Liebmann (1850) for the species since placed by Boeckeler (1874) in *Scleria* as *S. mexicana* (Liebm.) Boeck.

Prior to Nees' 1842 publication, Endlicher (1836) had proposed the division of the genus *Scleria* into three sections, namely *Scleria*, *Becquerela* and *Hypoporum*. Diagnoses and descriptions of the sections were given. In section *Scleria* he included *Scleria Bergius* and *Cylindropus* Nees; in section *Becquerela* he placed *Becquerela Brongniart* and *Calyptrocarya* Nees and his section *Hypoporum* comprised *Hypoporum Nees*.

The integrity of the genus *Scleria* was upheld by Kunth (1837) in his account in "Enumeratio Plantarum". He distinguished several sections of the genus but applied no names to them. His systematic treatment included keys to the "sections" and "sub-sections" and descriptions, among them the original descriptions of five South African species based on collections made by Drège. These were the first descriptions of Southern African
species of *Scleria* based on gatherings made in the region.

In a revision of the Brazilian Cyperaceae Boeckeler (1869) enumerated fourteen species of *Scleria*, three of them new. He rejected Nees' splitting of the genus and reduced *Hypoporum*, *Mastigoscleria*, *Ophryoscleria*, *Schizolepis* and *Macrolomia* to congenerity in *Scleria*. He subdivided this genus into three sections, *Spicatae*, *Paniculatae* and *Cymiferae*. He failed to provide diagnoses of the sections but included two species assigned by Nees to *Hypoporum* in section *Cymiferae*, and the species assigned by Nees to *Scleria*, *Mastigoscleria*, *Macrolomia*, *Ophryoscleria* and *Schizolepis* in section *Paniculatae*, thereby defining his concept of infragenetic limits by inference.

In a later publication Boeckeler (1874) reduced *Chondrolomia*, *Trachylomia* and *Hymenolytrum* to congenerity in *Scleria* and provided keys to the sections *Spicatae*, *Paniculatae*, *Cymiferae* and a group designated as having corymbose-cymose inflorescences which did not fit in any of the other three sections. Descriptions of 109 species, with distribution records and some synonymy were provided. Subsequently (Boeckeler, 1879) eleven more African species were listed, with descriptions of ten of them.

Clarke (1894) in his critical revision of *Cyperaceae* for the "Flora of British India", recognised two subgenera in *Scleria*, namely subgenus *Hypoporum* comprising the species with many bisexual spikelets (4 species represented) and subgenus *Scleria proper* (sic), with bisexual spikelets few or none (25 species represented). He further divided subgenus *Scleria* into three sections, *Tessellatae* (8 species), *Elatae* (16 species) and *Schizolepis* (1 species), basing his separation on a number of morphological characters. Section *Tessellatae* included those species of slender, sometimes tall habit with very short, slender rhizomes or lacking rhizomes; with leaves not "caudate-setaceous" at the tip, that is, not praemorse; with narrow terminal panicles and lower axillary panicles often remote, reduced
to "spikes" and sometimes very short. Section Elatae comprised robust plants with thick, sometimes woody rhizomes (one exception remarked); leaves in many (not all) species "caudate-setaceous" at the tip; with rigid, often pyramidal partial panicles and with the lobes of the disc-margin entire, or, in one species, digitate. The only species assigned to section Schizolepis, *S. bracteata* Cav. (syn. *Macrolomia bracteata* Nees) was characterised as having "character of Elatae, but rim of disc - margin with numerous triangular or lanceolate teeth". Descriptions of all the species listed were given.

In the following year Clarke (1895) in Durand and Schinz "Conspectus Florae Africae" listed alphabetically 55 species of *Scleria*. He included distribution records and some synonymy, but failed to recognise synonymy in some instances. No keys or descriptions were provided. Several new species and varieties were listed including some based wholly or in part on plants collected in Southern Africa (*S. rehmannii*, *S. woodii*, *S. natalensis*, *S. catophylla* and var. *tuberculata* of *S. hirtella* Sw. and var. *macrantha* of *S. melanomphala* Kunth). In this publication *Acriulus* was maintained as a separate genus.
Descriptions of the new Southern African species were published three years later in "Flora Capensis" (Clarke, 1898). The eleven species recorded from the region were grouped in three subgenera, Hypoporum, Eu-Scleria and Schizolepis. In Urban's "Symbolae Antillanae" (1900) Clarke designated all infrageneric groups of species as sections rather than as subgenera and sections. He provided diagnoses of sections Hypoporum, Brownieae, Tessellatae, Eu-Scleria, Ophryoscleria, Schizolepis and Becquerelia. Sections Hypoporum and Brownieae comprised those species with the nut-bearing spikelets androgynaeceous. Species with unisexual spikelets were distributed among the other sections. Section Hypoporum was diagnosed as having the disc of the achene obscure or obsolete, fused with the achene-stipe, whereas in section Brownieae the disc was described as having its margin produced into three scales or 3 - 6 glands. In the sections with unisexual spikelets, Tessellatae comprised those species with fibrous roots (annuals by implication), while Eu-Scleria, Ophryoscleria, Schizolepis and Becquerelia comprised perennial species. The distinction between sections Eu-Scleria and Becquerelia were not very clearly drawn, being more a matter of degree than one of absolute distinction. Eu-
Scleria was diagnosed as having the disc-margin neither ciliate nor fimbriate, Ophryoscleria as having the disc-margin ciliate and Schizolepis as having the disc-margin fimbriate or serrate.

The genus Acriulus Ridley was reduced to congenerity in Scleria by Clarke (1902). In this publication his reversion to the concept of the division of the genus into subgenera and sections was shown by his division of Hypoporum into Hirtellae and Lithospermeae. The 22 species placed in Hirtellae were characterised as "Slender plants. Spikelets small, mostly clustered. Clusters sessile in a simple spike or on the branches of a panicle. Inflorescence not leafy; bracts small or setaceous". Hirtellae comprised some annual and some perennial species. The single species, S. lithosperma, placed in Lithospermeae was diagnosed as "Less slender. Inflorescence very scattered; bracts leaf-like. Perennial".

Two sections were recognised in subgenus Scleria, Tessellatae, with "rhizome 0 or hardly any" and "all the species except S. gracillima very much alike", and a section to which no name was applied which was characterised as
having "rhizome thick, creeping. All stout plants, with copious inflorescence". Subgeneric rank was implied for Schizolepis, Ophryoscleria and Acriulus.

In a posthumous publication compiled from Clarke's notes (1908) several alterations were made. Seven subgenera were recognised, namely, subgenus Hypoporum, with four sections, A Pergraciles, Lithospermae and Corymbosae; subgenus Browneae; subgenus Tessellatae; subgenus Eu-Scleria with three sections, Asiaticae-Oceanicae, Africanae and Americanae; subgenus Ophryoscleria; subgenus Schizolepis and subgenus Becquerelia. The genus Acriulus was excluded from Scleria. Browneae and Tessellatae were elevated from sectional to subgeneric rank and the nameless section placed in subgenus Scleria in his 1902 classification, was accorded subgeneric rank as Eu-Scleria.

Core (1936) in his revision of the American species of Scleria, recognised five sections within the genus; Hypoporum, Hymenolytrum, Ophryoscleria, Schizolepis and Euscleria, section Hypoporum being distinguished only by the absence of any hypogynium. Section Hymenolytrum he characterised as having "Pistillate
spikelets lowest in each branch, sessile, one-flowered; the staminate on distinct long peduncles. The other sections with hypogyniate achenes lacked the combination of characters of section Hymenolytrum and were distinguished from each other solely on the morphology of the hypogynium, that of Ophryoscleria having a ciliate margin; of Schizolepis having a fimbriate or serrate margin and that of Euscleria having three lobes with entire margins. Species assigned by Core to section Hymenolytrum (Nees) Core were placed by Clarke (1908) in subgenus Eu-scleria, section Americanae, group Stipulares.

The system used by Chermezon (1936) was based on that of Clarke (1908). Acriulus was excluded from Scleria.

The system used by Piérart in his account of the genus in the Belgian Congo and Ruanda Urundi (1951) was based on that of Core. Acriulus was excluded from synonymy.

Nelmes, (1955, 1956) in his comprehensive account of the genus for the whole of Africa recognised four sections, Hypoporum (Nees) Endl., Scleria (Berg.) Endl., Schizolepis (Nees) C.B.Cl., and Ophryoscleria (Nees) C.B.Cl. Acriulus was
excluded from synonymy. Clarke's separation of the sections Hypoporum and Scleria into smaller groups of species was not upheld, which indicated Nelmes' awareness that the greater the number of species under consideration and the greater the geographical range of those species the less clearly defined the supraspecific and infrageneric limits become.

Two accounts of Scleria from Asian regions were published in 1961, namely Koyama's revision of Japanese species and Kern's of Malaysian species. Both authors included the genus Diplacrum in Scleria.

Koyama (1961) recognised two subgenera, namely Scleria, with three sections, Hypoporum, Elatae and Tessellatae; and Diplacrum with a single species represented, *S. caricina* (R.Br.) Benth. Subgenus Scleria was diagnosed as having "Partial inflorescences of a panicle" and Diplacrum as having "Partial inflorescences of head at axil of leaf-like bract; small annuals 3 – 20 cm tall".

Kern (1961) criticized Clarke's subdivision of Scleria and by way of correction proposed "the distinction of groups (sections) of apparently more or less closely related species".
Eight sections were proposed with the perennial species distributed among sections Brownieae, Scleria, Corymbosae and Carphiformes and annuals among Hypoporum, Tessellatae, Sphaeropus and Diplacrum. The distinctions between some of his sections were very minor indeed.

In a series of papers on East African species of *Scleria* which culminated in an account of the genus for the "Flora Zambesiaca" region (1966), Robinson progressively modified his concepts of infrageneric boundaries which were based in his earlier papers on full acceptance of Clarke's system. Critical re-assessment of the South-East African species led him to conclude that there is intergradation between sections Hypoporum (Nees) Endl., Scleria (Berg.) Endl., Acriulus (Ridl.) C.B.Cl. and Schizolepis (Nees) C.B.Cl. Accordingly he proposed that the African species be grouped in two subgenera, Scleria and Ophryoscleria. Subgenus Scleria was diagnosed as having the hypogynium not ciliate at the upper margin, never wider than the achene itself and often reduced to an undifferentiated stipe-like base to the achene, whereas the hypogynium of subgenus Ophryoscleria was defined as ciliate at the upper margin and enlarged at maturity into a cupola of hard corky tissue wider than the achene itself and in
1.2.1. History of the genus Scleria in Southern Africa

The first descriptions of species of Scleria based on plants collected in Southern Africa were published in "Enumeratio Plantarum" (Kunth, 1837). Five species were described, from collections made by J.F. Drège in 1832 (Gunn & Codd, 1981). These were S. drègeana, S. meyeriana, S. holcoides, S. melanomphala and S. angusta.

This was followed by Clarke's listing (1895) of eleven species from Southern Africa in Durand and Schinz "Conspectus Florae Africanae". (Table 1).

The publication of Clarke's descriptive account of Scleria in Southern Africa in "Flora Capensis" (1898) was the first comprehensive account of the genus for the region. It has never been superseded. In it, eleven species were described and notes on distribution, keys to identification and specimen citations were given.
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The description of a new species from Basutoland (Lesotho), *Scleria dieterlenii* Turrill (Turrill, 1914) increased the tally to twelve.

Schonland (1922) enumerated three species, none of them new records. Apart from illustrations of two of these by Stella Gower, Schonland's monograph added little information to that already available.

In his comprehensive revision of the genus in Africa Nelmes (1955, 1956) recorded fourteen species from Southern Africa with the exclusion of *S. catophylla* C.B.Cl. which he reduced to synonymy with *S. hirtella* Sw. and with the addition of *S. welwitschii* (Ridley) C.B.Cl., *S. foliosa* Hochstetter ex A. Richard and *S. pergracilis* (Nees) Kunth var. *brachystachys* Nelmes.

Kern (1963) published a re-assessment of the genus *Acirulus* Ridley which was once more reduced to synonymy in *Scleria*. Among the specimens cited was a gathering from Natal (K.D. Huntley 781) of *Scleria greigiifolia* (Ridl.) C.B.Cl.
Robinson (1966) in his descriptive account of the genus for "Flora Zambesiaca" included mention of those Southern African species common to both areas. He included both _S. nutans_ Willd. ex Kunth (syn. _S. hirtella_ Sw. var. _tuberculata_ C.B.Clm.) and _S. cataphylla_ C.B.Clm.: he placed _S. drègeana_ Kunth, _S. meyeriana_ Kunth and _S. holcoides_ Kunth in synonymy as _S. drègeana_: he included _S. dieterlenii_ Turrill but reduced this species to synonymy with _S. flexuosa_ Boeckeler and he recorded five additional species from our area, _S. longispiculata_ Nelmes, _S. achtienii_ DeWildeman, _S. lagoensis_ Boeckeler, _S. poaeformis_ Retzius and _S. veseyfitzgeraldii_ Robinson.

Thus by 1966 the total number of species recorded from Southern Africa, excluding _S. meyeriana_ and _S. holcoides_, had been increased to nineteen.

Podlech (1967) provided a key to and descriptions of three South West African species, none of them new records for Southern Africa.
Jacot Guillarmod (1971) enumerated three species in her "Flora of Lesotho", none new. No key or descriptions were given.

The taxonomic status of \( S. \) dieterlenii and \( S. \) flexuosa was reviewed by Napper (1971) who concluded that the two taxa are distinct, thereby re-establishing the valid name of the Southern African plants as \( S. \) dieterlenii. The taxon described by Clarke as \( S. \) catophylla was placed in synonymy with that originally named \( S. \) hirtella Sw. var. aterrima Ridl. and elevated from varietal to specific status as \( S. \) aterrima (Ridl.) Napper. Re-examination of American and African material assigned to \( S. \) hirtella Sw. and its varieties led to the conclusion that the African taxa are distinct from the American and therefore required re-naming.

In her account of the Cyperaceae in Ross' "Flora of Natal" (1972) Gordon-Gray recorded thirteen species in the province, together with specimen citations, synonymy, notes on distribution and on the taxonomic
status of some species, but without a key or descriptions. Robinson's treatment of *S. meyeriana* and *S. holcoides* as synonyms of *S. drègeana* and *S. dieterlenii* as a synonym of *S. flexuosa* was accepted. An un-named new species was listed, thereby bringing the total number of species recorded for Southern Africa to twenty.

Compton (1976) listed and provided descriptions of five species, including one new record, in his "Flora of Swaziland", so that by 1976 twenty-one species had been recorded for the area.

Yet, because of the difficulties inherent in attempting to correlate the available information on Southern African species of *Scleria* much of which is not in the literature of the region, Dyer (1976) in "The Genera of Southern African Flowering Plants" stated that twelve species were recorded from the region.

It is therefore obvious, as pointed out by Gordon-Gray (1965) that in dealing
with literature relating to *Scleria* and other genera of Southern African plants, it is imperative that consideration be given to literature relating to the genus under review throughout its distribution range.
2. **Materials and Methods**

2.1. **Preparations for examination by light microscopy**

Fresh vegetative material for use in anatomical studies was fixed in F.A.A. (40% formalin 8 ml : glacial acetic acid 5 ml : 70% aqueous ethanol 87 ml) for a minimum of seven days. Portions of the fixed material were desilicified by soaking in 10% aqueous hydrofluoric acid for from one to several weeks, washed in tap water for 24 hours and stored in F.A.A.

Dry vegetative material from herbarium sheets was, in the initial stages of the investigation, rehydrated by boiling in tap water for several hours prior to storage in F.A.A. Very poor results were obtained by this method (Fig. 2, A). Subsequently dry material was soaked in 1% aqueous potassium hydroxide for varying periods depending upon the response of the material, which could be gauged visually. When the organ had resumed normal shape the material was washed in tap water and stored in F.A.A. The staining reaction of
Fig. 2. Transverse sections of lamina of _S. greigiifolia_ (K.D. Huntley 781); A, material rehydrated by boiling in tap water; B, material rehydrated by soaking in 1% aqueous potassium hydroxide.
material treated in this manner was altered because of delignification effected by the alkali, but restoration of normal shape to cells resulted in very much better preparations than could be obtained by boiling in water (Fig. 2, B). Material which had been treated with alkali was not desilicified.

Freshly fixed, freshly fixed and desilicified, and fixed rehydrated material for sectioning was passed through a tertiary butanol dehydration series, embedded in wax and sectioned with a Leitz sledge-base microtome at a thickness of 15 μm. Sections were stained in a safranin and fast green series and mounted in Canada balsam, "Euparal" or "DPX" mountant (Johansen, 1940).

Leaf epidermal strips were made from freshly fixed or rehydrated material. A portion of leaf was laid flat on a glass slide with the epidermis to be stripped placed in contact with the glass, irrigated with a commercially available solution (c. 3.5%) of sodium hypochlorite ("Jik", "Javel", Jill's Bleach", etc.) and gently scraped with a scalpel or razor-blade until unwanted material was removed. A fine brush was used in the final stages to sweep away the less-tenacious mesophyll tissue.
The epidermis once freed from overlying tissue was trimmed, washed in tap water, placed right-side-up on a clean glass slide, covered with a thin layer of phenol crystals and gently heated on a slide drying plate until the phenol had liquefied and was reduced in volume to a thin film. A few drops of "DPX" mountant were then added to the preparation and a cover-slip placed in position. Permanent preparations were made by this method in which the silica deposits remained highly refractile indefinitely. The visibility of silica bodies was enhanced by phase-contrast microscopy.

A Zeiss semi-automatic photomicroscope was used to view and photograph anatomical preparations.

2.2.1. Preparation of camera-lucida drawings

Camera-lucida drawings of parts of transverse sections of different organs were made with the aid of a Zeiss drawing tube fitted to a monocular compound microscope. The scale of the drawings was measured with a stage micrometer. The drawings are provided as a guide to the interpretation of tissues shown in photomicrographs.
2.2. Preparations for use in SEM

Since the bulk of the material available for study was in the form of herbarium specimens it was considered desirable to establish at the outset whether such pressed, dry material should be rehydrated, then critical-point dried before coating and viewing or whether it could simply be coated and viewed. Preparations were made by both methods and these were compared with preparations made from freshly fixed material which had been critical-point dried and coated. The comparison showed no appreciable difference in the results obtained from the three different methods. All preparations for SEM were therefore made from dried specimens without recourse to critical-point drying.

Dry material was mounted on brass stubs using either double-sided adhesive tape or acrylic varnish. The specimens were then coated in vacuum with gold to a thickness of less than 150 Å in a Polaron Sputter Coating Unit E 5000, then examined in a Philips SEM 500 scanning electron microscope at a voltage of 25 kV. The images were photographed with a 35 mm camera.
2.3. **Silica deposits**

Portions of vegetative organs and whole achenes were macerated in concentrated nitric acid and concentrated perchloric acid (Hayward and Parry, 1975; Franklin, 1981) to remove organic constituents, and washed in tap water. Vegetative material yielded a sediment of particulate silica and some cell-shells and cell-sheets. The sediment was packed by centrifugation and the aqueous supernatant discarded. The sediment was stored in absolute methanol. Achenes shells remained whole after oxidation. The shells were transferred to absolute methanol with a fine brush. When required for SEM the siliceous material was transferred to adhesive-coated brass stubs (the methanol evaporating very rapidly), coated with gold and examined.

The siliceous nature of the achene shells was confirmed by analysis using a JEOL JSM U3 scanning electron microscope fitted with an energy dispersive X-ray analyser (EDX) Model 711. This was carried out at the National Physical Research Laboratory of the Council for Scientific and Industrial Research, Pretoria. EDX analyses were carried out on both outer and inner surfaces of achene shells (Franklin, 1979).
2.4. Preparation for use in Transmission Electron Microscopy (TEM)

Portions of fresh leaves were fixed in 3% glutaraldehyde in 0.05 M PIPES buffer, pH 7, for 24 hours, washed thrice with 0.05 M PIPES buffer at 10 minute intervals, post-fixed in 1% aqueous osmium tetroxide in cacodylate buffer for 1 hour and washed thrice with distilled water at 5 minute intervals. The fixed material was passed through an ethanol dehydration series (10%, 20%, 50%, 70%), then stained for 1 hour in saturated uranyl acetate in 70% aqueous ethanol. The dehydration process was continued (75%, 85%, 95%, 2 x 100%). The dehydrated material was passed through two changes of 100% acetone, then infiltrated with Spurr resin in three stages namely, acetone/resin 1:1 8 hours, the first under vacuum; acetone/resin 1:3 24 hours; resin 24 hours. After infiltration the material was placed in plastic boats, covered with resin and polymerised at 60°C in a vacuum oven for 24 hours, after which the blocks were stored in a desiccator.

The material was sectioned with either a diamond knife or glass knives on a Reichert OM U2 microtome. Sections were collected on 200
mesh copper grids, washed in distilled water, stained with lead citrate for 10 minutes, washed thrice in distilled water and dried.

Sections were viewed with a Philips 301 TEM. Images were photographed with a 35 mm camera.
CHAPTER 3

3. Morphology

The genus comprises monoecious annual herbs, with adventitious roots developed from the proximal nodes of the culms and monoecious perennial herbs with short or long, horizontal, oblique or descending fleshy or woody rhizomes, or more-or-less horizontal subterranean soboles or both rhizomes and soboles. Adventitious roots arise from the nodes of perennating organs. Culms are nodose, solitary or more-or-less tufted, stout or slender, erect or scandent, trigonous or triquetrous, leafy towards the base or throughout, smooth, scaberulous or scabrid on the angles, glabrous or hairy.

The leaves are three-ranked, narrowly to broadly linear with closed sheathing bases. They are smooth to scabrid on the margins and on the 3-5 principal ribs, glabrous or hairy and the lowermost are represented by almost bladeless or bladeless sheaths. The blades taper smoothly towards the apex except those of S. angusta which are suddenly narrowed on each side at unequal distances from the apex. In profile the blades are more-or-less V-shaped, flanged V-shaped or, in S. angusta flanged V-shaped distally and with additional lateral wings to the flanges proximally. The mouth of the sheath may be truncate, concave, convex or produced in a
short tongue with or without a membranous margin. In the species in which the leaves are crowded towards the base of the culm the sheaths may be split almost to the base at maturity.

The inflorescence is fundamentally paniculate in all sections of the genus. In members of sections Schizolepis, Acriulus and Scleria the proximal internodes of the main axis and of the proximal first and some higher orders of lateral axes are long so that the inflorescence appears to comprise a terminal panicle and usually one or more lateral panicles, subtended (except in *S. poaeformis*) by foliaceous bracts. In members of section Hypoporum proximal internodes of the main axis are usually short and internodes of all, or all but the proximal primary axillary axes, are so short that these inflorescences have been described as "simply glomerate-spicate" or "branched glomerate spicate" respectively. The glomerules (contracted panicle branches) are subtended by more-or-less glumaceous bracts.

The ultimate unit of the inflorescence is the spikelet which comprises an indeterminate axis, the rachilla and two to many glumes, the proximal 2-4 more-or-less distichous and the remainder spirally arranged. In the axils of the glumes unisexual flowers may be borne. In all sections the lowermost 1-4 glumes are empty. In section Hypoporum the spikelets are fully
androgyneceous with a single female flower towards the base and male flowers distally, or some of the spikelets may be male. In section Scleria the spikelets are usually functionally unisexual. Functionally female spikelets may be subandrogyneceous with a single sub-basal female flower and 1 - several inrolled empty glumes ("glumelllas") distally, or, less often, they may lack the distal male rudiments. In sections Schizolepis and Acriulus the spikelets are unisexual, the female spikelets lacking any distal male vestiges. Rare exceptions may occur in all sections of the genus.

Flowers are strictly unisexual. Male flowers consist of 1-3 free stamens with linear filaments and bithecate, apiculate anthers with longitudinal dehiscence which are exserted from the glumes at anthesis. Female flowers comprise a single tricarpellary, unilocular ovary with a terminal style branched above into three filiform stigmas and containing a single basal ovule. The fruit is a stipitate achene, the pericarp of which is silicified at maturity. In section Hypoporum the stipe is trigonous. In sections Scleria, Schizolepis and Acriulus the stipe is obpyramidal and is elaborated distally to form an hypogynium the shape of which is characteristic for each species. In sections Scleria and Acriulus the margin of the hypogynium is smooth; in section Schizolepis it is fimbriate and in section Ophryoscleria (no members of which have been recorded from our area) it is ciliate.
Members of section Hypoporum are slender, annual or perennial hygrophilous herbs of open habitats. The aerial parts of the perennial species die back at the end of each growing season. Members of section Scleria are stout or very stout (S. poaeformis) hygrophilous or hydrophilous annual or perennial herbs of open or partly sheltered frost-free (except S. transvaalensis) habitats. The aerial parts of the perennial species do not (except S. transvaalensis) die back each year. Scleria angusta (section Schizolepis) is a stout hydrophilous perennial inhabitant of swamp forests whose aerial parts do not die back annually. Scleria greigiifolia (section Acriulus) is a stout hydrophilous perennial inhabitant of open shallow lakes whose aerial parts do not usually die back each year.

3.1. Vegetative Organs

3.1.1. Roots

The rooting system, except for the primary embryonic root, is adventitious. In annual species the roots arise at the basal nodes of the culms. In perennial species roots develop at the nodes of the perennating organ(s). Roots of smaller species are slender while those of larger
3.1.2. Perennating Stems

Anatomical studies (see Chapter 4) have demonstrated that there are two fundamentally distinct types of subterranean perennating stem. The majority of perennial species have rhizomes, a few species have rhizomes and soboles ("stolons" of Holm, 1929), and one species has only soboles.

Rhizomes show a considerable range of morphological, but little anatomical, diversity. The morphology of the rhizome is relatively constant within a species and may provide key characters for use in separating taxa which are otherwise morphologically similar.
The rhizome represents the primary axis of the plant (Holm, 1929). Attempts to germinate seeds of locally available species were unsuccessful, therefore it is not known with certainty whether growth is monopodial or sympodial, but study of mature plants suggested that growth is sympodial. Successive aerial shoots are produced from the rhizomes, one or several in each growing season. All rhizomes bear sheathing scale leaves at the nodes. With age these may have disappeared or may be represented only by the fibrous remains of vascular bundles. Adventitious roots arise endogenously from the nodes. Internodes vary in length in different species with the result that some species have elongate rhizomes, described by Piérart (1953) as "rampant" whereas in other species these are very compact. The majority of rhizomes are more-or-less horizontal, straight or somewhat flexuous and often branched, but in two of the Southern African species, _S. veseyfitzgeraldii_ and _S. dieterlenii_ these are descending, almost vertical and usually unbranched.

The rhizomes of some species are of more-or-less uniform diameter throughout.
their length, whereas those of other species are variously swollen at intervals. Most rhizomes are hard, but the young rhizome of *S. woodii* is softly tuberous with swollen internodes and that of *S. dieterlenii* is very slender and descending with a soft, swollen, tuberous tip. The older parts of these organs "harden off" after sustaining the first new aerial growth of the next season. In addition to starch, which is the main storage product in all species of *Scleria*, there are volatile oils present which are very strongly scented. A description of the morphology of the rhizome is included in the formal description of each species in Chapter 6.

**Soboles** are subterranean propagative stems of adventitious origin. They originate from the bases of culms. My choice of the term "sobole" rather than "stolon" requires explanation. Holm (1929) referred to the subterranean adventitious stems as stolons, which he distinguished from runners on the basis of their being subterranean and runners being aerial. Holm did not define soboles. Jackson (1960) defined all three terms thus:
stolon - a sucker, runner, or any basal branch which is disposed to root

sobole - a shoot, especially from the ground

runner - a stolon, an elongated lateral shoot, rooting at intervals, the intermediate part apt to perish and thus new individuals arise

His definitions failed to distinguish subterranean from aerial axillary propagative stems, equated runners and stolons, and he failed to distinguish soboles adequately.

Stearn (1973) provided precise definitions of the three terms and clearly distinguished them thus:

sobol - soboles the underground creeping base of a stem, synonymous with caulis basi stoloniformis of some authors

runner - aboveground
73.

stolon - a runner leafy its whole length, and, "the term soboles is used for an underground runner"

Since the subterranean axillary propagative stems which arise from the culm bases of some species of Scleria precisely meet the definition of soboles given by Stearn, I have elected to use this term. Furthermore, in order to entrench its use I have applied the specific epithet sobolifer to a previously undescribed species (Franklin, 1983).

Among the Southern African representatives of the genus, three species are soboliferous. The possibility that other local species may occasionally produce soboles cannot be excluded. Robinson (1966) stated that the soboles (he did not use the term but recognised the organs) of many species are easily detached and therefore are rarely present on pressed specimens in the herbarium. He also pointed out (see also Chapter 4) that if their presence is not suspected by a collector they may not be dug from the soil.
Two of the three soboliferous Southern African species, *S. drègeana* and *S. aterrima*, do not perennate solely by soboles, but also possess rhizomes with very short internodes. Of the many herbarium sheets examined, only one sheet of each species had soboles present. Portions were detached for anatomical study and the findings are described in Chapter 4. The soboles of both species were approximately 2 cm long with overlapping sheathing scale leaves at the nodes. Robinson (1966), who knew *S. aterrima* in the field, stated that its soboles which he referred to as "many slender rhizomes", "form new plants at a distance of up to 10 cm from the parent plant which dies at the end of its flowering season. Only after the new plant is established do they harden off...."

The third soboliferous species is *S. sobolifer*, which perennates solely by means of soboles. Its soboles are very much longer than those of *S. drègeana* and *S. aterrima*, harder and, like the culms, trigonous. The distinctively wine-red mottled internodes are long, greatly exceeding the scale leaves which therefore
do not overlap. Wiry adventitious roots arise from the nodes.

Differences between rhizomes and soboles are summarised thus:-

**rhizome** - primary axis of plant, producing successive aerial shoots, one or several in each growing season

**soble** - subterranean culm branch, never arising directly from a rhizome, but from the bases of aerial shoots (culms) developed from the rhizome. In species such as S. sobolifer no rhizome exists; the soboles arise from the bases of culms.

3.1.3. Culms

The herbaceous, nodose, erect or semi-scandent culms of all Southern African species are trigonous. The angles are obtuse in most species but there is a tendency for them to become more acute in the distal part of the culm. In S. lagoensis
one side of the triquetrous culm is markedly concave and in several other species one of the three sides is slightly shorter than the other two. Immature culms of all species are solid but mature culms may have one or more central air cavities (see Table IV, Chapter 4). Internodes are wholly or partially enveloped by closed leaf-sheaths. In some species, such as S. greigiifolia and S. aterrima the proximal internodes are very short so that the three-ranked leaves are crowded towards the base. In the majority of species proximal and distal internodes are not markedly unequal so the leaves are more evenly spaced.

Assimilatory tissue is present in culms and this is best developed in those parts of the internodes that are not enveloped by leaf sheaths. Towards the base of the culm there is little or no chlorenchyma and most species display reddish coloration caused by flavonoid pigments.

The angles of the culms of most species are smooth or scaberulous, but in S. lacustris they are scabrid. Barbs and prickles
are heavily silicified. *Scleria* is unusual among Cyperaceae in that many species are hairy. Twelve of the twenty-three species recorded from our area may have hirsute culms. Of these *S. aterrima* is the most conspicuously hairy. The hairs, which are unicellular, are derived from epidermal cells. They are brittle, easily rubbed off, and can cause skin irritation because of silicification.

A culm hair is present in the transverse section of the culm of *S. dieterlenii* illustrated in Fig. 41,5 Chapter 4.

Dimensions of culms vary. In the tall-growing species of warm wet habitats the culms may attain a height of more than two metres, but even the tallest culms rarely exceed 1 cm in width. The more delicate grassland species have shorter, much more slender culms which, if the surrounding vegetation becomes unusually tall during the growing season, may be incapable of remaining upright and instead adopt a semi-scandent habit, relying on the neighbouring vegetation for support.
3.1.4. Leaves

The three-ranked, sessile foliage leaves have closed, sheathing bases and more-or-less linear-lanceolate laminas. Unlike the grasses there is no clearly defined collar at the junction of sheath and lamina; nor does a ligule arise from the adaxial surface of the leaf at this junction. However, the mouth of the sheath on the side opposite the lamina may be produced into a short tongue-like extension often with a membranous margin (Fig. 3).

This extension has been variously referred to as a tongue, ligule, pseudoligule (Chermezon, 1929), antiligule (Senay, 1950) and contraligule (Kern, 1961). Obviously the last three terms were coined in order to distinguish this outgrowth from the ligule of Poaceae.

Leaves of Scleria arise from culm nodes. The spacing of leaves along the culm depends upon the lengths of the internodes. The majority of local species have subequal internodes therefore the leaves are more-or-
Scanning Electron Micrographs of leaves of *Scleria* spp. at junction of sheath and lamina.

A. *S. woodii* C.B. Cl. (Acocks 21927), showing deeply concave mouth sparsely fringed with hairs (X 14)

B. *S. bulbifera* Hochst. ex A. Rich. (Acocks 10758), showing slightly concave mouth densely fringed with hairs and densely hirsute sheath. (X 14)

C. *S. welwitschii* C.B. Cl. (du Plessis 880), showing convex mouth with narrow membranous extension, the membrane glabrous, the sheath densely hirsute (X 14)

D. *S. rehmannii* C.B. Cl. (de Winter and Marais 5049) showing narrow triangular ligule with ill-defined membranous margin, the sheath very sparsely hirsute. (X 14)

E. *S. natalensis* C.B. Cl. (Ward 4716), showing shallowly convex mouth with broad, rounded membranous ligulate margin, the sheath glabrous (X 8)

F. *S. transvaalensis* E.F. Franklin (Hemm 563), showing shallowly convex mouth with triangular membranous ligulate margin, the sheath glabrous (X 8)

G, H. *S. angusta* Nees ex Kunth (Strey 9905). G. showing broadly triangular, densely hirsute ligule and region of lamina above the leaf—sheath in which lateral winged extensions develop, the vasculature of which originates from the major marginal v.b. (x 8)

H. showing hirsute ligule and major marginal v.b. passing from sheath into lamina (x 25)
less evenly spaced, but in *S. poaeformis*, *S. greigiifolia*, *S. veseyfitzgeraldii* and *S. aterrima* the proximal internodes are very short so that the leaves are crowded towards the base of the culm.

In all species the first-formed (oldest) leaves have shorter blades than the later-formed leaves. Blades may not develop at all in the basal leaves. Such bladeless sheaths occur in all species but they are less apparent and usually less numerous in those species which have the leaves crowded towards the bases of the culms.

Ontogenetically, inflorescence bracts are leaves. In the sub-genera Schizolepis, Acriulus and Scleria (excluding *S. poaeformis* as circumscribed by Clarke (1902) the bracts are foliaceous; in subgenus Hypoporum the bracts are reduced, glumaceous structures which Nelmes (1955) called *bracteoles*.

Leaf sheaths of *Scleria* are closed, triquetrous, with obtuse, acute or in *S. lacustris*, winged angles (Fig. 45, 6).
The angles may be smooth, scaberulous or scabrid and the sheaths may be glabrous or variously hairy. When present, hairs are most numerous below the mouth of the sheath, or may even be restricted to this area.

Leaf blades are dorsiventral. Two Southern African species have lamina profiles which are V-shaped, *S. woodii*, which has a narrowly V-shaped profile, and *S. perigracilis* var. *brachystachys* which has a broad, very nearly flat V-shaped profile with the margins slightly recurved. All other local species have flanged V-shaped laminas. Metcalfe (1961) distinguished flanged V-shaped and inversely W-shaped profiles, but I prefer not to separate two categories because they intergrade. The flanged V-shaped lamina of one species, *S. angusta* is modified, except in the distal part of the blade, by the addition of lateral extensions. These extensions stop short of the leaf-apex, usually unequally. This type of leaf has been called by Clarke, Nelmes and others, "praemorse" which, as Nelmes (1956) pointed out, is not really an appropriate term since it means "as though
Fig. 4. Unequally praemorse leaves of

*Scleria augusta* Nees ex Kunth
bitten off at the end". Since there seems to be no better descriptive term available for these distinctive leaves, the term "praemorse" is used in this account (see Fig. 4). The anatomical peculiarities of the lateral extensions, or "wings" are described in Chapter 4. Scleria angusta is the only Southern African species which possesses praemorse leaves but such leaves occur in other African, Madagascan and American species of sub-genera Schizolepis (Nees) Clarke and Ophryoscleria (Nees) Clarke and in some Madagascan and American and one Asian species of sub-genus Scleria (Berg.) Endl. (Kern, 1961).

Descriptions of Scleria usually include mention that the leaf-blades have three (or in the praemorse species five) principal nerves, and it has been stated that these principle nerves are prominent, namely, "midnerve prominent beneath, 2 lateral nerves prominent above" (Kern, 1961), and "For practical purposes these outwardly prominent veins are called costas" (Koyama, 1967). Even a cursory glance at the camera-lucida drawings of leaf profiles
in Fig. 43 (Chapter 4) is sufficient to reveal that leaves of *Scleria* have more than three principal nerves and that no nerves are prominent, if one considers as Stearn (1973) does, that the terms nerve and vein are synonymous. It is however true to say that the leaves of species of *Scleria* which have V-shaped lamina profiles have a median abaxial keel which may be acute or obtuse, and that the leaves of those species which have flanged V-shaped lamina profiles have a median abaxial keel and paired lateral adaxial ribs or ridges, that is, three parallel ribs, one below and two above. Praemorse leaves have five such parallel ribs proximally and three distally. The ribs may be antrorsely scabrid as may the margins, which makes the leaves difficult to handle with impunity because of these cutting edges. In addition to these silicified barbs, many species have silicified unicellular epidermal hairs which are usually most numerous on the ridges and margins. The distribution of hirsute leaves among Southern African species is enumerated in Chapter 6.
Fig. 5. Diagrammatic representation of inflorescence of *Scleria*. 
KEY to lettering of Fig. 5

A primary axis of inflorescence
a\textsuperscript{1} primary axillary axis
a\textsuperscript{2}, a\textsuperscript{3}, a\textsuperscript{4} second and subsequent orders of axillary axes
n node
in internode
l leaf
b bract of primary axis
b\textsuperscript{1} bract of primary axillary axis
b\textsuperscript{2} bract of secondary axillary axis
p\textsuperscript{1} prophyll of primary axillary axis
p\textsuperscript{2}, p\textsuperscript{3}, p\textsuperscript{4} prophylls of successive subsequent orders of lateral axes
ts terminal spikelet of inflorescence
s\textsuperscript{1} terminal spikelet of primary axillary axis
s\textsuperscript{2}, s\textsuperscript{3}, s\textsuperscript{4} terminal spikelets of successive subsequent orders of lateral axes
Dimensions of laminas vary. Those of *S. poaeformis* are the largest, reaching widths of up to 4 cm and attaining a thickness of 5 mm or more, whereas those of the smaller species may be less than 2 mm wide. Comparative dimensions of leaves are shown in Fig. 43 (Chapter 4).

3.2. **Flowering Organs**

3.2.1 **The Inflorescence**

The inflorescence of *Scleria* is paniculate. Difficulties arise in the interpretation of inflorescences because the panicles are contracted, sometimes so markedly so that they appear spiciform.

The main indeterminate axis of the inflorescence (A, Fig. 5) is the distal extension of the leafy, nodose culm. From each node of the main axis in the axil of a bract (b), an indeterminate branch (a<sup>1</sup>) arises. Successively higher orders of branching are the rhaches (a<sup>2</sup>), branches from the rhaches, rhachillas (spikelet axes) and ultimately, floral axes, all of which arise in the axils of bracts. Since the floral
axes are greatly reduced the rhachilla is, for practical purposes, the ultimate branch order of the inflorescence of *Scleria*.

Bracts are leaves which may retain their leaf-like appearance or may be reduced or modified. The terms bract, bracteole, prophyll, glume and glumella are applied to inflorescence leaves of *Scleria*. A bract (sometimes if it is reduced and not leaf-like (foliaceous) in appearance termed (Nelmes, 1955) a bracteole), subtends a culm-branch, rhachis, rhachis-branch and lateral rhachilla and has a well-defined midrib; a prophyll is the first-formed (proximal) appendage of a branch (Blaser, 1944) and differs from other appendages in that it has two (or 0) ribs or keels and a truncate or bicuspidate apex; a glume subtends a floral axis (or its aborted primordium) and usually has a well-defined midrib; a glumella is a glume which is membranous and lacks a midrib (Eiten, 1976).

When analysing extremely contracted inflorescences in which branching patterns are difficult to detect because of the
greatly reduced internodes, the
distinctive form of the prophyll is helpful
since it enables one to recognise the
beginnings of a new branch even when the
proximal, subprophyllar internode of that
branch is so greatly reduced that the
subtending bract and the prophyll appear
contiguous. A lateral sessile spikelet
has both subprophyllar and supraprophyllar
internodes greatly reduced so that the
bract, prophyll and proximal glumes are
closely adpressed. A spikelet which is
terminal on an axis which bears lateral
appendages (leaves, branches, spikelets)
is separated from its subtending bract and
prophyll by the length of the axis, for
example the terminal spikelet of the
inflorescence is separated from its
subtending bract and prophyll by the length
of the culm. Likewise the terminal
spikelet (s1, Fig. 5) of a primary axillary
axis is separated from its subtending bract
and prophyll by the length of the axis.

Two-dimensional plan drawings of the
distal part of the inflorescences of eight
Fig. 6. Analytical diagrams of apical portions of inflorescences of *Scleria* spp.

A, *S. angusta* (Ward 7911); B, *S. greigiifolia* (P.G. Stewart 293); C, *S. poaeformis* (Hennessy 374); D, *S. melanomphala* (Strey 5721);
E, S. natalensis (Ward s.n.); F, S. lacustris (P.A. Smith 2796); G, S. woodii (Devenish 1093); H, S. sobolifer (Strey 5711)
Southern African species of *Scleria*, *S. angusta* (section Schizolepis (Nees) C.B.Cl.), *S. greigiifolia* (section Acriulus (Ridley) C.B.Cl.), *S. poaeformis*, *S. melanomphala*, *S. natalensis* and *S. lacustris* (section Scleria (Bergius) Endlicher) and *S. woodii* and *S. sobolifer* (section Hypoporum (Nees) Endlicher) are shown in Fig. 6. These drawings which make no attempt to depict relative lengths of the axes of the inflorescences, serve to emphasise the fundamental similarity of species representing different section of the genus. This fundamental similarity is obscured in the living plants by shortening of some, or all, of the axillary axes which results in i) crowding of sessile, subsessile or shortly pedicillate spikelets in clusters or glomerules and ii) reduction in the number of spikelet-bearing branches in the lateral branch system, especially in the distal part of the inflorescence and the distal part of each primary axillary axis.

The so-called glomerate-spicate inflorescence which is characteristic of most members of section Hypoporum is not fundamentally different from the more laxly
branched inflorescence of other sections. Haines and Lye (1972) were mistaken in their statement that "in section Hypoporum the only bracts, as opposed to prophylls and glumes, in the whole inflorescence are those that subtend the glomerules as a whole". Such a condition may occur in some glomerules and possibly in all glomerules of some species, but at least some glomerules of most species retain second-order bracts (Fig. 6 G,H).

The "interrupted" or "terminal and lateral" inflorescence of sections other than Hypoporum are the results of development of long proximal internodes by some of the axillary axes. With the exception of S. poaeformis, the bracts of species of these sections are foliaceous.

3.2.2. **Spikelets**

Spikelets comprise an axis bearing glumes of which the proximal 1-4 are empty and each of the remainder may bear a single unisexual flower in its axil. Towards the proximal part of the axis the glumes are
distichous but distally they are spirally borne. Lower glumes all have a well-defined midrib which may be excurrent into an awn. Upper glumes are more delicate structures and usually lack a clearly defined midrib (glumellas of Eiten, 1976). Spikelets may be:

i. bisexual (androgynaecous)

ii. unisexual (male or female, monoecious)

iii. sterile

iv. functionally unisexual (female) with vestigial male rudiments (subandrogynaecous)

Historically the gender of the spikelets has provided, in part, the basis for separation of the sections, section Hypoporum (Nees) Endlicher having androgynaecous spikelets in the inflorescence and members of all other sections supposedly lacking them.
Fig. 7. Diagrammatic representation of spikelets of

Scleria spp. A, androgyneceous spikelet of
S. drègeana; B, subandrogyneceous spikelet of
S. melanomphala; C, subandrogyneceous spikelet
of S. boreformis; D, female spikelet
of S. angusta; g, glumes; f, filament of
sterile male flower; p, prophyll.
The androgynaecous spikelet of section Hypoporum has a single, basal female flower and 1 - several upper male flowers (Fig. 7 A). All spikelets in an inflorescence may be androgynaecous, for example S. motleyi C.B.Cl. from Malaysia (Kern, 1961) and S. poaeoides Ridl. from Africa north of our area (Haines & Lyc, 1972), or some spikelets may be androgynaecous and some male (lacking the basal female flower), or there may be androgynaecous, male and sterile spikelets in the same inflorescence.

The inflorescence of section Scleria (Bergius) Endlicher has unisexual spikelets and a few sterile spikelets. Functionally female spikelets are of two types; those which have a single basal female flower and a vestigial male part consisting of one to several empty glumellas (Fig. 7 B,C), and those which have no male vestige. Those with vestigial male parts are called subandrogynous (Robinson, 1966; Eiten, 1976) or subandrogynaecous. Rarely (Fig. 7 B) there may be staminodes present in subandrogynaecous spikelets.
The inflorescences of sections Acriulus (Ridley) C.B. Cl, Schizolepis (Nees) C.B. Cl. and Ophryoscleria (Nees) C.B.Cl., have unisexual spikelets and a few sterile spikelets. The female spikelets lack male rudiments (Fig. 7 D).

Among Southern African species of section Hypoporum, S. woodii comes closest to having all its spikelets androgynaeceous, there being only a few male and sterile spikelets in each panicle (Fig. 6 G).

Scleria lacustris (Fig. 6 F), which has hitherto been included in section Hypoporum, differs from other members of the section in that it has androgynaeceous, subandrogyneceous, male and sterile spikelets. There are fewer bisexual than there are functionally female spikelets.

Representatives of section Scleria in our area have functionally unisexual spikelets (and occasional sterile ones) of which the female almost invariably retain a few empty glumellas distally. In S. poaeformis the majority of female spikelets lack male rudiments, but I have found several with them (Fig. 22 A).
All specimens of *S. greigiifolia* (section Acriulus) examined have unisexual spikelets, the females without vestigial male parts.

The only species of section Schizolepis in our area, *S. angusta*, usually has a strictly unisexual spikelets, but one specimen (Ward 7911, Fig. 6 A) was exceptional in that it had a single, fully androgynaeceous spikelet.

It is not inconceivable that occasional bisexual and subandrogynaeceous spikelets may occur in all species which usually have unisexual spikelets.

It has been suggested (Holttum, 1948) that the spikelet of *Scleria* with its unisexual flowers may have been derived from an ancestral type in which all the flowers in the spikelet were hermaphrodite, through a stage such as is seen in *Cladium* in which the proximal flowers are hermaphrodite and the distal ones male. Loss of the androecial whorl from the proximal flowers would in turn lead to the condition found in section
Hypoporum and further loss of either male or female flowers from the androgynaecous spikelet to the subandrogynaecous and unisexual types of spikelet found in other sections.

The structure of androgynaecous spikelets has been interpreted in two ways. One interpretation is that the spikelet is a monopodial structure with a single, indeterminate axis bearing lateral flowers, each subtended by a glume with the single female flower situated proximally and the several male flowers distally. Nees (1842), Bentham (1883), Holttum (1948), Koyama (1961) and Eiten (1976) subscribe to this viewpoint. The other interpretation is that the spikelet comprises two axis systems, a sympodial axis which terminates in a female flower with a second, higher order axis system bearing male flowers arising laterally from the first axis. Proponents of this interpretation are Pax (1886), Core (1936), Kern (1961), Schultze-Motel (1964) and Koyama (1967, 1969).

Since the first appendage of a lateral branch is a prophyll which is recognisable
because of its position and its distinctive form, then if the second interpretation were correct, a prophyll would be present in the adaxial position near the base of the axis which bears male flowers. I have found no evidence of a prophyll in such a position in the androgynaeceous or subandrogyneceous spikelets of any species. Kern (1961) illustrates (Fig. 1; 1,II) prophylls in diagrams of spikelets of "bisexual Scleria species". It seems apparent that the diagrams were constructed to support an interpretation for which no direct evidence could be found and are hypothetical. Similarly, Koyama (1969) included a prophyll in illustrations (Figs. 5, 6 and 27) which appear to be based on an earlier drawing (Fig. 3 C, 1961) in which no prophyll was shown. Koyama (1961, p. 50) stated:—

"The staminate part, however, has no prophyll at its base, nor is found any bract scale from which the staminate part arises. Moreover in Scleria gracillima, which has more or less distichously arranged floral scales on the spikelets, the keel of the lowest scale of the staminate part faces the pistillate flower under it, and the second scale comes to
the same direction as the uppermost scale of the pistillate part. Accordingly the staminate part is a continuation of the pistillate part and not a side branch. Thus the pistillate flower is truly axillary."

I believe that the prophyll in the 1969 publication is a fabrication.

Since in the plants themselves no prophyll is interposed between the proximal female part of the spikelet and the distal male part, there is direct evidence that the spikelet is a monopodial structure. Further evidence obtained from analysis of branching patterns of the whole inflorescence also supports this interpretation.

If the androgynaeceous spikelet is interpreted as consisting of two axes, with the female flower terminating the first axis (thus sympodial) and the lateral (second) axis bearing male flowers, then in the species which have strictly unisexual spikelets, lateral branches of the axis which terminates in a female spikelet might be expected to bear terminal male spikelets. Only S. angusta, S. greigiifolia

...
and *S. poaeformis* among Southern African species have female spikelets which usually lack male rudiments. None of their inflorescences has such a branching pattern (Fig. 6 A,B,C). If a lateral axis is developed in these species from an axis with a terminal female spikelet, it too terminates in a female spikelet.

There is therefore no morphological evidence to support the interpretation of the androgynaecous spikelet as a double axis system with the female flower terminating a sympodial axis from which the second axis bearing male flowers arises laterally.

From examination of inflorescences of Southern African species I have, independently, come to the same conclusion as Eiten (1976) who worked with Brasilian species, that the bisexual spikelet of *Scleria* is a monopodial structure.

3.2.3. **Flowers**

Flowers of *Scleria* are invariably
unisexual and lack a perianth. Each is borne in the axil of a glume. The very shortly pedicillate female flower of Southern African species consists of a superior, syncarpous, tricarpellary, unilocular ovary with a terminal, deciduous style with three elongate stigmatic branches which are exserted from the glume at maturity. The ovary contains a single bitegmic, anatropous, crassinucellate ovule in centrally basal placentation. The pericarp is multilayered and at maturity the cell walls become silicified (Franklin, 1979). The ovary is shortly stipitate and the stipe or gynophore may be modified in the distal region to form a structure referred to as the disc or hypogynium, which will be described later.

The sessile male flower consists of 1-3 stamens with linear filaments and mucronate, basifixed, bithecate, tetrasporangiate anthers with longitudinal dehiscence, which are exserted from the glume at maturity. Pollen grains are circular in equatorial view and triangular in polar view.
Fig. 8. Diagrammatic representation of flowers of Scleria.

A, external morphology of female flower; B, external morphology of male flower; C, L/S female flower lacking hypogynium; D, L/S female flower with hypogynium.
Male and female flowers are illustrated diagrammatically in Fig. 8.

3.2.4. Fruit

The polycarpic, unilocular, dry, indehiscent, single-seeded fruit with its pericarp free from the integument of the seed and lacking a persistent style is classified as an achene, or nutlet.

The morphology of the achene of Scleria provides useful characters for the separation of taxa. Among the characters used are the size, shape and colour of the achene itself; the presence or absence of hypogynia; the shape, texture and colour of the hypogynium when present; the patterning, if any, of the achene surface and the presence or absence of hairs. While most of these characters are reasonably constant there are some species in which surface patterning of the achene is variable even on the same plant. It is noteworthy that most of the species in which variation in achene surface patterning has been recorded are members of
section Hypoporum (Nees) Endlicher.

3.2.4.1. Achene Surface Patterns

The terms used to describe achene surface patterns require explanation. Patterns may be either raised (projecting) or sunken (depressed). Projections may take the form of tubercles which are smooth rounded structures, warts or verrucae which are irregularly shaped low structures, trabeculae which are bar-shaped structures (Fig. 9), or a reticulum or network of sharply angled lines. An achene may have only one type of projection or a combination of types. For example, where an achene has only tubercles it is described as tuberculate, whereas one which has both tubercles and trabeculae is described as tuberculate-trabeculate.

Depressions if small and shallow are called alveolae and if
Fig. 9. Diagrammatic representation of main types of achene surface patterning in surface view and in profile.
large and shallow, lacunae (Fig. 9). If the arrangement or disposition of surface projections or depressions is regular, additional qualifying adjectives are used. For example an achene which has trabeculae arranged so as to form an irregular network is described as reticulate-trabeculate; one with lacunae arranged in a very regular pattern resembling that made by rectangular paving tiles is described as tesselate-lacunose; one with tubercles arranged in wavy bands is described as undulate-tuberculate and one with trabeculae arranged in the same manner is described as undulate-trabeculate. Similarly if a delicate pattern is present in conjunction with a more obvious one, such as fine linear markings in conjunction with a lacunose pattern, the achene is described as striate-lacunose.

In addition to the surface
patterns discernible with the aid of a hand-lens or a stereomicroscope, the occurrence of other, much smaller surface patterns has been revealed on some achenes by scanning electron microscopy (SEM). Most of these fine patterns are caused by differential deposition of silica in epidermal cells of the pericarp.

When the achene of *Scleria* is fully grown, silicon which is present in the plants in solution as a silicic acid is deposited in the cells of the pericarp as silica (Si (Franklin, 1979, 1981). Silicification of the achene proceeds progressively from the distal to the proximal end of the fruit. In the epidermal layer only the outer tangential walls of certain large, scattered or grouped epidermal cells of some species remain unsilicified or these may be very slightly silicified. The radial and the inner tangential
Fig. 10. Scanning Electron Micrographs of silicified achene shells of *Scleria* spp. after removal of organic matter by maceration.

A,B. *S. angusta* (R.H. Taylor 120)

A. achene shell showing smooth outer surface of body and "scar" remaining where the non-silicified hypogynium has been removed by maceration (X 26)

B. surface of "scar" showing silicified, proud-standing radial walls of cells and incompletely silicified, pitted inner tangential walls (X 450)

C,D. *S. poaeformis* (Ward s.n.)

C. achene shell showing smooth outer surface of body of achene and "scar" left by hypogynium (X 18)

D. half-shell, showing multilayered, wholly-silicified pericarp and stipe (X 15)

E,F. *S. aterrima* (Robinson 5055)

E. shell of achene with trigonous stipe (X 30)

F. view of fracture near base of stipe showing inflated epidermal cells in surface view and fractured cells of pericarp (X 250)

G. *S. aterrima* (Strey 7085), distal end of achene shell showing siliceous papillae protruberant from outer surface of pericarp (X 125)

H. *S. transvaalensis* (K.D. Gordon-Gray 6020), surface of achene shell showing protruberant siliceous papillae and a group of 3 inflated cells with their thinly silicified outer tangential walls partly collapsed (X 450)
walls of these cells are heavily silicified. (Siliceous achene-shells obtained by maceration are illustrated in Figs. 10, 54). South African species which have been found to possess enlarged epidermal cells of the type described are *S. bulbifera* (very rarely, Fig. 12 F); *S. dieterlenii* and *S. pergracilis* var. *brachystachys* (Fig. 14); *S. melanomphala* (rarely some achenes of *S. natalensis* and *S. transvaalensis* (Fig. 10 H); *S. achenii* (Fig. 20 C); *S. unguiculata* (Fig. 21 F); and *S. lagoensis* (Fig. 21 C). The last three species have patently hirsute achenes and the hair-shafts are derived from the outer tangential walls of enlarged epidermal cells. Deposition of silica in and on the inner tangential wall and radial walls of these cells effectively cuts off the supply of moisture to them with the result that the outer tangential wall tends to collapse inwards forming a "pit."
Fig. 11. Scanning Electron Micrographs of achenes of *Scleria* spp.

A-C. *S. bulbifera* (Vesey-Fitzgerald 1447)

A. distal end of shortly-beaked, obovoid achene showing very strongly trabeculate-lacunose surface and unicellular epidermal hairs of a type not seen in achenes of any other species (ringed) (X 60)

B,C. two views of proximal region of same achene showing trigonous stipe and series of ribs and valleys at junction of stipe with body (X 60)

D-F. *S. woodii* (Bolus 1893)

D. subglobose, shortly-beaked achene with trigonous stipe and very obscure and ill-defined surface patterning (X 35)

E. distal part of same achene (X 100)

F. proximal part of same achene (X 55)
Fig. 12. Scanning Electron Micrographs of achenes of *Scleria bulbifera*.

A-C. from K.D. Huntley 567

A. subglobose, shortly beaked achene showing lightly tuberculate-trabeculate surface and shrivelled, immature, trigonous stipe (X 30)

B. distal end of same achene showing sparse tubercles (X 60)

C. proximal end of same achene (X 60)

D-F. from Acocks 10758

D. subglobose, shortly-beaked achene showing tuberculate-trabeculate surface and trigonous stipe (X 30)

E. distal end of same achene showing tubercles crowned with inflated epidermal cells (X 100)

F. proximal end of same achene, the trigonous stipe slightly shrunken, showing one tubercle with outer tangential walls of inflated epidermal cells collapsed forming "pits" and few, short unicellular hairs distally (X 50)
A-C. one achene, D-F. another achene, both achenes from isotype, Robinson 4220

A,D. two strongly trigonous, shortly beaked achenes showing reticulate-trabeculate surface, and trigonous stipe with a series of ribs and valleys at junction of stipe and body, and in D, protruberant siliceous papillae which are absent from A (both X 30)

B,E. proximal part of same two achenes (both X 60)

C,F. surfaces of the two achenes, one without papillae (C) and one with them (F) (both X 220)
Fig. 14. Scanning Electron Micrographs of achenes of *Scleria* spp.

A-C. *S. dieterlenii* (isotype, Dieterlen 749)

A. subglobose, very shortly beaked achene with trigonous stipe, showing surface pattern of flat tubercles or warts and short transverse bars (verrucose - trabeculate surface), their crests strongly patterned by the proud-standing silicified radial walls of inflated epidermal cells whose outer, thin, tangential walls have collapsed (X 30)

B. proximal part of same achene (X 50)

C. distal part of same achene (X 100)

D-F. *S. pergracilis var. brachystachyx* (Pentz & Acocks 10277)

D. immature, damaged, subglobose, strongly-beaked, tuberculate - trabeculate achene showing the same type of pattern on the crests of the tubercles and trabeculae as that seen in *S. dieterlenii* (X 35)

E. proximal part of same achene (X 55)

F. distal part of same achene (X 55)
Fig. 15. Scanning Electron Micrographs of achenes of *Scleria* spp.

A-C.  *S. dregeana* (Galpin 9104), a gathering of tall plants with inflorescences simply glomerate-spicate or with 1 - 2 short basal branches and dark glumes made at an altitude of c. 1700 m.

A. subglobose, shortly-beaked achene showing numerous distal tubercles, numerous median and proximal trabeculae (horizontal bars) and trigonous stipe (X 40)

B. distal part of same achene (X 100)

C. surface of same achene (X 200)

D-F.  *S. sobolifer* (Strey 5711)

D. subglobose, shortly-beaked achene showing tuberculate - trabeculate surface, trigonous stipe and series of ribs and valleys at junction of stipe and body (X 34)

E. proximal part of same achene (X 55)

F. surface of same achene showing the distinctive pattern found on the crests of the tubercles and trabeculae of all achenes of this species (X 400)
Fig. 16. Scanning Electron Micrographs of achenes of *Scleria dregeana*.

A-B. from Lubke 181, a gathering of tall plants with simply glomerate-spicate inflorescences and dark glumes made at an altitude of c. 1500 m.

A. subglobose, shortly-beaked achene with smooth surface and trigonous stipe (X 40)

B. distal part of same achene (X 67.5)

C-D. from Doidge & Bottomley s.n., a gathering of tall plants with inflorescences simply glomerate-spicate or with 1 - 2 short basal branches and dark glumes made at an altitude of c. 1500 m

C. subglobose, shortly-beaked achene with sparse small, distal tubercles on otherwise smooth surface (X 40)

D. distal part of same achene (X 57)

E-F. from Drege 4381 (Type of *S. holcoides*), a gathering of tall plants with sparingly branched glomerate-spicate inflorescences and pale glumes made at an altitude below 150 m

E. subglobose, shortly-beaked achene with well-developed distal tubercles on otherwise smooth surface (X 40)

F. distal part of same achene (X 57)
Fig. 17. Scanning Electron Micrographs of achenes of Scleria spp.

A-C. *S. aterrima* (Strey 7085)

A. shortly beaked achene with subglobose body and trigonous stipe, the surface smooth except for protruberant siliceous papillae around the apical beak and somewhat inflated epidermal cells towards the base of the stipe (X 30)

B. stipe and base of achene (X 67.5)

C. distal region showing protruberant siliceous papillae (X 125)

D-F. *S. nutans* (Vesey-Fitzgerald 2301)

D. very shortly beaked achene with globose body and trigonous stipe, the surface smooth except for protruberant siliceous papillae towards the base of the stipe (X 30)

E. stipe and base of achene (X 67.5)

F. distal region of achene showing smooth surface (X 67.5)
Fig. 18. Scanning Electron Micrographs of achenes of *Scleria* spp.

A-C.  *S. welwitschii* (Acocks 22171)

A. ovoid, very shortly beaked, smooth achene with short trigonous stipe (X 38)

B. distal part of same achene (X 58)

C. proximal part of same achene (X 58)

D. *S. rehmannii* (de Winter & Marais 5049)

D. very badly damaged ovoid achene showing smooth surface, short beak with remains of style base still attached and multilayered construction of pericarp (X 33)

E-F.  *S. longispiculata* (Story 6464)

E. distal part of damaged, ovoid, shortly-beaked achene showing smooth surface and multilayered construction of pericarp (X 27)

F. proximal part of same achene showing trigonous stipe (X 27)
Fig. 19. Scanning Electron Micrographs of achenes of *Scleria* spp.

A-C. *S. natalensis* (Ward 4716)

A. obtusely trigonous, shortly beaked achene showing tuberculate-lacunose surface, well-developed hypogynium with rounded lobes and obpyramidal stipe (X 20)

B. proximal part of achene showing hypogynium and stipe (X 35)

C. distal part of trigonous achene showing distribution of "pits" which result from collapse of non-silicified outer tangential walls of scattered, inflated epidermal cells (X 30)

D-F. *S. transvaalensis* (Seagrief 18)

D. barrel-shaped, shortly beaked achene showing tesselate-lacunose surface, well-developed hypogynium with rounded lobes, the stipe obscured by partly collapsed hypogynium (X 20)

E. proximal part of achene showing hypogynium (X 25)

F. surface showing tesselate-lacunose surface with protruberant siliceous papillae (X 62.5)

Note: in both species the mature stipe is obpyramidal.
Fig. 20. Scanning Electron Micrographs of achenes of *Scleria* spp.

A-C. *S. achtenii* (Ward 9146)

A. subglobose, very shortly beaked achene showing lightly and obscurely lacunose, sparsely hirsute surface and well-developed hypogynium with ligulate lobe (tip broken off), the hypogynium partly collapsed obscuring the stipe (X 20)

B. apex of achene (X 33)

C. achene surface showing very numerous, protuberant siliceous papillae; non-silicified hairs, their collapsed bases forming "pits" and among them a few cells with non-silicified outer tangential walls which have not been produced as hairs (X 400). It is noteworthy that inflated epidermal cells with non-silicified outer tangential walls not produced as hairs have been observed in the distal region of some, but not all, achenes of *S. natalensis* and *S. transvaalensis*.

D-F. *S. foliosa* (Schweickerdt 2189)

D. ovoid achene, not fully mature so somewhat compressed towards the base which hardens later than the apex, showing beakless, smooth distal region and strongly alveolate-lacunose median and proximal regions, hypogynium and stipe (X 27)

E. distal part of achene (X27)

F. proximal part of achene showing three rounded lobes of hypogynium and shrivelled stipe (X 27)
Fig. 21. Scanning Electron Micrographs of achenes of Scleria spp.

A-C. *S. lagoensis* (Compton 2944) (damaged)

A. ovoid, very slightly beaked achene showing smooth surface which is glabrous distally and sparingly hirsute proximally (X 18)

B. distal end of achene (X 26)

C. proximal, damaged end of achene showing collapsed hypogynium with narrowly lanceolate lobes (1,2) (X 26)

D-F. *S. unguiculata* (P.A. Smith 1980)

D. proximal part of ovoid, densely hirsute achene showing unguiculate lobe of hypogynium and obpyramidal stipe (X 28)

E. distal part of achene, the point of attachment of the style completely obscured by the hairy indumentum (X 36)

F. surface showing non-silicified hairs and collapsed hair bases forming "pits", the surface between the "pits" smooth, without protuberant papillae (X 400)

Note: in both species the mature stipe is obpyramidal.
Fig. 22. Scanning Electron Micrographs of achenes of *Scleria* spp.

A-C. *S. poaeformis* (Ward 4024)

A. female spikelet with achene in situ and empty glumes (eg) representing the sterile remains of the male part of the ancestral androgynaeceous spikelet (X 12)

B. subglobose achene showing smooth surface, narrow hypogynium and obpyramidal stipe (X 17)

C. base of achene showing stipe and hypogynium with very short triangular lobes (X 27)

D-F. *S. lacustris* (Robinson 4700)

D. ovoid achene showing smooth surface, narrow hypogynium and obpyramidal stipe (X 20)

E. apex of achene with fungal contaminant (X 58)

F. base of achene showing stipe and hypogynium with very poorly developed lobe (X 35)
Fig. 23. Scanning Electron Micrographs of achenes of Scleria spp.

A-C. S. greigiifolia (W. Siame Z 09)

A. strongly-beaked ovoid-globose achene showing smooth surface, zoniform hypogynium and shrivelled (not fully mature) stipe (X 15)

B. surface showing faint outlines of radial walls of silicified epidermal cells (X 125)

C. proximal part of achene (X 30)

D. S. melanomphala (F. Bayer s.n.)

D. ovoid, beakless achene showing smooth surface, zoniform hypogynium, stipe and the unusual feature of a persistent style base, which is not normal for the section Scleria (X 15)

E-F. S. melanomphala (Ward 3648)

E. ovoid, beakless achene with immature, crumpled hypogynium: no style base present in this specimen (X 15)

F. proximal part of same immature achene with crumpled zoniform hypogynium and shrivelled stipe and a group of three unsilicified epidermal hairs (X 30)

Note: in both species the mature stipe is obpyramidal.
Fig. 24. Scanning Electron Micrographs of achenes of *Scleria* spp.

A-C. *S. angusta* (Strey 11306)

A. ovoid-globose achene showing smooth surface, hypogynium with fimbriate margin and obpyramidal stipe (X 20)

B. proximal part of same, not fully mature achene, the lobes of the hypogynium not clearly defined (X 26)

C. surface of marginal fimbriae showing non-silicified papillae (X 400)

D. *S. angusta* (R.H. Taylor 120)

D. proximal part of a fully mature achene showing three short rounded lobes of hypogynium with their fimbriate margins and the obpyramidal stipe (X 28)

E-F. *S. racemosa* (Bock s.n.)

E. part of achene showing cupuliform, marginally ciliate hypogynium which exceeds the achene in width (X 15)

F. ciliate margin of hypogynium (X 125)
as the cell desiccates. If the outer tangential wall has been produced as a hair-shaft, that also collapses. The result of this process is illustrated at high magnification in Figs. 20 C and 21 F.

The position on the achene surface occupied by the enlarged epidermal cells is characteristic for each of the species which possesses them. In the species of section Scleria which have patently hirsute achenes, *S. achtenii* with reticulate-lacunose achenes and *S. unguiculata* with striate-lacunose achenes have these cells (and therefore the hairs) on the crests of the interlacunar ridges. In *S. lagoensis* which has smooth or very faintly striate-lacunose achenes these cells together with their hairs occur only in isolated lines and patches on the proximal two-thirds of the achene-surface. The achenes of *S. melanomphala* are
smooth and usually glabrous, but some achenes (Fig. 23 F) have a few, or rarely, many hairs at the proximal end of the body of the achene which may be obscured by the upper margin of the zoniform hypogynium. The glabrous, strongly-patterned achenes of *S. natalensis* and *S. transvaalensis* may have some inflated epidermal cells and these occur only towards the distal end of the achene where they crown some of the tubercles or interlacunar ridges.

Among members of section *Hypoporum*, *S. dieterlenii* and *S. pergracilis* var. *brachystachys* have inflated cells on the crests of the protuberances from the achene surface and they are so well-developed that they account for the verrucose surface which is discernible without SEM. In *S. sobolifer* they also crown superficial projections but are more subtle and are not discernible without SEM. Of the
achenes of *S. bulbifera* examined, only one, from Acocks 10758 (Fig. 12) shows inflated cells and a few "pits" on the crests of some tubercles, but both this achene and one from Vesey-Fitzgerald 1447 (Fig. 11 A) possess a few tiny, pointed, apparently unicellular hairs with inflated bases in the distal region which are only discernible with SEM. It would seem that all species with scattered, enlarged epidermal cells with non-silicified outer tangential walls may have the potential to be hirsute but that this potential has only been realised in some species of section Scleria (Berg.) Endl.

Another type of surface pattern discernible on some achenes with SEM is that created by the aggregation of silica in nodules which project from the epidermis as papillae. This type of pattern has been observed on some achenes of *S. aterrima* (Fig. 17 C), some
145.

Achene patterns of *S. veseyfitzgeraldii* (Fig. 13) and all achenes thus far examined of *S. achatenii*, *S. natalensis* and *S. transvaalensis* (Figs. 19, 20).

The Southern African species which show the greatest range of variation in achene surface patterning discernible without SEM are *S. drègeana* and *S. bulbifera* and a lesser degree of variation is found in *S. woodii*. Slight variation, from smooth to lightly and obscurely tuberculate, may also occur in *S. nutans* and *S. rehmannii*. At higher resolutions afforded by SEM variations are discernible in the achene surface patterns of *S. aterrima* and *S. veseyfitzgeraldii* which may or may not possess protruberant siliceous papillae. All other Southern African species have reasonably constant achene surface patterning.
3.2.4.2. The Hypogynium

The presence or absence of a hypogynium or disc is a key character which has been used to aid in separation of the sections of the genus. Members of section Hypoporum lack a hypogynium whereas members of other sections have one. The hypogynium is three-lobed with the margins of the lobes entire in section Scleria (Figs. 19-23) fimbriate in section Schizolepis (Fig. 24 B) and ciliate in section Ophryoscleria (Fig. 24 E).

It has been suggested (Johnson, 1931) reported by Core, 1936) that the hypogynium may represent a greatly modified perianth. I am of the opinion that it is a derivative of the stipe of the achene and thus a new modification rather than the vestige of a disappearing perianth. Nelmes (19 considered section Hypoporum to be
more advanced than the other sections of the genus, arguing that in Hypoporum the hypogynium has become reduced and vestigiate. Robinson (1962) presented a cogent counterargument and my own observations support those of Robinson. Morphological features which suggest that section Hypoporum is less advanced than other sections of the genus include, 1) the possession by members of section Hypoporum of androgyneceous spikelets whereas members of other sections have unisexual spikelets of which the functionally female spikelet is often subandrogyneceous possessing sterile male rudiments, a condition which suggests reduction; 2) the least-modified panicles are to be found in some species of section Hypoporum, e.g. S. motleyi, S. poaeoides, S. woodii; 3) most members of section Hypoporum produce a simultaneous inflorescence whereas members of other sections produce staged
inflorescences, which is a more advanced state; 4) inconstancy of achene surface-patterning is more common in species of section Hypoporum than in species of any other section and such inconstancy suggests a greater degree of flexibility in the genetic code or in other words, a lower level of specialisation.

If, as the evidence suggests, section Hypoporum is more primitive than other sections, the lack of an hypogynium in its members is unlikely to be the result of reduction, but rather provides evidence of failure of this structure to develop.

Robinson (1962) expressed the view that the hypogynium in members of section Scleria serves the function of attaching the immature achene securely to the concave "receptacle" (which I consider to be a short pedicel). Expansion,
drying out and hardening of the hypogynium take place in these species only when the achene is mature and it is at this stage that abscission occurs. Prior to this the achene is firmly held and very difficult to detach from its pedicel. He pointed out that the inflorescence of most members of section Hypoporum is erect therefore the achenes are held in situ by the enveloping glumes even after they are fully mature and ready to fall, and attributed to the hypogynium the important rôle of keeping the achene securely attached to the plant until it has achieved maturity. He did not mention the achenes of section Schizolepis which is represented on the African mainland only by $S$. angusta, or those of $S$. greigiifolia the only member of sect. Acriulus, but if his explanation of the rôle of the hypogynium in sect. Scleria were correct, it would fit the achenes of $S$. angusta and $S$. greigiifolia equally well.
Robinson considered that the rôle of the hypogynium in members of section Ophryoscleria (which has not been recorded from our area) has been expanded to fulfil the rôle of a buoy in addition to serving as a secure means of attachment for the immature achene. Whereas mature achenes of S. angusta and S. greigiifolia (my own observations) and of species of section Scleria (his observation, confirmed by me), do not float in water those members of section Ophryoscleria do, with the very well-developed corky, cupuliform hypogynium (Fig. 24 E, F ) remaining uppermost. Using achenes obtained from a gathering of S. racemosa Poir. made in Mozambique (Ward 7912) I have confirmed that the hypogynium of this species does indeed buoy the fruit in water. Robinson considered that the development of the hypogynium as a flotation device in Ophryoscleria is associated with the aquatic
habitats occupied by plants of this section. In such habitats buoyant fruit are advantageous because buoyancy permits wider dispersal than could occur if achenes sank to the bottom. It is noteworthy that the stipe of achenes which lack hypogynia is trigonous and is from $\frac{1}{3}$ - $\frac{1}{7}$ the total length of the achene, whereas that of achenes which possess hypogynia is obpyramidal and is in comparison with the trigonous stipes far shorter in proportion to the achene as a whole. It would appear that elaboration of the distal part of the stipe to form an hypogynium has resulted in shortening of the stipe, sometimes almost to the point of obsolescence. Mature achenes (which are very rarely present on herbarium sheets) of species with well-developed hypogynia are very nearly sessile. It has been observed that the free part of the hypogynium is not
silicified even at maturity (Fig. 10) whereas the body and stipe of the achene are.
Silicification is progressive, proceeding from the distal end downwards so that the stipe is the last part of the achene to become silicified. It is only when the stipe silicifies that the connexion with the pedicel is broken and the achene is shed. This is as true for achenes without hypogynia as it is for those with them.

I am therefore not convinced that Robinson's interpretation of the rôle of the hypogynium as a means to provide secure attachment is correct. Immature achenes of species which lack hypogynia are as difficult to detach from their pedicels as are those which possess them. The fact that they remain in situ longer than do those of hypogyniate species is simply the consequence of their being held upright in an erect inflorescence.
What, if any, is the function of the hypogynium in sections other than Ophryoscleria remains obscure. That selection pressure has operated in favour of those individuals with buoyant hypogynia to permit the development of the group of aquatic species which constitute section Ophryoscleria seems to be a logical assumption. Whether, in time, the hypogynia of achenes of hydrophilous species other than those of section Ophryoscleria will become elaborated as flotation devices is a matter for speculation.
3.2.4.3. Achene shape and colour

All Scleria achenes are fundamentally trigonous, but the body of the mature achene of most species is often very obscurely so. Of the species recorded from Southern Africa only one, \textit{S. veseyfitzgeraldii} has an achene the body of which is very strongly trigonous at maturity. The shape of the body of the achene of each species is recorded in the description of the species in Chapter 6 and all are illustrated (Figs. 11-24). The measurements given in the descriptions are overall length, measured with callipers from the base of the stipe to the base of the style and width measured at the broadest part of the body of the achene.

Although the body of the achene is usually only very obscurely trigonous, the stipe, and the hypogynium are usually clearly trigonous. When fully mature the
trilateral symmetry of the hypogynium of *S. greigiifolia* and *S. melanomphala* becomes obscured as these structures assume a zoniform shape.

None of the species represented in our area has a persistent style, but the distal part of the body of the fruit may be produced as a plinth to which the style-base is attached. This plinth may persist as the beak on the achene. The only local species which has a strongly beaked achene is *S. greigiifolia*, all others are beakless or almost so.

It is commonly believed that the achenes of most species of *Scleria* are white, because the achenes which remain attached to dry herbarium specimens are usually white. As has already been stated, fully mature achenes do not remain attached to their pedicels, therefore it is only rarely that mature
achenes, even of species with erect inflorescences, will remain in situ through the handling process involved in preparing herbarium specimens. Young achenes are green. When dried, such achenes turn white. These prematurely dried white achenes in which the silicification process is not complete, usually remain attached to the herbarium specimens, thereby creating the false impression that the achenes of Scleria are white.

Sometimes white achenes may be found on fresh specimens. If opened they will prove to be empty shells. A white achene is therefore either a prematurely dried green one which has changed colour in drying or one with an aborted embryo.

Fully mature achenes if they can be found will invariably, as Robinson (1962) pointed out, be
coloured. In some species the colour is strong and striking; in most it is dull, usually pale brown or grey and often with darker longitudinal zones in the three interangular regions. The local species with strikingly coloured achenes are *S. angusta* whose achenes change colour from green through mauve and violet to deep purple as they mature, *S. greigiiifol* whose achenes change from green through beige to pinkish brown, sometimes developing violet blotches, *S. melanomphala* whose mature achenes are grey or brown with deep purple (almost black) area apically from which the species gets its name and *S. longispiculata*, the body of whose achene is brown and the stipe black.

Patterned achenes when mature usually have the crests of the surface projections either paler or darker than the intervening
surface areas, or they may be differently coloured. For example, the mature achene of *S. dieterlenii* is grey and the crests of the projections are bright reddish-gold, while that of *S. unguiculata* is grey or light brown and the hairs are golden or white.

Hypogynia may also change colour as they mature. White, brown, golden and reddish hypogynia occur among local species (Table II).
<table>
<thead>
<tr>
<th>HYPOGYNIUM</th>
<th>ACHENE</th>
<th>SPECIES</th>
<th>SECTION</th>
</tr>
</thead>
<tbody>
<tr>
<td>Very narrow with three short, obtusely triangular lobes: margin entire</td>
<td>brown X X</td>
<td>grey to brown</td>
<td>lacustris</td>
</tr>
<tr>
<td></td>
<td>white/brown X X</td>
<td>brown</td>
<td>poaeformis</td>
</tr>
<tr>
<td>+ Zoniform without lobes: margin entire</td>
<td>brown X X X</td>
<td>brown/violet</td>
<td>greigiifolia</td>
</tr>
<tr>
<td></td>
<td>brown X X X X</td>
<td>grey/black</td>
<td>melanomphala</td>
</tr>
<tr>
<td>With three rounded lobes: margin entire</td>
<td>yellow X X</td>
<td>grey</td>
<td>foliosa</td>
</tr>
<tr>
<td></td>
<td>yellow X X</td>
<td>brown</td>
<td>natalensis</td>
</tr>
<tr>
<td></td>
<td>yellow X X</td>
<td>brown</td>
<td>transvaalensis</td>
</tr>
<tr>
<td>With three acutely triangular (sometimes divided) lobes: margin entire</td>
<td>cream X X X X</td>
<td>grey to brown</td>
<td>lagoensis</td>
</tr>
<tr>
<td></td>
<td>brown X X X</td>
<td>grey to brown</td>
<td>unguiculata</td>
</tr>
<tr>
<td></td>
<td>white X X X</td>
<td>grey to brown</td>
<td>achtenii</td>
</tr>
<tr>
<td>With three obtuse lobes: margin fimbriate</td>
<td>brown X X</td>
<td>violet to purple</td>
<td>angusta</td>
</tr>
<tr>
<td><em>Cupuliform, broader than achene: margin ciliate</em></td>
<td>brown X X</td>
<td>brown</td>
<td>racemosa</td>
</tr>
</tbody>
</table>

*NOT REPRESENTED IN AREA OF FLORA OF SOUTHERN AFRICA*
3.3. **Summary and Discussion**

As a result of observations of morphology of Southern African species of *Scleria* it has become evident that, while the fundamental branching pattern of the inflorescence of all species examined is the same, this underlying uniformity is obscured by differences in degree of contraction or elongation of subordinate branch orders in the panicle in different groups of taxa.

Two types of inflorescence occur, namely, one with the internodes of inflorescence branches of primary and higher orders extremely contracted, resulting in the type of inflorescence referred to as "glomerate-spicate", which has glumiform bracts (Group A), and the other with the proximal internodes of lateral inflorescence branches, particularly those arising from the lowermost nodes of the inflorescence greatly elongated, resulting in the type of inflorescence described either as "interrupted-paniculate" or, as having "terminal and lateral panicles", which has foliaceous bracts (Group B).

The ultimate branch orders of inflorescences are (excluding floral axes) the rhachillas of the spikelets. Spikelet structure is fundamentally uniform in all Southern African representatives of
the genus, all spikelets comprising a monopodial (indeterminate) axis bearing spirally arranged glumes in the axils of which solitary, unisexual flowers may be borne. The basic pattern of spikelet morphology may be modified by abortion of flowers so that among extant taxa spikelets occur which are androgynaeceous, subandrogyneceous, female, male and occasionally, sterile.

It is suggested that the sequence of reduction in the spikelets of Scleria has been from taxa having all spikelets in an inflorescence androgynaeceous → taxa with spikelets androgynaeceous and male → taxa with spikelets androgynaeceous (few), subandrogyneceous and male → taxa with spikelets subandrogyneceous (few), female and male → taxa with spikelets female and male. Separation of the sexes in the spikelets seems to be a trend which reaches its highest level of expression in taxa with interrupted-paniculate inflorescences, unisexual female spikelets being unknown in the group with glomerate-spicate inflorescences.

On the basis of spikelet form, two groups of taxa are distinguishable, namely, a group which has androgynaeceous spikelets and male
spikelets in the same inflorescence (Group A), and one which has subandrogyneceous, female and male spikelets in the same inflorescence, or has female and male spikelets, or, rarely, has androgyneceous, subandrogyneceous and male spikelets (Group B).

Two types of achene are distinguishable, namely, a type which has a trigonous stipe which is not elaborated distally to form an hypogynium (Group A), and a type which has an obpyramidal stipe which is elaborated distally to form an hypogynium (Group B).

Two types of plants are distinguishable, namely, slender, more-or-less hygrophilous, narrow-leaved herbs of open, often temperate, seasonally dry grassland habitats, which are either annuals, or perennials with annual aerial parts (Group A), and stout or very stout hygrophilous or hydrophilous, usually wide-leaved herbs of tropical and subtropical stream-bank, forest or lacustrine habitats, most of which are evergreen perennials (Group B).
Morphological evidence indicates clearly that in *Scleria* two distinct groups have evolved in response to different factors. One group comprises slender plants with glomerate-spicate inflorescences, androgynaeceous and male spikelets, and achenes with trigonous stipes which lack hypogynia (Group A). The other comprises relatively stout plants with interrupted-paniculate inflorescences, sometimes with some androgynaeceous spikelets but more often with spikelets female and male, the functionally female spikelets with male rudiments present (sub-androgynaeceous), or without such vestigial male parts, and achenes with obpyramidal stipes and hypogynia (Group B).

Elaboration of the distal part of the achene stipe to form an hypogynium is a modification which occurs only in taxa with interrupted-paniculate inflorescences, and reaches the highest levels of development in certain groups of shade-dwelling hydrophilous plants which have strictly unisexual spikelets. Evidence exists that in one of these groups the hypogynium functions as a flotation device which may assist in dissemination of the fruit. Such hypogynia exceed the achene in width, are
cupuliform and are ciliate on the margin. The group which possesses these morphologically distinctive hypogynia which serve a biologically important function not attained in any other group, may have reached the most specialised level of development in the interrupted-paniculate line. Another specialised feature of this group of plants is the development of pseudodorsiventral lateral extensions which greatly increase the width of the lamina. It is suggested that this type of leaf, referred to as praemorse, may, because of its increased surface-area and volume, increase the photosynthetic capacity of plants which occupy shady habitats.

Another group which has unisexual spikelets has morphologically distinctive, elaborate hypogynia with fimbriate margins. It has been demonstrated that the hypogynium in this group does not function as a flotation device, therefore does not assist in fruit dissemination in water. This group is probably less specialised than the group with buoyant hypogynia, although its members also have praemorse leaves.

The hypogynia of all other members of the interrupted-paniculate line have an entire
margin and do not function as flotation devices. Many of these taxa have functionally female spikelets with distal male rudiments present, and a few may have some androgynaeceous spikelets in the inflorescence. Some have strictly unisexual female spikelets. While the majority of taxa which have hypogynia with entire margins do not have praemorse leaves, a few species (none Southern African) are reported to have developed this type of lamina.

It is suggested that, in Scleria, evolution of two different types of plants, two different types of inflorescence and two different types of achene has occurred in response to differences in habitat.

Annual plants and plants with annual aerial parts and protected subterranean perennating organs have been able to exploit temperate habitats in open, seasonally dry areas. Such plants, whose aerial parts complete their growth and sexual reproductive cycles in less than a year, are slender, with narrow laminas. These plants have glomerate-spicate inflorescences which are often held stiffly erect. The achenes are held in an upright position by the clasping glumes and are mostly
shed when, during winter, the aerial parts of the plant die back to ground level. It is suggested that, since germination is likely to occur more-or-less simultaneously with the onset of favourable conditions in spring, shedding of achenes over an extended period is not advantageous. Since the majority of these plants occupy seasonally damp habitats, dissemination of fruit beyond the limits of the areas occupied by the parents, that is, into drier areas, might be disadvantageous. Since by the time the inflorescence together with its tightly held achenes falls, the habitat is dry, the development of an hypogynium which may serve as a flotation device, or may serve to prise the glumes apart in order to facilitate shedding of the achene, is unnecessary. Thus, despite retention of androgynaeceous spikelets, which is a primitive condition, these plants are highly specialised and very well adapted to the seasonally dry, often temperate habitats which they have succeeded in exploiting.

Evergreen perennial plants are limited to permanently damp or wet, open or shady, tropical and subtropical habitats. The growth and sexual reproductive cycle of such plants extends over periods longer than a year since
there is little seasonal fluctuation in temperature and availability of water is not a limiting factor. Such plants are stout or very stout herbs, usually with broad laminas, which, in those taxa which are denizens of deeply shaded habitats such as swamp forest, are further broadened by the development of pseudodorsiventral lateral wings which extend beyond the margins of the true lamina. These plants have interrupted-paniculate inflorescences. Elongation of the proximal internodes of many of the lower branches of the inflorescences results in the partial panicles becoming wholly or partly pendulous. It is suggested that the loss of the distal male part of the functionally female spikelet in taxa with pendulous inflorescences may be advantageous in that its loss may permit the female glumes to spread apart more widely, as such spreading is not physically impeded by the distal extension of the rhachilla and its other appendages and achene fall is not obstructed. Elaboration of an hypogynium may, by increasing the breadth of the achene towards its base, force the glumes apart as the achene matures so that they grip the mature achene, in which the hypogynium shrinks slightly, less firmly than they would do if no hypogynium were elaborated, thereby facilitating shedding of
the achene. The achenes, which mature progressively, are therefore able to drop out of the spikelets.

Among taxa with interrupted-paniculate inflorescences a few exist which are not tied to permanently damp or wet habitats. Such taxa include a few annual species of seasonally dry tropical habitats, and one Southern African species is known which has annual aerial parts and subterranean perennating organs, which occurs at higher, therefore more temperate altitudes than other Southern African species of this group.

It is suggested that each of the two morphologically distinct groups of taxa be accorded subgeneric rank, as originally proposed by Clarke (1894).

To subgenus Hypoporwn (Nees) C.B.CI. are assigned taxa with glomerate-spicate inflorescences, androgynaecious and male spikelets and achenes without hypogynia (Group A).

To subgenus Scleria (Bergius) C.B.CI. are assigned taxa with interrupted-paniculate inflorescences, functionally female and male spikelets (with or without androgynaecious
spikelets in the same inflorescence) and achenes with hypogynia (Group B).

Sufficient evidence to permit further subdivision of subgenus Hypoporum has not been accumulated in this study, therefore it is proposed that, until a world-wide revision of the genus is made, provisional recognition be given to a single section, section Hypoporum (Nees) Endlicher, in subgenus Hypoporum, and that the section shall include the following supraspecific taxa: subgenus Hypoporum, sections Pergraciles, Hirtellae, Lithospermeae and Corymboae of Clarke (1894, 1900, 1902, 1908); section Hypoporum of Core (1936); section Hypoporum of Fierárt (1951); section Hypoporum (excluding S. lacustris) of Nelmes (1955); sections Hypoporum and Corymboae of Kern (1961, 1974); subgenus Scleria, section Hypoporum of Koyama (1961); subgenus Scleria (pro parte, species 1-27) of Robinson (1966).

Four sections are recognised in subgenus Scleria, namely:-

1. Scleria (Bergius) Endlicher, diagnosed as having leaves tapering smoothly towards the tips, or, rarely, with leaf-tips narrowed suddenly to a point (praemorse);
at least some subandrogyneaceous spikelets in the inflorescence; female glumes adaxially glabrous; achenes beakless or almost so; hypogynia with entire margins:

2. Acriulus (Ridley) C.B. Clarke, diagnosed as having leaves tapering smoothly towards the tips, or, rarely, with leaf-tips narrowed suddenly to a point (praemorse); female spikelets without male rudiments; female glumes adaxially hairy; achenes strongly beaked; hypogynia with entire margins:

3. Schizolepis (Nees) C.B. Clarke, diagnosed as having leaves usually praemorse; female spikelets without male rudiments; female glumes adaxially glabrous; achenes beakless or almost so; hypogynia with fimbriate margins:

4. Ophryoscleria (Nees) C.B. Clarke, diagnosed as having leaves usually praemorse; female spikelets without male rudiments; female glumes adaxially glabrous; achenes beakless, with persistent style-base; hypogynium cupulate, broader than the achene, with ciliate margins.
Section Scleria may comprise several natural groups, the delimitation of which cannot be attempted until a world survey is made. Although Acriulus is here maintained as a section, the distinction between it and section Scleria is a fine one which may, when other species assigned to Scleria are better known, prove untenable.

Subgenus Scleria, section Scleria includes the following supraspecific taxa: subgenus Scleria, sections Tessellatae and Elatae of Clarke (1894); subgenera Browneae, Tessellatae and Euscleria of Clarke (1908); sections Euscleria and Hymenolytrum of Core (1936) and of Piérart (1951); section Scleria (with the addition of *S. lacustris*) of Nelmes (1956); sections Brownieae, Carphiformes, Tessellatae and Scleria of Kern (1961, 1974); subgenus Scleria, series Tessellatae and Elatae of Koyama (1961), subgenus Scleria (pro parte, species 28-55 and 57 of Robinson (1966).

Subgenus Scleria, section Acriulus includes subgenus Acriulus of Clarke (1902); *Acriulus* of Clarke (1908) and subgenus Scleria (species 56) of Robinson (1966).
Subgenus Scleria, section Schizolepis includes
subgenus Scleria, section Schizolepis of Clarke
(1894); subgenus Schizolepis of Clarke (1898,
1902, 1908); section Schizolepis of Core
(1936) and of Piérart (1951); section
Schizolepis of Nelmes (1956) and subgenus
Scleria (species 58) of Robinson (1966).

Subgenus Scleria, section Ophryoscleria
includes section Ophryoscleria of Clarke (1900);
subgenus Ophryoscleria of Clarke (1902, 1908);
section Ophryoscleria of Core (1936) and of
Piérart (1951); section Ophryoscleria of
Nelmes (1956) and subgenus Ophryoscleria of
Robinson (1966).
ABBREVIATIONS USED IN PLAN DRAWINGS

ac - air cavity
aer - aerenchyma
c - cortex
cc - central cylinder
ch - chlorenchyma
en - endodermis
end - endodermoid region
ep - epidermis
gc - guard cell
hb - hair base
hyp - hypodermis (= outer cortex)
ic - inner cortex
is - inner sheath of vascular bundle
ls - leaf sheath
mx - metaxylem
mxv - metaxylem vessel
oc - outer cortex (= middle cortex)
os - outer sheath of vascular bundle
p - pericycle
pal - palisade chlorenchyma
ph - phloem
px - protoxylem
pxv - protoxylem vessel
sb - silica body
st - sieve tube
sub c - subsidiary cell
tc - translucent cell
tr - trabecula
vb - vascular bundle
vp - vascular plexus
KEY TO SHADING OF PLAN DRAWINGS

parenchyma

chlorenchyma of culms (leaf chlorenchyma not shown)

sclerenchyma

phloem

xylem (proto- and metaxylem not distinguished in plan drawings of organs with collateral and amphivasal vascular bundles)

protoxylem

metaxylem

distinguished in drawings of roots only

epidermis with stoma

endodermis of root
Fig. 25. Camera-lucida drawings of T/S root of Scleria achtenii (Ward 7743): a, plan; b, detail of fibrous inner cortex, endodermis and polyarch stele.
Fig. 26. Camera-lucida drawings of T/S root of *Scleria angusta* (Ward 8083): a, plan; b, detail of outer cortical region showing fibrous hypodermal zone (outer cortex) and parenchyma cells of trabecula of middle cortex; c, detail of fibrous inner cortex, endodermis and polyarch stele.
Fig. 27. Camera-lucida drawings of T/S young tuberous rhizome of *Scleria woodii* (Hennessy 409): a, plan; b and c, details of peripheral zone; d, detail of amphivasal vascular bundle.
Fig. 28. Camera-lucida drawings of T/S culm, leaf and rhizome of *Scleria welwitschii* (Hennessy 408): a, plan of culm; b, plan of flanged V-shaped amphistomatic lamina with bulliform cells restricted to median adaxial groove; c, plan of part of heavily lignified rhizome.
Fig. 29. Camera-lucida drawings of T/S rhizome of *Scleria poaeformis* (Hennessy 374):
a, outline; b, plan; c, detail of amphivasal vascular bundle.
Fig. 30. Camera-lucida drawings of T/S leaf and sobole of *Scleria drègeana* (Moll 1424): a, plan of lamina; b, outline of sobole within leaf-sheath; c, plan of sobole showing cortical air cavities and collateral vascular bundle.
Fig. 31. Camera-lucida drawings of T/S culm of *Scleria bulbifera* (Hennessy 407): a, outline; b, plan of corner; c, detail of two vascular bundles with their associated sclerenchyma, chlorenchyma and translucent ground tissue.
Fig. 32. Camera-lucida drawings of T/S culm of Scleria melanomphala (Ward 7708): a, outline of culm within leaf-sheath; b, plan of corner showing distribution of chlorenchyma, collateral vascular bundles and mechanical tissue; c, detail of stoma.
Fig. 33. Camera-lucida drawings of T/S culm of \textit{Scleria angusta} (Ward 8083): a, plan showing distribution of vascular bundles and centrally situated schizogenous air cavities; b, plan of corner showing distribution of chlorenchyma, collateral vascular bundles and mechanical tissue; c, detail of stoma.
Fig. 34. Camera-lucida drawings of T/S leaf and culm of *Scleria woodii* (Hennessy 409): a, plan of V-shaped amphistomatic lamina with bulliform cells restricted to median adaxial groove; b, plan of culm; c, detail of lamina showing an adaxial stoma, chlorenchyma, vascular bundle with adaxial and abaxial sclerenchyma girders and conical silica bodies in epidermal cells overlying the sclerenchyma girders.
Fig. 35. Camera-lucida drawing of T/S flanged V-shaped amphistomatic lamina of *Scleria aterrima* (Strey 7035), showing distribution of vascular bundles and their associated sclerenchyma and large translucent cells subjacent to the adaxial epidermis.
Fig. 36. Camera-lucida drawings of T/S leaf of *Scleria achtenii* (*Ward* 7743): a, plan of flanged V-shaped hypostomatic lamina; b, detail showing vascular bundle with its associated sclerenchyma girders.
4. Anatomy

4.1. Subterranean organs

4.1.1. Roots

The rooting system of *Scleria* is adventitious. No description of root anatomy of the genus has been found in the literature.

As a source of taxonomically useful information root anatomy has proved disappointing. The stelar anatomy of the roots of all the species investigated is fundamentally similar. Differences in position of metaxylem vessels are associated with root diameter, the same species sometimes having metaxylem vessels distributed in a ring around a central medulla in large diameter roots and occupying a central position in small diameter roots. Slight variations in cortical anatomy were observed which are associated with the age of the root (Beckel, 1956).
General Description (Refer Figs. 25, 26, 37)

Diameter from less than 1 mm to 5 mm.

Epidermis (piliferous layer) single layered, of small, more-or-less isodiametric parenchyma cells, not persisting in mature roots. Hypodermis (exodermis) of one or two layers of lignified cells, polygonal to isodiametric in transverse section, axially elongated. Cortex of three zones of radially arranged cells, the number of layers differing according to the diameter of the roots; outer zone not always clearly defined, consisting of few layers of compact polygonal parenchyma cells with small intercellular air spaces; middle zone in very young roots of large rounded parenchyma cells with small intercellular air spaces, in older roots the cells of some of the radiating rows become tangentially stretched and contrast conspicuously with the rounded cells of remaining rows and eventually the tangentially stretched cells break down to produce large air cavities and the rounded cells persist as uniseriate trabeculae which traverse the lacunar middle cortex radially; inner
Fig. 37. Photomicrographs of transverse sections of roots of *Scleria* spp. 1, *S. poaeformis* X 20; 2, *S. poaeformis* X 128; 3, *S. melanomphala* X 20; 4, *S. natalensis* X 20; 5, *S. achtenii* X 52; 6, *S. foliosa* X 20.

Note: cortex differentiated into three zones, an outer hypodermal zone 1 - several cell layers broad, of lignified cells; a middle zone of thin walled cells which break down leaving residual radial trabeculae between large air cavities; an inner zone of lignified cells, very regularly arranged in radial rows, separated from the stele by an endodermis the cells of which may be evenly lignified (2) or the outer tangential wall may be thin (5): polyarch stele with metaxylem vessels situated in a ring (1, 2, 3, 4) or centrally situated (5, 6); secretory cells with dark-stained contents most numerous in stele.

1, 2, from *Hennessy* 374; 3, from *Ward* 7708; 4, from *Hennessy* 372; 5, from *Ward* 7743; 6, from *Merxmüller* and *Giess* 2081.
zone 3 - 5 cell layers wide, of lignified cells of smaller diameter than cells of middle zone, regularly arranged with small or no intercellular air spaces. Endodermis clearly defined, the cells in transverse section taller than broad, axially elongated to $\pm 3$ times their diameter; either heavily and evenly lignified with lumina greatly reduced, or with inner tangential wall and radial walls heavily lignified and outer tangential wall only slightly lignified (U-shaped thickening). Stele polyarch, protostelic with fibrous pith in roots of large diameter.

Pericycle either an uninterrupted single layer of small, axially slightly elongated, thin- or thick-walled cells, or the layer interrupted by protoxylem vessels abutting directly on the endodermis. Number of alternating phloem and protoxylem groups variable even within the same species depending upon the diameter of the root; protoxylem vessels spirally thickened, of small diameter compared with that of metaxylem vessels. Metaxylem
in most species centrally situated, the vessel elements of very large diameter, with scalariform or reticulate thickening, several in large diameter roots or single in small diameter roots, or situated in a single peripheral ring and the medullary region fibrous. (In *S. pcaeformis* large diameter roots have the metaxylem vessels in a ring around a fibrous medulla and small, branch roots have a single central metaxylem vessel). End walls of xylem vessel elements + horizontal, simply perforate or scalariform. Secretory cells few or many, most numerous in pith of medullated roots, cells axially elongated, of small diameter.

4.1.2. **Stems**

On the basis of their vascular anatomy two fundamentally different kinds of underground stems are distinguishable in the Southern African representatives of the genus, rhizomes and soboles. **Rhizomes** show a range of morphological diversity but whether they have long or very abbreviated internodes, whether they are
straight or flexuous, whether they are horizontal or descending, whether they are more-or-less the same diameter throughout their length or variously swollen, whether they are hard and woody or soft and fleshy, they have *amphivasal* vascular bundles. *Soboles* which are subterranean horizontal propagative stems arising from culm-bases are distinguished by their possession of collateral vascular bundles.

The species of *Scleria* in our area fall into four categories on the basis of the type(s) of subterranean stems they possess or lack.

A. Those which have rhizomes and no other type of underground stem.

B. Those which have rhizomes and may also produce one or several short soboles.

C. Those which have no rhizomes, spreading exclusively by means of long, remarkably culm-like soboles.
D. Those which have no perennating stems (annual or ephemeral plants).

These four categories do not mirror taxonomic relationships.

The distribution of Southern African species among the four categories described above is shown in Table III.

4.1.2.1. Rhizomes, despite morphological differences and differences in the degree of lignification of the cortex and the ground tissue of the stele which may be associated with habitat, are fundamentally alike anatomically.

*General Description (Refer Figs. 27, 28, 29, 38, 39)*

*Epidermis* of a single layer of small cuboidal or slightly thick-walled cells, some at least containing amorphous silica or cone-shaped silica bodies. *Cortex* either uniform, of \( \pm \) polygonal
TABLE III. Distribution of Southern African species of *Scleria* among four categories based on the nature of their subterranean stems.

<table>
<thead>
<tr>
<th>CATEGORY</th>
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<th>SPECIES</th>
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<tbody>
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<td>Schizolepis</td>
<td>angusta</td>
</tr>
<tr>
<td></td>
<td>Acriulus</td>
<td>greigiifolia</td>
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<tr>
<td></td>
<td>Scleria</td>
<td>achtenii</td>
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<td></td>
<td>Scleria</td>
<td>unguiculata</td>
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<td>Scleria</td>
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<td></td>
<td>Scleria</td>
<td>natalensis</td>
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<td></td>
<td>Scleria</td>
<td>transvaalensis</td>
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<td>Scleria</td>
<td>melanomphala</td>
</tr>
<tr>
<td></td>
<td>Scleria</td>
<td>poaeformis</td>
</tr>
<tr>
<td></td>
<td>Hypoporum</td>
<td>bulbifera</td>
</tr>
<tr>
<td></td>
<td>Hypoporum</td>
<td>veseyfitzgeraldii</td>
</tr>
<tr>
<td></td>
<td>Hypoporum</td>
<td>welwitschii</td>
</tr>
<tr>
<td></td>
<td>Hypoporum</td>
<td>rehmannii</td>
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<tr>
<td></td>
<td>Hypoporum</td>
<td>longispiculata</td>
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<tr>
<td></td>
<td>Hypoporum</td>
<td>nutans</td>
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<td></td>
<td>Hypoporum</td>
<td>woodii</td>
</tr>
<tr>
<td></td>
<td>Hypoporum</td>
<td>dieterlenii</td>
</tr>
<tr>
<td>B (rhizomes &amp; soboles)</td>
<td>Hypoporum</td>
<td>aterrima</td>
</tr>
<tr>
<td></td>
<td>Hypoporum</td>
<td>drègeana</td>
</tr>
<tr>
<td>C (soboles only)</td>
<td>Hypoporum</td>
<td>sobolifer</td>
</tr>
<tr>
<td>D (none)</td>
<td>Scleria</td>
<td>foliosa</td>
</tr>
<tr>
<td></td>
<td>Scleria</td>
<td>lacustris</td>
</tr>
<tr>
<td></td>
<td>Hypoporum</td>
<td>pergracilis</td>
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</tbody>
</table>
Fig. 38. Photomicrographs of transverse sections of rhizomes of *Scleria* spp. 1, *S. bulbifera* X 52, material damaged in sectioning because outer cortex (right) of heavily silicified stone cells has torn away leaving (bottom left) endodermoid region only in places and within the stele the darkly stained crescentiform sclerenchyma caps of the inner vascular bundles also heavily silicified resulting in tearing of sections; 2, portion of rhizome of *S. drègeana* X 52, showing part of stele (left) and cortex (right), 3, portion of rhizome of *S. aterrima* X 52 showing part of stele (left) and cortex (right); 4, portion of rhizome of *S. veseyfitzgeraldii* X 52 showing part of stele (left) and cortex (right); 5, young tuberous rhizome of *S. woodii* X 20 parenchymatous except for 1 - few amphivasal vascular bundles (ringed); 6, portion of young tuberous rhizomes of *S. woodii* X 52 with the solitary amphivasal vascular bundle ringed.

Note: secretory cells with dark-staining contents present in all rhizomes.

1, from Hennessy 407; 2, from Vesey-Fitzgerald 10007; 3, from Ward 2924; 4, from Robinson 4220; 5, 6, from Hennessy 409.
Fig. 39. Photomicrographs of transverse section of rhizomes of *Scleria* spp. 1, portion of stele of *S. poaeformis* X 128, with amphivasal vascular bundles (left), peripheral vascular plexus in contact with lignified endodermoid region of cortex (right of centre) and portion of aerenchymatous cortex (right); 2, portion of peripheral region of cortex of *S. poaeformis* X 28, with aerenchyma (left) outer zone of parenchyma and distorted tissue of sheathing scale (right); 3, portion of rhizome of *S. angusta* X 52, showing part of stele (left), broad, heavily lignified endodermoid region and cortical tissue (right); 4, portion of rhizome of *S. natalensis* X 20, showing part of stele (left), narrow endodermoid region and cortex (right); 5, portion of rhizome of *S. achtenii* X 20 showing part of stele (left), the amphivasal vascular bundles towards the centre with heavy crescentiform sclerenchyma caps, and part of cortex (right); 6, portion of rhizome of *S. unguiculata* X 20 showing part of stele and cortex and T/S fibrous root (top left).

Note: secretory cells with dark-staining contents present in all rhizomes.

1, 2, from Hennessy 374; 3, from Ward 8083; 4, from Hennessy 372; 5, from Ward 7743;
lignified cells or more often of two zones; bounded on the inside by an endodermoid region: outer cortex narrow or broad, compact, usually without air-spaces, parenchymatous or the cells lignified to a lesser or greater degree (stone cells present in some species and the walls of such cells silicified): inner cortex often broader than outer, of rounded parenchyma cells with small intercellular air spaces or of stellately lobed cells with large interstitial air cavities; secretory cells sometimes present in inner cortex, few: in young, tuberous rhizomes of S. woodii, S. dieterlenii ground tissue parenchymatous throughout and no endodermoid region or stelar region distinguishable. Endodermoid region of 1 - 10 or more layers of axially elongate, heavily lignified cells; in those
rhizomes with broad endodermoid zone, cells of layer nearest the stele either more heavily lignified than those nearer cortex or physiologically differentiated from them as evidenced by different staining reaction with safranin.

Stele not usually delimited by a clearly-defined pericycle; if recognisable the pericycle of a single or double, interrupted layer of ± isodiametric cells: periphery of stele occupied by an almost complete ring of vascular elements several layers broad, comprising an anastomosing system of xylem and phloem elements, the "vascular plexus" of Plowman (1906). In the vascular plexus phloem elements lie external to xylem elements. Internal to the vascular plexus is ground tissue in which numerous vascular bundles are embedded. Ground tissue wholly parenchymatous
or wholly lightly or heavily lignified, or zones of thin-walled and lignified cells differentiated: secretory cells present, usually numerous.

Vascular bundles numerous in mature rhizomes, their courses through the ground tissue tortuous so that very few are seen in transverse view in a transverse section of the rhizome, most being cut obliquely; distributed throughout ground tissue with peripheral bundles less crowded than central ones, or absent from central (medullary) region; peripheral bundles smaller than those towards centre; circular or oval in T/S, amphivasal with protoxylem pole directed towards centre of rhizome; protoxylem vessels spirally thickened, metaxylem vessels reticulate or scalariform; fibrous bundle sheaths usually present, sometimes absent from peripheral bundles; sheaths often broader
adjacent protoxylem than metaxylem pole: in species with fibrous ground-tissue bundle sheaths distinguishable because sheath fibres more heavily lignified than cells of ground-tissue.

4.1.2.2. Soboles

Of the three Southern African species of Scleria which have been found to possess soboles, two, S. drègeana and S. aterrima, also have abbreviated rhizomes. The rhizomes are so short that the plants appear to be caespitose. Production of soboles in these two species seems, from examination of a number of herbarium specimens to be a rare occurrence. However, many herbarium specimens are incomplete with regard to their subterranean organs either because the collector has failed to dig the specimen, or because fragile structures such as the
soboles of these species have been inadvertently detached in handling. I believe that soboles occur more frequently than present evidence suggests.

Robinson (1966) writing of the species of Scleria in the "Flora Zambesiaca" area, has noted the presence of what I have designated soboles in S. aterrima (as S. catophylla C.B.C.I.) and S. polyrrhiza E.A. Robinson. In a note following his description of the latter species, he compares it with S. woodii (a rhizomatous species in which the young rhizome is softly tuberous, composed of parenchymatous storage tissue and a few amphivasal bundles) and S. hilsenbergii Ridley, a species which has not yet been found outside Madagascar. Of S. polyrrhiza he writes, "This species comes very close to the polymorphic S. woodii, but differs from it in its root (sic) system" Of S. hilsenbergii he says, "It
is true that none of the eleven sheets of *S. hilsenbergii* examined by me in the Paris Herbarium had any signs of the storage rhizomes so characteristic of *S. polyrrhiza*, but the very greatest care is needed to gather the plant intact, and, where a storage rhizome (sic) is not suspected to exist, it is unlikely to be found". He concluded, "In these geophytic species, by the time the achenes have reached maturity the old (storage) rhizomes have usually begun to disintegrate".

Writing of the distinction between *S. aterrima* (as *S. catophy* and *S. nutans* he said that the former may always be distinguished from the latter "by ........ and by its many slender rhizomes, which descend obliquely and rise up again to form new plants at a distance of up to 10 cm from the parent plant, which dies at the end of its flowering season. Only
after the new plant is established do they harden off, and even then can hardly be mistaken for the woody storage-rhizomes of *S. nutans*.

It is noteworthy that Robinson, with no knowledge of the anatomy of the subterranean stems, was able to distinguish true rhizomes from soboles on morphological grounds alone. Although his terminology is confused, his concept of the distinction between the two types of stem is clear.

The third soboliferous species in our area, *S. sobolifer* differs from the other two in that it has no rhizome at all, habitually spreading and perennating by means of long, tough, culm-like soboles. Although there is no fundamental difference in the vascular anatomy of the three species, there are individual differences in tissue distribution and in the amount of
Fig. 40. Photomicrographs of transverse sections of soboles of *Scleria* spp. 1, *S. sobolifer* X 52; 2, *S. sobolifer* X 128; 3, *S. drègeana* X 52; 4, *S. drègeana* X 128; 5, *S. aterrima* X 52; 6, *S. aterrima* X 128.

Note: collateral vascular bundles in all three species; vascular bundles scattered throughout ground tissue in *S. sobolifer*, confined to central region of *S. drègeana*, arranged in a ring (cylinder) in *S. aterrima*; schizogenous air cavities in centre in *S. sobolifer*, in a ring (cylinder) outside the central vascular region in *S. drègeana*, in centre and outside the vascular ring in *S. aterrima*; mechanical tissue sheathing each vascular bundle in *S. sobolifer*, the sheaths of adjacent bundles not confluent, absent from *S. drègeana*, sheathing each vascular bundle in *S. aterrima*, the sheaths of adjacent bundles confluent; outline of sobole trigonéus (culm-like) in *S. sobolifer*, basically terete in *S. drègeana* and *S. aterrima* (distortion the result of imperfect reconstitution of material taken from dried herbarium specimens); secretory cells with dark-staining contents present in all three species.

1, 2, from Ward 4737; 3, 4, from Moll 1424; 5, 6, from Robinson 5055
fibrous tissue which distinguish them and which are clearly shown in Fig. 40.

Description (Refer Figs. 30, 40)

Shape in transverse section basically terete in S. aterrima and S. drègeana, obtusely triangular in S. sobolifer.

Epidermis of brick-shaped, axially slightly elongate thin-walled cells of similar size to subjacent cells of ground-tissue. Ground-tissue fundamentally parenchymatous, breaking down to form air-cavities in different regions relative to the vascular tissue in the three species. Vascular bundles in a single ring in S. aterrima, a roughly double ring in S. drègeana and more-or-less evenly distributed through the ground-tissue in S. sobolifer, oval or rhomboid in T/S, collateral, with the phloem pole
directed towards the periphery of the stem; fibrous bundle sheath lacking in S. drègeana, many-layered in S. sobolifer and in S. aterrima many layered and the sheaths of adjacent bundles confluent so that the ring of bundles is mechanically supported in a sclerenchymatous cylinder.

4.2. Culms

Although there are individual differences in culm anatomy among Southern African species of Scleria, there is, except for the occurrence of some amphivasal vascular bundles in one species, S. greigiifolia, overall similarity among them.

The culm in transverse section is triangular, with some slight variation in the acuteness of the angles, most being more-or-less obtuse. There is a suggestion of a wing at one angle of the culms of S. greigiifolia (Fig. 42, 3) and S. foliosa. The sides are usually straight or slightly convex and a tendency exists for one side to be slightly shorter than the other two.
Fig. 41. Photomicrographs of transverse sections of culms of Scleria spp. 1, S. woodii X 52; 2, S. woodii X 128; 3, S. welwitschii X 128; 4, S. bulbifera X 128; 5, S. dieterlenii X 128; 6, S. pergracilis var. brachystachys X 128.

Note: variation in acuteness of angles; few or no central air cavities; absence of "ring" of mechanical tissue separating chlorenchyma from translucent ground tissue; thick-walled (silicified) unicellular epidermal hair in 5; enlarged schizolysigenous protoxylem cavities of larger vascular bundles in 6, and in some deeply-seated vascular bundles in 4; conical silica bodies clearly visible in 2 in epidermal cells overlying sclerenchyma strands/girders.

1, 2, from Hennessy 409; 3, from Hennessy 408; 4, from Hennessy 407; 5, from Hoener 2040; 6, from Pentz and Acocks 10777.
Fig. 42. Photomicrographs of transverse sections of culms of *Scleria* spp. 1, corner of culm of *S. angusta* X 52; 2, portion of side of culm of *S. poaeformis* X 52; 3, portion of culm of *S. greigiifolia* X 20; 4, corner of culm of *S. greigiifolia* X 52; 5, corner of culm of *S. natalensis* X 52; 6, portion of side of culm of *S. lacustris* X 128.

Note: net-type of translucent ground tissue in 1, 2, 3; mechanical tissue forming a continuous "ring" separating chlorenchyma from translucent ground tissue in 1, 2, 3, 4; very heavy sclerenchyma sheaths/girders associated with vascular bundles in 6; relatively little development of mechanical tissue in 5 except in corner; enlarged schizolysigenous protoxylem cavities of largest vascular bundles in 1, 2, 3, 6; presence of some amphivasal vascular bundles in *S. greigiifolia* (3, 4); few or no secretory cells with dark-staining contents.

1, from Ward 8083; 2, from Hennessy 374; 3, 4, from P.G. Stewart 293; 5, from Hennessy 372; 6, from P.A. Smith 2718.
All species have a subepidermal chlorenchymatous zone interrupted by girders or strands of fibrous mechanical tissue associated with peripheral vascular bundles. In the species with the largest culms, *S. poaeformis*, there is a narrow hypodermal zone of sclerenchyma between neighbouring girders and strands which is continuous except where interrupted by stomata. The amount of fibrous tissue varies from species to species and is often better developed towards the base than the apex of the culms. In three species, *S. poaeformis*, *S. angusta* and *S. greigiifolia* the mechanical tissue links adjacent vascular bundles immediately inside the chlorenchymatous zone (Fig. 42, 1-4). This "ring" of sclerenchyma is best-developed in *S. greigiifolia*. In *S. lacustris* the sclerenchyma associated with the vascular bundles is very well developed (Fig. 42, 6), forming a heavy sheath around the peripheral vascular bundles, but each vascular bundle together with its sheath remains discrete. Particularly massive girders occur in *S. bulbifera*, *S. vescyfitzgeraldii* and *S. longispiculata*, and *S. nutans* is unusual in that the most deeply seated vascular bundles have very heavy fibrous sheaths, while the peripheral vascular bundles have a lesser amount of associated sclerenchyma.
The chlorenchyma of the culm is similar to that of the leaf of the same species. The type of chlorenchyma present in each species is tabulated in Table V.

Translucent ground tissue is present towards and in the centre of the culms of all species and in most comprises large round parenchyma cells with small or large intercellular air spaces. In four species, *S. angusta*, *S. greigiifolia*, *S. poaeformis* (Fig. 42) and *S. unguiculata*, which are hydrophilous plants, the translucent ground tissue consists of a three-dimensional network of narrow, elongated parenchyma cells, designated by Metcalfe (1971) as "net-type" ground tissue.

In those Southern African species belonging to sections *Schizolepis*, *Acriulus* and *Scleria*, as circumscribed by Clarke (1902), the central ground tissue breaks down to form large air cavities. Among the Southern African species in section *Hypoporum*, some have solid culms, some have a few, rather small central air cavities and one, *S. rehmannii* has large schizogenous central air cavities. It is perhaps significant that this species is hydrophilous and that stellate chlorenchyma is present in leaf and culm. Although
Table IV. Synopsis of features of interest in the anatomy of the Sclerenchyma Associated with Schizogenous Peripheral vascular bundles

<table>
<thead>
<tr>
<th></th>
<th>Discrete girders/strands/caps</th>
<th>Laterally confluent, uniting adjacent v.b's. in a ring</th>
<th>Schizogenous Peripheral</th>
</tr>
</thead>
<tbody>
<tr>
<td>S. angusta</td>
<td></td>
<td>X</td>
<td></td>
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<tr>
<td>S. greigiiifolia</td>
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<td>X</td>
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<td>S. poaeformis</td>
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<td>X</td>
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<td>S. melanomphala</td>
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<td>S. transvaalensis</td>
<td>X</td>
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<td></td>
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<tr>
<td>S. natalensis</td>
<td>X</td>
<td></td>
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</tr>
<tr>
<td>S. lagoensis</td>
<td>X</td>
<td></td>
<td></td>
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<tr>
<td>S. achtenii</td>
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<td></td>
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<td>S. unguiculata</td>
<td>X</td>
<td></td>
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<tr>
<td>S. foliosa</td>
<td>X</td>
<td></td>
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<tr>
<td>S. lacostris</td>
<td>massive, almost confluent</td>
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<tr>
<td>S. sobolifer</td>
<td>X</td>
<td></td>
<td></td>
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<tr>
<td>S. drègeana</td>
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<td>S. dieterlenii</td>
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<td>S. pergracilis</td>
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<td>S. woodii</td>
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<td>S. bulbifera</td>
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<td>S. veseyfitzgeraldii</td>
<td>X</td>
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<tr>
<td>S. nutans</td>
<td>massive</td>
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<td>S. aterrima</td>
<td>X</td>
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<td>S. welwitschii</td>
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<td>S. longispiculata</td>
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<tr>
<td>S. rehmannii</td>
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culms of Southern African species of Scleria

<table>
<thead>
<tr>
<th>Air Cavities</th>
<th>Central</th>
<th>Net type central ground tissue</th>
<th>Vascular bundles</th>
</tr>
</thead>
<tbody>
<tr>
<td>Enlarged protoxylem cavities of largest v.b's.</td>
<td>Present</td>
<td>Absent</td>
<td>Collateral</td>
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<tr>
<td>X</td>
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S. lacustris is reported by Robinson (1966) to have hollow culms, the culms of the material examined in this study (P.A. Smith 2118) had remarkably few, small, central air cavities. It is probable that in this aquatic species the mature culms, or at least their basal parts, are hollow. The Smith gathering examined was immature, lacking fully-hardened achenes.

Peripheral, extravascular air cavities of schizogenous origin are rare and have been observed in S. poaeformis, where small cavities appear in the stellate chlorenchyma (Fig. 42 2). Metcalfe (1971) in his description of culm anatomy of S. greigiifolia (as Acriulus greigiifolius) mentions slit-shaped air cavities "embedded in peripheral sclerenchyma, formed by breakdown of two distinct types of cells, one subcircular and the other in the form of narrow, lobed cells". The material examined in this study shows no evidence of air cavities of this nature. It has however been observed that the schizolysigenous protoxylem cavities of the peripherally situated collateral vascular bundles of S. greigiifolia are large, especially those of the largest bundles situated near each angle (Fig. 42, 4). This feature is shared by several other species (Table IV) although it is less marked in the other
species except perhaps in *S. pergracilis*
(Fig. 41, 6). It is my opinion that Metcalfe, perhaps because of inadequate material, failed to recognise the enlarged protoxylem cavities of *S. greigiifolia* for what they are, thereby attributing to *S. greigiifolia* an unique type of peripheral air cavity which it perhaps does not possess.

The only features of culm anatomy which *S. greigiifolia* possesses which are not shared by at least some other Southern African species of *Scleria*, are the rather odd admixture of collateral and amphivasal vascular bundles and the absence of fibrous bundle sheaths. The vascular bundles of the culms of all other local species are strictly collateral. *S. greigiifolia* has a "ring" of collateral bundles towards the periphery of the culm, the largest of which are in the angles. Other vascular bundles, especially the smaller ones, are strictly amphivasal, and others are transitional between the two types with the metaxytem arranged in a broad V with the phloem between the open arms of the V.
General Description (Refer Figs. 28, 31, 32, 33, 41, 42)

**Epidermis** of small, more-or-less isodiametric or brick-shaped thin-walled or lignified, cuticularised cells; stomata usually few.

**Hypodermis** in *S. poaeformis* of 1 - few layers of axially elongate sclerenchyma. **Chlorenchyma** limited to peripheral zone, interrupted by sclerenchyma girders and strands associated with peripheral vascular bundles; substomatal air cavities small; schizogenous air cavities small, few, in stellate chlorenchyma of *S. poaeformis*.

**Translucent ground tissue** parenchymatous, cells small or large, round or polygonal with small or large intercellular air spaces, or, in *S. angusta*, *S. greigiifolia*, *S. poaeformis* and *S. unguiculata* of narrow elongated cells forming a three-dimensional meshwork of fine strands. **Air cavities** absent, few and small, or many and large, situated towards centre of culm. **Vascular bundles** collateral or, in *S. greigiifolia*, collateral and amphivasal; many, more congested towards periphery than towards centre of culm from which they are usually absent; some peripheral vascular bundles relatively small; bundle sheaths two, the inner sclerenchymatous, the outer parenchymatous, continuous around associated sclerenchyma in some species and not thus continuous in others, as in the leaves (Table V);
sclerenchyma sheath absent from culm bundles of \textit{S. greigiifolia}; phloem pole directed towards periphery. Mechanical tissue associated with vascular bundles sclerenchymatous, most fully developed towards periphery especially near angles; not symmetrical in the three angles of all species; peripheral vascular bundles often with massive girders or caps and strands at phloem poles, caps at xylem poles, sometimes the whole bundle surrounded by a sclerenchyma sheath one to several layers broad; adjacent sub-peripheral bundles of \textit{S. angusta}, \textit{S. greigiifolia} and \textit{S. poaeiformis} more-or-less united by a "ring" of sclerenchyma several to many layers broad; more deeply seated vascular bundles with narrow sclerenchyma caps at one or both poles. Secretory cells few or many, extrafascicular in chlorenchyma and translucent ground tissue and intrafascicular in xylem. Silica bodies present in epidermal cells of all species; conical bodies in cells overlying sclerenchyma and amorphous masses in other epidermal cells. Hairs present in some species; unicellular, silicified, of epidermal orgin (Fig. 41, 5).
Fig. 43. Camera-lucida drawings of lamina profiles of Southern African species of *Scleria* to show relative sizes, and indicating, semi-diagrammatically, distribution of bulliform epidermal cells, translucent hypodermal cells, schizogenous air-cavities, mechanical tissue and vascular bundles.

1. *S. greigiifolia* K.D. Huntley 781
2. *S. poaeformis* E.F. Hennessy 374
3. *S. welwitschii* E.F. Hennessy 408
4. *S. woodii* E.F. Hennessy 406
5. *S. aterrima* M. McCallum-Webster s.n.
6. *S. nutans* T.H. Arnold 796
7. *S. rehmannii* de Winter and Marais 5049
8. *S. longispiculata* Story 6467
10. *S. pergracilis* Pentz and Acocks 10277
11. *S. drègeana* Acocks 10850
12. *S. veseyfitzgeraldii* Robinson 4220
13. *S. dieterlenii* Hoener 2040
14. *S. sobolifer* T.H. Arnold 467
15. *S. foliosa* Merxmüller and Giess 2081
16. *S. lacustris* P.A. Smith 2718
17. *S. melanomphala* Ward 7708
18. *S. angusta* Ward 8083
19. *S. natalensis* E.F. Hennessy 372
20. *S. unguiculata* P.A. Smith 1980
21. *S. achtienii* Ward 7710
22. *S. lagoensis* Compton 29644
23. *S. transvaalensis* P.J. Müller 2031
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Table V. Synopsis of features of interest in lamina anatomy of leaves of Southern African species of *Scleria.*
Fig. 44. Photomicrographs of transverse sections of leaves of *Scleria* spp. 1, midrib region of *S. poaeformis* X 20 showing median adaxial bulliform cells and subjacent translucent cells; 2, part of lamina of *S. poaeformis* X 20 showing distribution of vascular bundles on both sides and in the trabeculae of translucent cells which traverse the lamina, large air cavities, scattered remnants of stellate, silicified translucent mesophyll cells, and chlorenchyma limited to a narrow zone on both sides of the lamina; 3, enlarged view (X 52) of part of abaxial side of lamina of *S. poaeformis* showing outer parenchymatous and inner schlerenchymatous bundle-sheaths, several rows of palisade chlorenchyma and secretory cells with darkly-stained contents; 4, midrib region of *S. greigiifolia* X 52 showing median adaxial bulliform cells; 5, part of lamina of *S. greigiifolia* X 52 showing distribution pattern of vascular bundles and chlorenchyma; 6, enlarged view (X 128) of part of lamina of *S. greigiifolia* showing major vascular bundle with adaxial and abaxial sclerenchyma girders and outer and inner bundle-sheaths, adaxial and abaxial palisade chlorenchyma and stellate chlorenchyma.

1,2,3, from Hennessy 374; 4,5,6, from K.D. Huntley 781.
Fig. 45. Photomicrographs of transverse sections of leaves of *Scleria* spp. 1, *S. angusta* X 128, midrib region near leaf apex showing translucent cells subjacent median adaxial bulliform cells and bases of three epidermal hairs, two adaxial and one median abaxial; 2, *S. angusta* X 52, in region of junction of lamina proper (left), and marginal wing (right) showing adaxial bulliform cells of true lamina and groups of abaxial bulliform cells of wing; 3, *S. melanomphala* X 52 in angle region showing major vascular bundle of angle with adaxial and abaxial sclerenchyma girders; 4, *S. melanomphala* X 52, in angle region showing major vascular bundle of angle with adaxial sclerenchyma strand and abaxial sclerenchyma girder; 5, *S. melanomphala* X 52, portion of lamina of wet form showing air cavities resulting from breakdown of stellate translucent mesophyll and trabeculae of translucent cells traversing lamina; 6, portion of winged leaf sheath of *S. lacustris* X 20, showing wing.

1,2 from Ward 8603; 3,4 from Ward 7708; 5 from Ward s.n.; 6 from P.A. Smith 2718.
Fig. 46. Photomicrographs of transverse sections of leaves of *Scleria* spp. 1, portion of lamina of *S. lacustris* X 128, showing stellate chlorenchyma; 2, marginal region of lamina of *S. foliosa* X 128, showing stellate chlorenchyma; 3, angle region of lamina of *S. achtenii* X 52, showing adaxial sclerenchyma strand remote from major vascular bundle of angle region and the intervening tissue chlorophyllous; 4, angle region of lamina of *S. natalensis* X 52, showing the same features as 3; 5, angle region of lamina of *S. transvaalensis* X 52, showing the same features as 3 & 4; 6 angle region of lamina of *S. transvaalensis* X 52, showing translucent cells between adaxial sclerenchyma strand and vascular bundle.

1, from P.A. Smith 2718; 2, from Merxmüller and Giess 2081; 3 from Ward 7743; 4, from Hennessy 372; 5, from Arnold 336; 6, from P.J. Müller 2031.
Fig. 47. Photomicrographs of transverse sections of leaves of *Scleria* spp. 1, *S. woodii* X 52, V-shaped lamina with bulliform cells restricted to median adaxial groove, adaxial and abaxial epidermal cells equal in size; 2, *S. welwitschii* X 52, flanged V-shaped lamina with bulliform cells restricted to median adaxial groove, adaxial and abaxial epidermal cells equal in size; 3, *S. drègeana* X 52, flanged V-shaped lamina with bulliform cells in median adaxial groove and in intercostal regions of adaxial epidermis; 4, *S. drègeana* X 128, part of lamina showing amorphous silica bodies in bulliform adaxial epidermal cells and uniform chlorenchyma; 5, *S. aterrima* X 20, showing flanged V-shaped lamina, translucent cells subjacent adaxial epidermal cells in median and intercostal regions and several hair-bases; 6, *S. nutans* X 128, lamina near margin showing adaxial intercostal bulliform cells, clearly differentiated adaxial and abaxial palisade mesophyll and the dense nature of the chlorenchyma.

1, from Hennessy 409; 2, from Hennessy 408; 3,4, from L. Smook 1055; 5, from M. McCallum-Webster s.n.; 6, from Arnold 786.
4.3. **Leaves**

Differences in anatomical structure of leaves of Southern African species of *Scleria* appear to be associated with the habitats of the plants. Lamina profiles of all Southern African species are shown in Fig. 43, and anatomical features of the laminae of these species are summarised in Table V and illustrated in Figs. 28, 34, 35, 36, 44, 45, 46, 47. Those perennial species which inhabit more-or-less permanently wet habitats in open, frost-free areas, *S. poaeformis*, *S. greigiifolia*, *S. melanomphala*, and the annual aquatic species *S. lacustris* have broad leaves, in which the mesophyll is differentiated into palisade and more-or-less well-developed aerenchyma in the form of lobate or stellate cells which in *S. poaeformis* and *S. lacustris* break down to form large air cavities. *Scleria foliosa*, another, less robust annual species, of seasonally wet habitats, has less broad leaves but also possesses palisade and stellate mesophyll and schizogenous air cavities. The stellate mesophyll of *S. greigiifolia* in the the specimens examined remains intact. In *S. melanomphala* only those specimens collected from truly wet localities have stellate mesophyll, while those from slightly drier localities have spongy mesophyll of the more
Koyama (1967) tentatively classified members of the Sclerieae into three types on the basis of mesophyll structure: Type A in which the mesophyll is not differentiated into palisade and spongy portions (a condition considered by him to be the least specialised); Type B in which the mesophyll is differentiated into palisade and spongy portions and Type C in which the mesophyll is differentiated into palisade and spongy portions and the cells of the spongy portion are markedly lobate or stellate with large intercellular air spaces, which he considers to be the most specialised type. Using his criteria, *S. poaeformis*, *S. greigiifolia*, *S. lacustris* and *S. foliosa* belong to Type C and *S. melanomphala*, depending upon its habitat belongs to either Type B or Type C. This flexibility indicates that production of Type C mesophyll in *S. melanomphala* may be a response dictated by ecological factors (Kawase and Whitmoyer, 1980).
Another broad-leaved species which occupies permanently wet habitats is the shade-dwelling swamp-forest species, S. angusta. Anatomically the leaf is distinguished from the leaves of other species which are fundamentally similar by the possession of wings which extend beyond the true margin on each side of the lamina. Several other species from areas outside Southern Africa have such winged leaves and as far as I am able to determine all are shade-dwellers, which suggests that wing production with its associated anatomical peculiarities may be a device to increase the photosynthetic capacity of the plants in the low light intensities of their forest environment by increasing leaf surface area and volume.

Anatomical and morphological evidence (Fig. 3 G) suggests that the wing may have originated by lateral growth of laminar tissue in the region external to the major marginal vein, the new tissue being supplied with ramuli from the main marginal vein. Since the orientation of the vascular bundles in the wing varies, some bundles having their phloem poles directed towards the abaxial surface
Fig. 48. A, diagrammatic representation of T/S lamina of Scleria angusta; B, putative interpretation of structure of lateral extension ("wing").

**KEY.**
- **sclerenchyma**
- **xylem**
- **stoma**
- **bulliform cells**
- **midrib**
(normal), some having their phloem poles directed towards the adaxial surface (inverted) and some bundles lying obliquely, and since the wing is amphistomatic whereas the lamina proper is hypostomatic it is suggested that there has been infolding of the new tissue and connation in the plane of the contact faces. This hypothesis is illustrated diagrammatically in Fig. 48.

The Southern African species whose leaf anatomy except for the absence of wings is fundamentally similar to that of S. angusta are are S. transvaalensis, S. natalensis, S. achtenii S. lagoensis and S. unguiculata. All but one are perennial plants of warm or at least partially sheltered damp habitats whose aerial parts do not usually die back in winter. The exception is S. transvaalensis, whose aerial parts may, in the less favourable habitats in which it occurs in parts of the Transvaal, die back in winter. The most striking anatomical character which these species, S. angusta and S. melanomphala have in common is that except for the region overlying the sclerenchyma strands or girders of major vascular bundles, and the extreme marginal area, the adaxial epidermis is wholly bulliform. Such leaves are in effect hypostomatic. All have both palisade and spongy mesophyll of the
type designated by Koyama (1967) as Type B, although one species, *S. unguiculata* has some markedly lobate cells in the spongy tissue such as are characteristic of the Type C condition. The laminas of all five species and of *S. angusta* are thickest in the angle region and the major vascular bundle in the angle has an adaxial sclerenchyma strand remote from the bundle cap. This feature is also shared by the previously mentioned species, *S. lacustris*, and by some specimens of *S. melanomphala*. The leaves of some, but not all, plants of *S. angusta* and *S. transvaalensis* have large translucent cells subjacent to the adaxial epidermis in the median groove and in the angle region, a feature shared by *S. lacustris* and in a more extreme form, *S. poaeformis* and some specimens of *S. melanomphala* of those species previously mentioned. In addition, *S. angusta* may have translucent cells subjacent the abaxial bulliform cells which are present near the true margin of the lamina.

With the exception of *S. lacustris* and *S. foliosa* which are annuals, all the species mentioned thus far are more-or-less robust perennials with evergreen (except *S. transvaalensis*) aerial parts and all except *S. transvaalensis* are restricted in their distribution to warm, wet, subtropical or tropical areas. They comprise all the Southern
African representatives of section *Scleria*, section *Acriulus* (*S. greigiifolia*) and section *Schizolepis* (*S. angusta*).

All other species in Southern Africa fall within section *Hypoporum* and with the exception of *S. pergracilis* var. *brachystachys* which is annual, all have perennial rootstocks and rather slender, annual aerial parts which die back under unfavourable climatic conditions.

Although several of these species have distinctive types of leaf anatomy few clearly defined groups can be discerned as there is intergradation between types.

All the species are amphistomatic. Two species, *S. woodii* and *S. pergracilis* var. *brachystachys* have V-shaped lamina profiles while all the others have flanged V-shaped profiles. The profiles of these two species differ in that the V-shaped profile of the leaf of *S. woodii* is narrow whereas that of *S. pergracilis* var. *brachystachys* is somewhat flattened. One species, *S. vesseylfitzgeraldii* has the arm of the flange much longer than the arm of the V whereas all others with flanged laminas have the arm of the V longer than or equalling the flange. Two
species, S. woodii and S. welwitschii have bulliform cells restricted to the median adaxial groove whereas all others have the adaxial epidermis bulliform except where interrupted by stomata and where overlying mechanical tissue. One species, S. aterrima, has translucent cells subjacent to the adaxial epidermis in the median groove and intercostal regions, which feature distinguishes this species from all others. Three species, S. pergracilis, S. welwitschii and some specimens of S. drègeana lack palisade mesophyll (mesophyll Type A of Koyama, 1967) while all others except S. vesevfitzgeraldii have Type B mesophyll and of these, two species, S. nutans and S. rehmannii have palisade differentiated both adaxially and abaxially whereas the rest have adaxial palisade only, or, if some palisade is differentiated abaxially it is confined to the margin region and the midrib region.

4.3.1. Leaf Surface

Prickles (barbs) generally present at leaf margins, especially towards leaf apex, on lateral ribs adaxially and midrib abaxially, the walls invariably silicified (Fig. 50 E) and the lumina sometimes more-or-less filled with amorphous silica.
Fig. 49. Phase-contrast photomicrographs of leaf epidermes of some amphistomatic Scleria spp. viewed after treatment with phenol to reveal silica-deposits which show up as pale, highly refractile areas.

A. S. woodii C.B.Cl. (Hennessy 406); adaxial epidermis; intercostal region with relatively few stomatal files; crescentiform silica deposits in sinuosities of anticlinal walls; subsidiary cells silicified and guard cells partly silicified. (X 260)

B. S. woodii C.B.Cl. (Hennessy 406); abaxial epidermis showing costal and intercostal regions; stomata more numerous than in adaxial epidermis: short cells present in intercostal files, their lumina filled with silica. (X 260)

C. S. bulbifera Hochst. ex A. Rich. (Hennessy 407); adaxial epidermis with files of bulliform cells alternating with stomatal files in intercostal region: silica deposition as in A. (X 260)

D. S. bulbifera Hochst. ex A. Rich. (Hennessy 407); abaxial epidermis showing costal and intercostal regions: apices of conical silica bodies in costal cells visible as white dots (X 260)

E. S. poaeformis Retz. (Hennessy 374); adaxial epidermis showing costal and intercostal regions with stomatal files: silica deposition as in A: cells relatively small (X 260)

F. S. sobolifer E.F. Franklin (Ward s.n.); abaxial epidermis showing costal and intercostal regions with short cells present in intercostal files as in D (X 260)
Fig. 50. Phase - contrast photomicrographs of leaf epidermes of some hypostomatic \textit{Scleria} spp. viewed after treatment with phenol to reveal silica-deposits which show up as pale highly-refractile areas.

A. \textit{S. achtenii} De Wild. (Ward 5508); abaxial epidermis showing intercostal regions with stomata in files, and costal region of narrower cells with scattered unicellular hairs: stomatal subsidiary cells filled with silica, guard cells partly silicified. Costal and intercostal cells with silica deposits in the sinuosities of the anticlinal walls: costal cells with conical bodies based on inner periclinal walls visible as shadows because not in focus. (X 260)

B. \textit{S. natalensis} C.B.Cl. (Hennessy 410); abaxial surface; silica deposits as in A. (X 260).

C. \textit{S. melanomphala} Kunth (Ward 8874); adaxial surface, intercostal region without stomata; sinuosities in anticlinal walls heavily silicified; few spherical silica bodies in lumina of some cells (X 260).

D. \textit{S. melanomphala} Kunth (Ward 8874); abaxial surface with stomata in intercostal regions; conical silica bodies with satellite rings in costal cells: sinuosities in anticlinal walls silicified: subsidiary cells and guard cells silicified as in A. (X 260)

E. \textit{S. angusta} Nees ex Kunth (Ward s.n.); adaxial surface showing silicified marginal bars; no stomata; cells with heavily silicified tangential walls not markedly sinuous (X 260).

F. \textit{S. angusta} Nees ex Kunth (Ward s.n.); abaxial surface showing files of costal and intercostal cells, stomata with silicified subsidiary cells and guard cells; crescentiform silica bodies in sinuosities of anticlinal walls of costal and intercostal cells; hemispherical silica bodies based on transverse anticlinal walls of some cells and shadowy conical bodies in costal cells (X 260).
Hairs confined to certain species (see Chapter 6): when present more numerous in, or restricted to narrow zones adjacent to the principal ribs and the margins: only one type of hair seen, namely, thick-walled, flexuous, unicellular type with inflated base, the wall silicified (Fig. 50 A) and the lumen sometimes more-or-less filled with amorphous silica.

Stomata usually more numerous in abaxial than in adaxial surface of amphistomatic species, absent from adaxial surface except possibly extreme margins of other (hypostomatic) species; invariably paracytic, the subsidiary cells broadly triangular to dome-shaped in the same specimen, silicified; guard cells also silicified (Figs. 49, 50); arranged at intervals in longitudinal files of cells lying parallel to the long axis of the leaf in all species.

Silica bodies of several types.  
1) conical bodies based on inner periclinal walls of cells overlying sclerenchyma associated with vascular
strands invariably present, 1-2 or up to 4 per cell, usually with a "ring" of satellites (Fig. 50 D). Maceration has shown that the inner periclinal wall is silicified and the conical bodies are therefore based on a siliceous plate; the satellite "ring" is a thicker, verrucose zone of silica which is raised above the surface of the baseplate with the cone standing proud in its centre.

2) Coarsely verrucose/echinulate bodies which are sometimes spherical but more often more-or-less hemispherical, solitary or more often paired, the two members of a pair separated from each other by the thickness of the anticlinal wall between their bases (Fig. 50 F).

3) Amorphous or finely granular silica present in some cells, more-or-less completely filling their lumina.

4) Small siliceous bodies, usually crescentiform, in the sinuosities in anticlinal walls of intercostal cells (Figs. 49, 50).

5) Other types of silica deposits include the amorphous deposits in the lumina of subsidiary cells and guard cells of stomata. The walls of all epidermal cells of all species examined
are silicified, so that maceration yields sheets of cell-shells.

**Epidermal cells** seldom more than slightly elongated, those overlying the sclerenchyma associated with v.b's narrower than those of intercostal regions: abaxial epidermal cells of most species smaller than adaxial; adaxial cells bulliform in median adaxial groove in all species; all adaxial cells from median groove to major marginal v.b. bulliform except those overlying sclerenchyma in lateral rib in seven species (see Key); some adaxial cells other than those in median groove bulliform in twelve species (see Key) and bulliform cells restricted to median adaxial groove in four species (see Key). Heavily silicified short cells such as may occur in grasses (Metcalfe, 1960) which are more-or-less isodiametric have been found in both epidermes of three species, *S. woodii* (Fig. 49 A,B), *S. pergracilis* and *S. sobolifer* (Fig. 49 F). Anticlinal walls of all epidermal cells sinuate, the degree of sinuation more marked in intercostal cells and varying from species to species:
the lobed sinuations reported (Metcalfe, 1971) for S. welwitschii not detected in material examined.

Papillae such as reported by Metcalfe (1971) not detected in any species, but solitary, non-protruberant dome-shaped cells next to and in the same files as stomata present in all species in small numbers, often filled with amorphous silica.
4.3.2. **Descriptions of Leaf Anatomy**

4.3.2.1. **Scleria woodii**

**LEAF SURFACE** (Fig. 49 A,B)

Amphistomatic, stomata paracytic; subsidiary cells more-or-less triangular, short cells present in intercostal files in both surfaces. *Silica bodies*: conical bodies, without satellites present in cells overlying sclerenchyma in both surfaces. 1-2 per cell; amorphous silica present in lumina of short cells; small crescentiform bodies present in sinuosities in anticlinal walls of long and short intercostal cells.

**T/S LAMINA** (Fig. 43, 4; Fig. 34 A; Fig. 47)

Narrowly V-shaped, thickest towards the obtuse subequal margins; keel obtuse. *Epidermis*: adaxial cells slightly larger than abaxial cells, bulliform cells restricted to median groove, with cells overlying sclerenchyma conspicuously smaller than the remainder; abaxial cells slightly smaller than most adaxial cells, the smallest overlying sclerenchyma. *Hypodermis*: nil. *Sclerenchyma*: eccentric median v.b. with crescentiform girder to one side of keel apex and with small adaxial rectangular girder major v.b.'s nearest margins with abaxial pulviniform or triangular girders and adaxial pulviniform strands; other major v.b.'s with variously shaped abaxial and abaxial girders, or abaxial girders and adaxial strands; minor v.b.'s nearest midrib with abaxial pulviniform girders and no adaxial sclerenchyma; one minor v.b. in margin in each half of lamina with no
adaxial sclerenchyma; one minor v.b. in margin in each half of lamina with an adaxial pulviniform strand and other minor v.b's without associated sclerenchyma. Mesophyll: chlorenchyma differentiated as palisade and spongy tissue, the palisade 1-2 rows deep adaxially and abaxially; spongy tissue composed of slightly lobed cells. Air cavities not developed except for small sub-stomatal cavities. Vascular bundles c. 10 in each half of the lamina, the major v.b's oval or pyriform, the minor v.b's rounded. Bundle sheaths: inner sheaths fibrous, outer sheaths parenchymatous. Secretory cells numerous in chlorenchyma.

4.3.2.2. Scleria welwitschii

LEAF SURFACE

Amphistomatic, stomata paracytic; subsidiary cells more-or-less triangular. Silica bodies: conical bodies present 1-2 per cell, without satellites, in cells overlying sclerenchyma associated with v.b's in both surfaces; small crescentiform bodies in sinuosities in anticlinal walls of intercostal cells.

T/S LAMINA (Fig. 433; Fig. 28 b; Fig. 47 2

Flanged V-shaped; keel prominent obtuse; margins rounded, equal. Epidermis: adaxial not conspicuously larger than abaxial cells but those overlying sclerenchyma smaller than remainder; bulliform cells restricted to median adaxial region.
Hypodermis: nil. Sclerenchyma: median v.b. with eccentric descending crescentiform abaxial girder and adaxial rectangular or pulviniform girder; other major v.b's with abaxial pulviniform or triangular girders and abaxial pulviniform or secundiflor girders; minor v.b's on each side of major marginal v.b. in each half of lamina without sclerenchyma, other minor v.b's mostly with abaxial and abaxial girders, or with abaxial girders and no adaxial sclerenchyma or the converse, or rarely, without sclerenchyma. Mesophyll: chlorenchyma spongy throughout, the cells slightly lobed, very densely packed. Air cavities: only small substomatal cavities present. Vascular bundles: c. 9 in each half of the lamina, oval or rounded. Bundle sheaths: inner sheath fibrous, outer sheath parenchymatous, those of major v.b's of some specimens extended to epidermis as sheaths to sclerenchyma girders. Secretory cells numerous in chlorenchyma.

4.3.2.3. Scleria rehmannii

LEAF SURFACE

Amphistomatic, stomata paracytic, subsidiary cells more-or-less triangular. Silica bodies: conical bodies present, 1-2 per cell in both epidermes, some with low satellite ring; numerous hemispherical echinulate bodies in pairs in intercostal cells in both surfaces, the two members of each pair separated by the thickness of
the anticlinal wall lying between their bases; small crescentiform bodies in sinuosities in anticlinal walls of intercostal cells.

T/S LAMINA (Fig. 437)

Flanged V-shaped, the flanges slightly shorter than the arms of the V; margins unequal, one broad, obtuse, the other tapered abruptly downward to an acute point; keel prominent, rounded. **Epidermis**: most adaxial cells much larger than adaxial, bulliform except where overlying sclerenchyma and where interrupted by stomata and at margin; abaxial cells smaller, smallest over sclerenchyma. **Hypodermis**: nil. **Sclerenchyma** median v.b. with eccentric descending crescentiform or broadly subtriangular girders and adaxial rectangular girder; other major v.b's with abaxial rectangular or subtriangular girders and adaxial securiform or subtriangular girders; minor v.b's in arms of V and in flange with abaxial subtriangular or rectangular girders except one small v.b. next to major marginal v.b. on each side of lamina without associated sclerenchyma; minor v.b's in margin several, the largest with adaxial cap and bulliform strand, the remainder (3 in each margin) without associated sclerenchyma. **Mesophyll**: chlorenchyma differentiated as palisade and spongy tissue, the palisade of 1-2 rows adaxially and abaxially; spongy tissue composed of strongly lobed cells; stellate achlorophyllous tissue present in the vicinity of the lateral ribs. **Air cavities**: only small substomatal cavities present
in specimen examined but the presence of stellate achlorophyllous tissue suggests that air cavities may develop in this species. **Vascular bundles** c. 14 in each half of lamina, the median v.b. much larger than other major v.b's; major v.b's oval or pyriform, smaller v.b's rounded. **Bundle sheaths**: inner fibrous, outer parenchymatous, those of major v.b's sometimes continuous around associated sclerenchyma. **Secretory cells** numerous in chlorenchyma.

4.3.2.4. *Scleria longispiculata*

**LEAF SURFACE**

Amphistomatic, stomata paracytic; subsidiary cells more-or-less triangular. **Silica bodies**: conical bodies present, 1-2 per cell in cells overlying sclerenchyma associated with v.b's in both surfaces, without satellites; numerous hemispherical echinulate bodies in pairs in the arm of the V in adaxial surface, the two members of each pair separated by the thickness of the anticlinical wall lying between their bases; small crescentiform bodies in sinuosities in anticlinical walls of intercostal cells.

**T/S LAMINA** (Fig. 43 8)

Flanged V-shaped, with conspicuous median adaxial groove; flanges shorter than the arms of the V; margins subequal, rounded to acute; keel prominent, rounded.
Epidermis: most adaxial cells much larger than adaxial, bulliform except where overlying sclerenchyma and where interrupted by stomata and at margin; abaxial cells smaller, smallest over sclerenchyma. Hypodermis: nil. Sclerenchyma: median v.b. with abaxial massive, descending crescentiform girder and adaxial pulviniform/bulbiform girder; other major v.b's and most minor v.b's with abaxial pulviniform or subtriangular girders and adaxial subtriangular girders; one minor v.b on each side of median v.b. with abaxial girder only and smallest bundles without associated sclerenchyma. Mesophyll: chlorenchyma differentiated as palisade and spongy tissue, the palisade of 1-2 adaxial rows; spongy tissue of slightly lobed cells. Air cavities not developed except for small substomatal cavities. Vascular bundles c. 12 in each half of lamina, the larger v.b's oval, the smaller rounded. Bundle sheaths: inner sheaths fibrous, outer parenchymatous. Secretory cells numerous in chlorenchyma.

4.3.2.5. Scleria bulbifera

LEAF SURFACE (Fig. 49 C,D)

Amphistomatic, stomata paracytic; subsidiary cells more-or-less triangular. Silica bodies: conical bodies present, 2-4 per cell in cells overlying sclerenchyma associated with v.b's in both surfaces, usually without satellites; very numerous
hemispherical echinulate bodies in pairs in both epidermes, the two members of each pair separated from each other by the thickness of the anticlinal wall lying between their bases; few spherical echinulate bodies in adaxial cells; small crescentiform bodies in sinuosities in anticlinal walls of intercostal cells.

**T/S LAMINA (Fig. 43 9)**

Flanged V-shaped, the flanges slightly shorter than the arms of the V; the margins rounded, subequal; keel prominent rounded. **Epidermis**: most adaxial cells much larger than abaxial, bulliform except where overlying sclerenchyma and where interrupted by stomata and at margins; abaxial conspicuously smaller than adaxial, smallest over sclerenchyma. **Hypodermis**: nil. **Sclerenchyma**: median v.b. with eccentric abaxial pulviniform/securiform girder and small adaxial pulviniform girder; major v.b.'s in ribs with small or large abaxial pulviniform girders and adaxial securiform or pulviniform girders; major marginal v.b.'s with abaxial pulviniform girder, adaxial pulviniform strand and with or without small adaxial cap; minor marginal v.b. with adaxial pulviniform girder or strand; minor v.b. on flange side of major marginal v.b. without associated sclerenchyma; other minor v.b.'s with abaxial pulviniform girders and with or without small adaxial caps. **Mesophyll**: chlorenchyma differentiate as palisade and spongy tissue, the palisade adaxial, of 1-2 rows; spongy tissue composed of slightly lobed cells. **Air**
cavities not developed except for small substomatal cavities. Vascular bundles c. 10 in each half of the lamina, the major v.b.'s oval or pyriform, the smaller ones rounded. Bundle sheaths: inner sheaths fibrous, outer sheaths parenchymatous. Secretory cells numerous in chlorenchyma.

4.3.2.6. Scleria veseyfitzgeraldii

LEAF SURFACE

Amphistomatic, stomata paracytic; subsidiary cells more-or-less triangular. Silica bodies: conical bodies present in cells overlying sclerenchyma associated with v.b.'s in both surfaces, 1-2 per cell, usually with a satellite ring; few amorphous masses more-or-less filling the lumina of some large adaxial cells; small crescentiform bodies present in sinuosities in anticlinal walls of intercostal cells.

T/S LAMINA (Fig. 43 12)

Widely flanged V-shaped, the flanges much longer than the arms of the V, thickest in the region of the major marginal v.b.; tapering abruptly to a downward-directed point at the margins; keel prominent, obtuse. Epidermis: adaxial cells unequal in size, bulliform in the median groove, with alternating files of bulliform cells and stomata in intercostal regions and with smallest cells overlying sclerenchyma; abaxial cells smaller than
most abaxial cells, the smallest overlying sclerenchyma. **Hypodermis**: nil. **Sclerenchyma**: median v.b. with abaxial descending crescentiform girder, with or without small adaxial cap; major v.b's near margin and in ribs with abaxial pulviniform girders and adaxial pulviniform or securiform strands; one large v.b. nearest rib in flange region in each half of lamina with abaxial pulviniform girder and adaxial pulviniform or securiform girder; minor v.b's in arms of V with abaxial pulviniform girders and no adaxial sclerenchyma; minor v.b's in flange mostly with abaxial pulviniform girders and adaxial pulviniform strands, or rarely with both abaxial and adaxial strands; the smallest without sclerenchyma and the marginal minor vib's with adaxial strands and no abaxial sclerenchyma. **Mesophyll**: chlorenchyma differentiated as palisade and spongy tissue, the palisade of 1-2 adaxial rows; the spongy tissue composed of strongly lobed cells. Air cavities not developed except for small sub-stomatal cavities. **Vascular bundles** c. 14 in each half of the lamina, the major v.b's oval or pyriform, the minor v.b's rounded. Bundle sheaths: inner sheaths fibrous, outer sheaths parenchymatous. Secretory cells numerous in chlorenchyma.

4.3.2.7. **Scleria drègeana**

**LEAF SURFACE**

Amphistomatic, stomata paracytic; subsidiary cells more-or-less triangular. **Silica bodies**: conical bodies present, 2–4 per cell in cells overlying sclerenchyma.
associated with v.b's in both surfaces, with low satellite ring; numerous hemispherical echinulate bodies in pairs especially in adaxial epidermis, the two members of each pair separated from each other by the thickness of the anticlinal wall lying between their bases; few spherical echinulate bodies in adaxial cells; small crescentiform bodies in sinuosities in anticlinal walls of intercostal cells.

T/S LAMINA (Fig. 43 11; Fig. 30 a; Fig. 47 3,4)

Flanged V-shaped, the flanges shorter and slightly thicker than the arms of the V; the margins subequal, rounded; keel prominent, acute or rounded. Epidermis: most adaxial cells much larger than abaxial, bulliform except where overlying sclerenchyma and where interrupted by stomata and at margins; abaxial cells conspicuously smaller than adaxial, smallest over sclerenchyma. Hypodermis nil. Sclerenchyma: median v.b. with abaxial descending crescentiform girder which in some specimens is eccentric (K.D. Huntley 425); major v.b's in ribs with abaxial pulviniform girders and with adaxial securiform or sub-triangular or sub-T-shaped girders; major marginal v.b's with abaxial pulviniform girders and with adaxial subtriangular or sub-T-shaped girders or with small cap and pulviniform strand; minor v.b's with abaxial and adaxial girders, or with abaxial girders and adaxial strand or with abaxial girder, or the marginal minor v.b. with adaxial girder, or the minor v.b's on either side of the major marginal v.b. without associated sclerenchyma. Mesophyll chlorenchyma either spongy throughout, composed of slightly-lobed cells, or with a single
layer of palisade differentiated adaxially. Air cavities not developed except for small substomatal cavities. Vascular bundles c. 8 in each half of lamina, the major v.b's pyriform or oval, minor v.b's oval or rounded. Bundle sheaths : inner sheath fibrous, outer parenchymatous. Secretory cells numerous in chlorenchyma.

4.3.2.8. Scleria sobolifer

LEAF SURFACE (Fig. 49 F.)

Amphistomatic, stomata paracytic, subsidiary cells more-or-less triangular; short cells present in intercostal files in both surfaces. Silica bodies : conical bodies present 1-2 per cell in cells overlying sclerenchyma associated with v.b's in both surfaces; usually without satellites; spherical echinulate bodies fairly numerous in adaxial cells; amorphous silica present in lumina of short cells; small crescentiform bodies present in sinuosities in anticlinal walls of intercostal cells.

T/S LAMINA (Fig. 43 14)

Flanged V-shaped, the flanges slightly shorter and thicker than the arms of the V; the margins subequal, broadly rounded; keel prominent, rounded. Epidermis : most adaxial cells much larger than adaxial, bulliform except where overlying sclerenchyma and where interrupted by stomata and at margins; abaxial cells conspicuously smaller than adaxial, smallest over sclerenchyma. Hypodermis : nil. Sclerenchyma : median v.b. with abaxial slightly eccentric low pulviniform girder and adaxial
pulviniform girder; major v.b's in ribs with abaxial pulviniform/rectangular girders and adaxial bulbiform strand, with or without tiny adaxial cap; major marginal v.b's with abaxial pulviniform girders and either adaxial crescentiform cap (Ward 4737) or adaxial bulbiform strand, with (Ward 4935) or without (Baijnath 126; Arnold 467) tiny adaxial cap; minor v.b's with abaxial pulviniform girders except v.b's on each side of major marginal v.b's which either lack associated sclerenchyma or (Arnold 467) the marginal minor v.b. with adaxial bulbiform strand. Mesophyll: chlorenchyma differentiated as palisade and spongy tissue; palisade of 1 adaxial row, spongy tissue of slightly lobed cells. Air cavities not developed except for small substomatal cavities. Vascular bundles c. 7-8 in each half of lamina, the major v.b's oval, the smaller ones rounded. Bundle sheaths inner sheaths fibrous, outer parenchymatous, sometimes continuous around associated sclerenchyma. Secretory cells numerous in chlorenchyma.

4.3.2.9. Scleria pergracilis var. brachystachys

LEAF SURFACE

Amphistomatic, stomata paracytic; subsidiary cells more-or-less triangular; numerous short cells present in intercostal files in both surfaces. Silica bodies: conical bodies without satellites present in cells overlying sclerenchyma in both surfaces, 1-3 per cell; amorphous silica present in lumina of short cells; small crescentiform bodies present in sinuosities in anticlinal walls of intercostal cells.
T/S LAMINA (Fig. 43 10)

Broadly V-shaped, thickness more-or-less uniform; the margins subequal, obtuse; keel obtuse. Epidermis: most adaxial cells much larger than abaxial, bulliform except where overlying sclerenchyma and in files in which stomata and short cells are situated; abaxial cells smaller than most adaxial cells, smallest over sclerenchyma. Hypodermis: nil. Sclerenchyma: median v.b. with massive descending crescentiform girder; major v.b's nearest margins with abaxial pulviniform girder and adaxial bulbiform strands; some v.b's with abaxial and adaxial girders, or abaxial girder and adaxial strand; some with abaxial girders only; those on each side of the major marginal v.b. without sclerenchyma and one or two others without sclerenchyma. Mesophyll: chlorenchyma spongy throughout, of slightly lobed cells. Air cavities not developed except for small substomatal cavities. Vascular bundles: c. 7 in each half of the lamina, oval or rounded. Bundle sheaths: inner sheaths fibrous, outer parenchymatous, sometime more-or-less continuous around associated sclerenchyma. Secretory cells numerous in chlorenchyma.

4.3.2.10. Scleria dieterlenii

LEAF SURFACE

Amphistomatic, stomata paracytic; subsidiary cells more-or-less triangular. Silica bodies: conical bodies present, 1-2 per cell in cells overlying sclerenchyma in both surfaces, usually with a satellite ring;
few large amorphous masses more-or-less filling the lumina of some large adaxial cells; small crescentiform bodies in sinuosities in anticlinal walls of intercostal cells.

T/S LAMINA (Fig. 43 13)

Flanged V-shaped; the flanges slightly thicker than the arms of the V; the margins rounded, subequal; keel prominent obtuse. 

Epidermis : most adaxial cells much larger than adaxial, bulliform except where overlying sclerenchyma and where interrupted by stomata and at margins; abaxial cells conspicuously smaller than adaxial, smallest over sclerenchyma.

Hypodermis : nil. Sclerenchyma : median v.b. with abaxial slightly eccentric descending crescentiform girder and adaxial pulviniform/ baculiform girder; major v.b's in ribs with abaxial pulviniform or subtriangular girders and adaxial securiform or sub-T-shaped girder or bulbiform strand; major marginal v.b's with abaxial pulviniform or subtriangular girder and bulbiform strand; minor v.b's with abaxial pulviniform or subtriangular girders, or without associated sclerenchyma. 

Mesophyll : chlorenchyma either not differentiated as palisade and spongy tissue or with a single, poorly-defined adaxial row of palisade, the spongy tissue composed of slightly-lobed cells. Air cavities not developed except for small substomatal cavities. Vascular bundles c. 7 in each half of lamina, the major v.b's oval, the smaller ones rounded. Bundle sheaths : inner sheaths fibrous, outer parenchymatous. Secretory cells few in chlorenchyma.
4.3.2.11. Scleria nutans

**LEAF SURFACE**

Amphistomatic, stomata paracytic; subsidiary cells more-or-less triangular.

Silica bodies: conical bodies present, 1-2 per cell in cells overlying sclerenchyma associated with v.b.'s in both surfaces, without satellites; few amorphous masses more-or-less filling lumina of some abaxial cells; few spherical echinulate bodies present in both epidermes; small crescentiform bodies in sinuosities in anticlinal walls of intercostal cells.

**T/S LAMINA (Fig. 43 6; Fig. 47 6)**

Flanged V-shaped, the flanges slightly shorter than the arms of the V; the margins subequal, broadly rounded; keel prominent, rounded. Epidermis: most adaxial cells much larger than abaxial, bulliform except where overlying sclerenchyma and in files in which stomata are situated which are most numerous adjacent to the lateral rib on the arm of the V, and at margins; abaxial cells conspicuously smaller than adaxial, smallest over sclerenchyma. Hypodermis: nil. Sclerenchyma: median v.b. with abaxial pulviniform or rectangular girder and adaxial subtriangular girder; major v.b.'s in ribs and margins with abaxial pulviniform or subtriangular girders and adaxial oblique subtriangular girders; minor v.b.'s nearest median v.b. and major marginal v.b.'s without associated sclerenchyma, the remainder with abaxial girders or, rarely, abaxial and abaxial girders. Mesophyll: chlorenchyma differentiated as palisade and spongy tissue, the palisade 1-2 rows deep adaxially and
abaxially; spongy tissue composed of slightly lobed cells. **Air cavities** not developed except for small substomatal cavities. **Vascular bundles** c. 9 in each half of the lamina, the major v.b's pyriform or oval, the minor v.b's rounded. **Bundle sheaths**: inner sheaths fibrous, outer parenchymatous, sometimes more-or-less continuous around associated sclerenchyma. **Secretory cells** numerous in chlorenchyma.

4.3.2.12. **Scleria aterrima**

**LEAF SURFACE**

Amphistomatic, stomata paracytic; subsidiary cells more-or-less triangular. **Silica bodies**: conical bodies present, 1-2 per cell, without satellites, in cells overlying sclerenchyma associated with v.b's in both surfaces; finely particulate silica in lumina of some adaxial bulliform cells; few spherical echinulate bodies and very few paired hemispherical echinulate bodies in adaxial cells; small crescentiform bodies in sinuositi in anticlinal walls of cells in both surfaces.

**T/S LAMINA** (Fig. 43 5; Fig. 35; Fig. 47 5)

Flanged V-shaped with conspicuous median adaxial groove; keel prominent, acute; margins obtuse or rounded, subequal. **Epidermis** most adaxial cells much larger than abaxial, bulliform except where overlying sclerenchyma and where interrupted by stomata and at margins abaxial cells conspicuously smaller than adaxial smallest over sclerenchyma. **Hypodermis**:
groups of inflated translucent cells in intercostal regions subjacent adaxial bulliform cells. Sclerenchyma: median slightly eccentric v.b. with strongly eccentric abaxial crestiform girder and small adaxial cap, other major v.b's and middle-sized v.b's with abaxial and adaxial girders of various shapes; most minor v.b’s without sclerenchyma but minor v.b’s adjacent median v.b. with abaxial girders and with or without adaxial caps. Mesophyll: chlorenchyma differentiated as palisade and spongy tissue, the palisade of 1-2 rows adaxially and abaxially, the spongy tissue composed of slightly lobed cells. Air cavities: only small substomatal cavities present. Vascular bundles: c. 14 in each half of the lamina, larger and smaller v.b’s mostly alternating, the larger v.b’s oval or pyriform, the smallest rounded. Bundle sheaths inner sheath fibrous, outer sheath parenchymatous. Secretory cells present in chlorenchyma.

4.3.2.13. Scleria lacustris

LEAF SURFACE

Amphistomatic, stomata paracytic, subsidia cells more-or-less triangular. Silica bodies: conical bodies present 1-2 per cell in cells overlying sclerenchyma associated with v.b’s in both surfaces, with a satellite ring; very numerous hemispherical echinulate bodies with their bases resting against outer periclinal walls in both surfaces; few spherical echinulate bodies in both surfaces; small crescentiform bodies in sinuosities in anticlin
walls of intercostal cells. In addition, the lumina of many cells of sclerenchyma girders/strands filled with granular accretions of silica.

T/S LAMINA (Fig. 43 16; Fig. 46 1)

Widely flanged V-shaped; keel prominent, obtuse; greater part of each half thick especially near lateral ribs; margins rounded, equal. **Epidermis**: adaxial cells variable in size, bulliform in median region and on both sides of ribs and those overlying sclerenchyma much the smallest; abaxial cells less variable but those overlying sclerenchyma smaller than remainder. **Hypodermis** represented by trabeculae of translucent cells extending from outer sheaths of median v.b. and major v.b's of ribs to adaxial epidermis. **Sclerenchyma**: median v.b. with abaxial descending crescentiform cap; other major v.b's and a few minor v.b's with abaxial pulviniform girders, small adaxial caps and adaxial pulviniform strands, those of the major v.b's of ribs separated from their bundles by translucent cells; minor v.b's mostly without sclerenchyma but a few near midrib with abaxial pulviniform girders and a few with adaxial small pulviniform strands. **Mesophyll**: chlorenchyma slightly differentiate as palisade and spongy tissue, the palisade limited to a single adaxial row in the vicinity of the lateral rib in each half of the lamina and a single adaxial and abaxial row near each margin; the spongy tissue composed of stellately lobed cells. **Air cavities** present, formed by breakdown of stellate chlorenchyma; substomatal cavities small. **Vascular bundles**
c. 28 in each half of the lamina, of three sizes; the largest oval or pyriform, the middle-sized v.b's oval or rounded, the smallest rounded; the larger v.b's closer to abaxial than to adaxial epidermis, the medium sized and small v.b's unevenly distributed with some closer to the abaxial epidermis, some closer to the adaxial epidermis and some about midway between the two epidermes.

Bundle sheaths: inner sheaths fibrous, outer sheaths parenchymatous, those of larger v.b's extended to the abaxial epidermis as sheaths to sclerenchyma girders. Secretory cells: few in chlorenchyma.

4.3.2.14. Scleria transvaalensis

LEAF SURFACE

Hypostomatic, stomata paracytic; subsidiary cells more-or-less triangular. Silica bodies: conical bodies present 1-3 per cell in cells overlying sclerenchyma associated with v.b's in both surfaces, with a satellite ring; few large amorphous masses more-or-less filling the lumina of some large adaxial cells; small crescentiform bodies in sinuosities in anticlinal walls of intercostal cells.

T/S LAMINA (Fig. 43 23; Fig. 45 5,6)

Flanged V-shaped, the arms of the V and the flange more-or-less equal in length; thickest near the lateral ribs; the margins subequal, acute; keel small, prominent, acute. Epidermis: adaxial cells bulliform except those overlying sclerenchyma of lateral ribs and margins; abaxial cells smaller, the
smallest overlying sclerenchyma. Hypodermis: nil (Arnold 336; Seagrief 18) or of large translucent cells subjacent bulliform cells in median adaxial groove and in region of lateral ribs where they may form partial trabeculae (Müller 2031; Gordon-Gray 6020; Compton 24985; Smuts & Gillett 3260).

Sclerenchyma: median v.b. with abaxial large descending crescentiform girder, and small or large adaxial cap or girder; major v.b's in ribs with abaxial large crescentiform or pulviniform girder, small crescentiform adaxial cap and massive bulbiform strand remote from the bundle; major marginal v.b's with abaxial pulviniform or subtriangular girder and adaxial subtriangular or securiform girder; two minor v.b's in each margin with adaxial pulviniform or subtriangular girders; other minor v.b's with abaxial and adaxial girders variously shaped, or a few with abaxial or adaxial girders only and some without associated sclerenchyma, the v.b's with sclerenchyma more-or-less alternating with those lacking sclerenchyma. Mesophyll: chlorenchyma differentiated as a single adaxial row of palisade and spongy tissue of strongly-lobed cells. Air cavities not developed except for small substomatal cavities. Vascular bundles: c. 26 in each half of the lamina; the larger v.b's oval or pyriform, the smaller rounded. Bundle sheaths: inner sheaths fibrous, outer sheaths parenchymatous, those of major v.b's extended as sheaths around sclerenchyma girders. Secretory cells numerous in chlorenchyma.
4.3.2.15. Scleria natalensis

**LEAF SURFACE** (Fig. 50 B)

_Hypostomatomic_, stomata paracytic; subsidiary cells more-or-less triangular; conical bodies present, 1-2 per cell usually with a low satellite ring; numerous hemispherical echinulate bodies in pairs in both epidermis, the two members of each pair separated by the thickness of the anticlinal wall lying between their bases and sometimes with two pairs at right angles to each other forming a "tetrad"; small crescentiform bodies in sinuositites in anticlinal walls of intercostal cells.

**T/S LAMINA** (Fig. 43 19; Fig. 46 4)

Flanged V-shaped, the flanges slightly shorter than the arms of the V; thickest near the lateral ribs; the margins subequal, acute; keel small, prominent, acute. **Epidermis**: adaxial cells bulliform except those overlying sclerenchyma of lateral ribs and margins; abaxial cells much smaller, the smallest overlying sclerenchyma. **Hypodermis**: nil. Sclerenchyma: median v.b. with abaxial large ascending crescentiform girder and with or without tiny adaxial cap; major v.b’s in ribs with abaxial pulviniform or crescentiform girders, adaxial crescentiform caps and massive bulbiform strands remote from the bundles; major marginal v.b’s with abaxial subtriangular or pulviniform girders and adaxial subtriangular girders: minor marginal v.b’s two in each margin, the outer without associated sclerenchyma, the inner with adaxial subtriangular girder and small abaxial cap; other minor v.b’s
with small abaxial and adaxial girders or with abaxial girders only, or without associated sclerenchyma. **Mesophyll** : chlorenchyma differentiated as a single adaxial row of palisade and slightly and strongly lobed chlorenchyma, the strongly-lobed cells in the vicinity of the lateral ribs. **Air cavities** not developed except for small substomatal cavities. **Vascular bundles** c. 16 in each half of the lamina, oval, or the smaller ones rounded, the median v.b. much smaller than the other major v.b's. **Bundle sheaths** : inner sheaths fibrous, outer parenchymatous, those of the major v.b's extended as sheaths around sclerenchyma girders. **Secretory cells** : numerous in chlorenchyma.

4.3.2.16. *Scleria foliosa*

**LEAF SURFACE**

**Amphistomatic**; stomata paracytic, subsidiary cells more-or-less triangular. **Silica bodies** : conical bodies present, 1-2-3 per cell in cells overlying sclerenchyma in both surfaces, without satellites; numerous echinulate plates in pairs in both epidermes especially in arms of median V, the two members of each pair separated by the thickness of the anticlinal wall lying between their bases; finely particulate silica masses present in a few adaxial intercostal cells; small crescentiform bodies in sinuosities in anticlinal walls of intercostal cells.
T/S LAMINA (Fig. 43 15; Fig. 46 2)

Widely flanged V-shaped; keel prominent, obtuse; margins rounded, equal. Epidermis: most adaxial cells much larger than abaxial, bulliform except where overlying sclerenchyma strands and where interrupted by stomata and at margin; abaxial cells conspicuously smaller than adaxial, smallest over sclerenchyma. Hypodermis: none seen in sections examined. Sclerenchyma: median v.b. with abaxial pulviniform girder and small adaxial cap. Other major v.b's with abaxial pulviniform girders and adaxial pulviniform strands. Minor v.b's mostly with abaxial pulviniform girders and no adaxial sclerenchyma except minor v.b's nearest margin in each half of lamina with adaxial pulviniform girder and no abaxial sclerenchyma and one minor bundle in each half of lamina without sclerenchyma. Mesophyll: chlorenchyma slightly differentiated as palisade and spongy tissue, the palisade a single adaxial layer, the spongy tissue composed of stellately lobed cells. Air cavities present between many v.b's, formed by breakdown of stellate cells. Vascular bundles c. 10 in each half of the lamina, oval or rounded. Bundle sheaths: inner sheaths fibrous, outer sheaths parenchymatous, those of major v.b's extended to epidermis as sheaths to sclerenchyma girders. Secretory cells: few in chlorenchyma near major v.b's.
4.3.2.17. *Scleria unguiculata*

**LEAF SURFACE**

Hypostomatic, stomata paracytic; subsidiary cells more-or-less triangular. Silica bodies: conical bodies present, 1-2 per cell in cells overlying sclerenchyma associated with v.b's in both surfaces, usually with a satellite ring; few large amorphous masses more-or-less filling the lumina of some large adaxial cells; small crescentiform bodies in sinuosities in anticlinal walls of intercostal cells.

**T/S LAMINA** (Fig. 43 20)

Flanged V-shaped, the flanges shorter than the arms of the V; thinnest towards the midrib, thickest on each side of the lateral ribs, tapering abruptly to acute margins, the margins equal; keel prominent, obtuse. Epidermis: adaxial cells bulliform except those overlying sclerenchyma of ribs and margins; abaxial cells much smaller, the smallest overlying sclerenchyma. Hypodermis: nil. Sclerenchyma: median v.b. with abaxial massive, eccentric crescentiform girder and adaxial securiform girder; major v.b's in ribs with abaxial very narrow rectangular, or sub-T-shaped girders, adaxial caps and narrow rectangular adaxial strands remote from the bundles; major marginal v.b's with abaxial pulviniform girders and adaxial securiform girders; minor marginal v.b's with adaxial pulviniform girders; other minor v.b's with adaxial pulviniform girders; other minor v.b's in flange without sclerenchyma; minor v.b's in arms of V with abaxial and adaxial girders variously shaped or with adaxial girders and no abaxial sclerenchyma, or with adaxial girders and tiny abaxial strands, or without associated sclerenchyma. Mesophyll: chlorenchyma
differentiated as palisade and spongy tissue, the palisade comprising a single adaxial row; the spongy tissue composed of strongly lobed cells. Air cavities not developed except for small sub-stomatal cavities. Vascular bundles c. 10 in each half of the lamina, the major v.b's oval or pyriform, the minor v.b's rounded. Bundle sheaths: inner sheaths fibrous, outer sheaths parenchymatous, those of the major v.b's extended as sheaths around sclerenchyma girders. Secretory cells present in chlorenchyma.

4.3.2.18. Scleria achtenii

LEAF SURFACE (Fig. 50 A)

Hypostomatic, stomata paracytic; subsidiary cells more-or-less triangular. Silica bodies: conical bodies present, 1-3 per cell in cells overlying sclerenchyma associated with v.b's in both surfaces, usually with a low satellite ring; few large amorphous masses more-or-less filling the lumina of some large adaxial cells; small crescentiform bodies in sinuosities in anticlinal walls of intercostal cells.

T/S LAMINA (Fig. 43 21; Fig. 36 a,b; Fig. 46 3)

Flanged V-shaped, the flanges slightly short than the arms of the V; thickest near the lateral ribs; margins narrowly rounded, equal; keel prominent, subacute. Epidermis: adaxial cells bulliform except those overlying sclerenchyma of lateral ribs and margins; abaxial cells much smaller, the smallest overlying sclerenchyma. Hypodermis nil, or (Ward 7743) a few large translucent cells subjacent bulliform cells in
median adaxial groove. Sclerenchyma: median v.b. with abaxial massive ascending crescentiform girder and adaxial pulviniform or securiform girder; major v.b's in ribs with abaxial pulviniform girders, adaxial caps and bulbiform strands remote from the bundles; major marginal v.b's with abaxial crescentiform girder and adaxial securiform or subtriangular girders minor marginal v.b's with adaxial pulviniform girders; other minor v.b's in flange without sclerenchyma except those adjacent rib with small abaxial girders; minor v.b's in arms of V with small abaxial and adaxial girders, mostly pulviniform or securiform, or those adjacent the midrib without associated sclerenchyma.

Mesophyll: chlorenchyma differentiated as palisade and spongy tissue, the palisade comprises a single adaxial row except sometimes 2-3 rows adjacent the lateral ribs; the spongy tissue composed mainly of slightly lobed cells except near the lateral ribs where the cells are strongly lobed. Air cavities not developed except for small substomatal cavities. Vascular bundles c. 12 in each half of the lamina, the major v.b's oval or pyriform, the minor v.b's rounded or oval. Bundle sheaths: inner sheaths fibrous, outer sheaths parenchymatous, those of major v.b's extended as sheaths around sclerenchyma girders. Secretory cells present in chlorenchyma.
4.3.2.19. Scleria lagoensis

**LEAF SURFACE**

*Hypostomatic, stomata paracytic; subsidiary cells more-or-less triangular. Silica bodies: conical bodies present, 1-3 per cell in cells overlying sclerenchyma associated with v.b's in both surfaces, usually with a satellite ring; few large amorphous masses more-or-less filling the lumina of some large adaxial cells; small crescentiform bodies in sinuositites in anticlinal walls of intercostal cells.*

**T/S LAMINA (Fig. 43 22)**

Flanged V-shaped, the flanges slightly shorter than the arms of the V; thickest near the lateral ribs and the submarginal region; the margins rounded, unequal; keel small, prominent, acute. **Epidermis**: adaxial cells bulliform except those overlying sclerenchyma of lateral ribs and margins; abaxial cells much smaller, the smallest overlying sclerenchyma. **Hypodermis nil. Sclerenchyma**: median v.b. with abaxial massive ascending crescentiform girder and with or without very small adaxial cap; major v.b's in ribs with abaxial crescentiform or pulviniform girders, adaxial crescentiform caps and buliform strands remote from the bundles; major marginal v.b's with abaxial crescentiform or pulviniform girders and small buliform strands remote from the bundle; minor marginal v.b's with small adaxial pulviniform or securiform girders, and in one margin, a minor v.b. without associated sclerenchyma; minor v.b's adjacent to the lateral ribs without sclerenchyma, most of the remainder with abaxial pulviniform girders.
and no adaxial sclerenchyma. **Mesophyll**: chlorenchyma differentiated as palisade and spongy tissue, the palisade comprising a single adaxial row; the spongy tissue composed of slightly lobed cells except near major lateral ribs and towards margins where the cells are strongly lobed. **Air cavities** not developed except for small sub-stomatal cavities. **Vascular bundles** c. 14 in each half of the lamina, oval or the smaller ones rounded; the median v.b. much smaller than the other major v.b’s. **Bundle sheaths**: inner sheaths fibrous, outer sheaths parenchymatous, those of the major v.b’s extended as sheaths around sclerenchyma girders. **Secretory cells** present in chlorenchyma.

4.3.2.20. *Scleria melanomphala*

**LEAF SURFACE** (Fig. 50 C,D)

**Hypostomatic**, stomata paracytic; subsidiary cells more-or-less triangular. **Silica bodies**: conical or dome-shaped bodies present, usually 1 per cell in cells overlying sclerenchyma associated with v.b’s in both surfaces, each body based on a more-or-less circular, coarsely echinulate plate the diameter of which almost equals that of the cell; small **spherical and hemispherical** bodies present in intercostal cells; small crescentiform bodies in sinuosities in anticlinal and periclinal walls of intercostal cells.

**T/S LAMINA** (Fig. 43 17; Fig. 45 3,4,5)

Flanged V-shaped, the flanges and the arms of the V subequal; not conspicuously thicker in the region of the lateral ribs, the margins.
rounded, equal; keel prominent, subacute. 

**Epidermis**: adaxial cells bulliform except those overlying sclerenchyma of lateral ribs and margins; abaxial cells smaller, the smallest overlying sclerenchyma. **Hypodermis** absent from plants of drier habitats; present as large translucent cells subjacent the adaxial epidermis (also see Mesophyll) in plants of wet habitats. 

**Sclerenchyma**: median v.b. with abaxial massive ascending, straight or descending crescentiform girder and adaxial pulviniform girder; major v.b's in lateral ribs and near margins with abaxial pulviniform girders and adaxial pulviniform or bulbiform (in rib) girders, or adaxial bulbiform strands in rib: 2-3 minor v.b's on either side of major marginal v.b without sclerenchyma; the remainder with abaxial pulviniform girders and adaxial subtriangular girders; or with abaxial girders and no adaxial sclerenchyma; or without sclerenchyma. **Mesophyll** chlorenchyma differentiated in "dry" form as palisade and spongy tissue, the palisade comprising 2-3 adaxial rows and 1 abaxial row limited to marginal and midrib regions; the spongy tissue composed of strongly lobed cells: in plants of wet habitats chlorenchyma and achlorophyllous cells present, the achlorophyllous cells of two types, namely, large, oblong or round cells forming conspicuous trabeculae, and stellately lobed cells filling (in the young leaf the mid-laminar region not occupied by chlorenchyma or trabeculae. **Air cavities** except substomatal cavities absent from "dry" form; very large and conspicuous cavities formed by breakdown of stellate translucent cells in mature leaves of wet form. **Vascular bundles** c. 20 in each half
of the lamina, the major v.b's oval or pyriform, the minor v.b's oval or rounded. Bundle sheaths inner sheaths fibrous, outer sheaths parenchymatous, those of major v.b's extended as sheaths around sclerenchyma girders. Secretory cells present in chlorenchyma.

4.3.2.21. Scleria poaeformis

**LEAF SURFACE** (Fig. 49 E)

Amphistomatic, stomata paracytic, subsidiary cells more-or-less triangular. Silica bodies: conical bodies present, usually 3 per cell in cells overlying sclerenchyma associated with vascular bundles (v.b's) in both surfaces, usually with a ring of satellites; crescentiform bodies in sinuosities in anticlinal walls of intercostal cells.

**T/S LAMINA** (Fig. 43 2; Fig. 44 1,2,3)

Widely flanged V-shaped with prominent V-shaped keel; greater part of each half thick but thinning on either side of midrib; margins gradually tapered to narrowly rounded ends, equal Epidermis: adaxial cells not conspicuously larger than abaxial cells; cells overlying sclerenchyma only slightly smaller than remainder; bulliform cells restricted to median adaxial region. Hypodermis of 3-4 layers of translucent cells subjacent median adaxial bulliform cells (also see Mesophyll). Sclerenchyma: median v.b. with abaxial ascending crescentiform strand, abaxial cap and adaxial cap: largest adaxial v.b's with abaxial crescentiform cap, with or without adaxial cap and with pulviniform adaxial strand;
middle-sized adaxial v.b's with or without abaxial crescentiform cap and with adaxial pulviniform strand separated from v.b. by trabeculae of translucent cells, with or without adaxial cap, or with adaxial pulviniform girder (v.b. 1 from margin), or without adaxial sclerenchyma; smallest adaxial v.b's without sclerenchyma or with very small adaxial caps: largest abaxial v.b's with abaxial securiform girders, with or without adaxial crescentiform caps and with adaxial pulviniform or triangular (v.b. of angle region) strand separated from v.b. by trabeculae of translucent cells; middle-sized abaxial v.b's with abaxial pulviniform strands or with abaxial pulviniform, sub-T or triangular girders, without or rarely with adaxial caps, or without sclerenchyma: smallest abaxial v.b's without sclerenchyma: vascular bundles situated in trabeculae with crescentiform cap at phloem pole and very small cap at xylem pole, or with small cap at phloem pole and no sclerenchyma at xylem pole, or without sclerenchyma. Mesophyll chlorenchyma and achlorophyllous translucent tissue present; chlorenchyma differentiated as palisade and spongy tissue, the palisade 3-4 rows deep adaxially and abaxially, the spongy tissue composed of stellately lobed cells situated in a narrow zone subjacent the palisade layers and adjacent to the trabeculae; achlorophyllous translucent cells of two types, namely, large oblong or round cells of the same type as the hypodermis, extending from adaxial poles of largest v.b's to adaxial epidermis forming very conspicuous trabeculae or partial trabeculae, and stellately lobed cells with silicified walls filling (in the young leaf)
the mid-laminar region not occupied by chlorenchyma or trabeculae. Air cavities very large and conspicuous, located between adjacent trabeculae in the mature leaf, formed from breakdown of stellate translucent cells, with few to many relict stellate translucent cells present in them; substomatal cavities small and well defined. Vascular bundles c. 318 in each half of the lamina, of three sizes, the largest oval or pyriform, the middle-sized v.b's oval or rounded, the smallest rounded; distributed adaxially, abaxially and in the trabeculae. Bundle sheaths: inner sheaths fibrous; outer sheaths parenchymatous, those of large v.b's extend to the epidermis nearest them as sheaths to sclerenchyma. Secretory cells: conspicuous in chlorenchyma, most numerous towards margins.

4.3.2.22. Scleria greigiifolia

LEAF SURFACE

Amphistomatic, stomata paracytic, subsidiary cells more-or-less triangular. Silica bodies: conical bodies present, 1-2 per cell in cells overlying sclerenchyma associated with vascular bundles (v.b's) in both surfaces, usually without but sometimes with a ring of satellites; finely particulate silica masses present in a few adaxial intercostal cells; small crescentiform bodies in sinuosities in anticlinal wall of intercostal cells.
T/S LAMINA (Fig. 43 1; Fig. 44 4,5,6)

Widely flanged V-shaped; keel prominent, rounded; margins rounded, equal. Epidermis: adaxial not conspicuously larger than abaxial cells but those overlying sclerenchyma smaller than remainder, bulliform cells restricted to median adaxial region. Hypodermis absent, or comprising a single layer of translucent cells subjacent median adaxial bulliform cells. Sclerenchyma: median v.b. with abaxial pulviniform girder and adaxial small pulviniform girder; other major v.b.'s with abaxial pulviniform or sub-T-shaped girders or partial girders and adaxial triangular, sub-T-shaped girders or partial girders, the girders of the major marginal bundles more massive than the rest; minor v.b.'s mostly without sclerenchyma; a few with sub-T-shaped or triangular adaxial girders and rarely, with very small abaxial caps. Leaf margins without sclerenchyma. Mesophyll: chlorenchyma differentiated as palisade and spongy tissue, the palisade 2-3 rows deep adaxially, the spongy tissue composed of stellately lobed cells. Air cavities: none in chlorenchyma; substomatal cavities small and well-defined. Vascular bundles c. 27 in each half of lamina, oval or pyriform, of 2 distinct sizes, principal and minor
v.b's mostly alternating. Bundle sheaths: inner sheath fibrous; outer sheath parenchymatous, those of principal v.b's extended to each epidermis as sheaths to sclerenchyma girders. Secretory cells frequent in chlorenchyma, most numerous in vicinity of v.b's with one end in contact with a cell of the outer bundle sheath.

4.3.2.23. Scleria angusta

LEAF SURFACE (Fig. 50 E,F)

Hypostomatic (except wing which is amphistomatic), stomata paracytic, subsidiary cells more-or-less triangular. Silica bodies: conical bodies present, 1-3 per cell in cells overlying sclerenchyma associated with v.b's mainly abaxial, usually with a ring of satellites; hemispherical echinulate bodies in pairs in abaxial epidermis, the two members of each pair separated from each other by the thickness of the anticlinal wall lying between their bases; small crescentiform bodies in sinuosities of anticlinal walls of abaxial intercostal cells.
T/S LAMINA (Fig. 43 18; Fig. 45 1,2)

Widely flanged V-shaped with additional lateral wings; keel small, prominent, acute; margins (of wings, not true margins of leaf) gradually tapered to narrowly rounded points.

**Epidermis**: adaxial of true lamina bulliform except overlying sclerenchyma strand at angle; abaxial of conspicuously smaller cells with those overlying sclerenchyma smaller than remainder: adaxial and abaxial cells of wing like those of abaxial surface of true lamina except for a conspicuous abaxial group of bulliform cells adjacent the true lamina.

**Hypodermis**: absent or comprising a single layer of translucent cells subjacent adaxial bulliform cells of midrib region, and subjacent abaxial bulliform cells of wing. **Sclerenchyma**: median v.b. with ascending crescentiform abaxial girder (which is sometimes eccentric) and adaxial crescentiform cap; v.b. opposite largest adaxial rib in each half of lamina with pulviniform or rectangular girder, adaxial crescentiform cap and massive adaxial pulviniform strand remote from v.b.; most other v.b's of true lamina with pulviniform, triangular, or sub-T-shaped abaxial girders and without adaxial sclerenchyma, but a few with tiny adaxial caps, or strands and usually one in the flange of the true lamina with both abaxial and adaxial girders, and one, obliquely oriented v.b. in the true margin with a crescentiform cap at each pole, and a few without any sclerenchyma: in wing some v.b's with abaxial and adaxial triangular girders; some with abaxial triangular or pulviniform girders or strands and without adaxial sclerenchyma or, rarely, with tiny adaxial caps; some with adaxial triangular or pulviniform girders only
and a few without any sclerenchyma. Pointed apices of margins of wings completely filled with well-developed sclerenchyma strands.

**Mesophyll**: chlorenchyma differentiated as palisade and spongy tissue, the palisade adaxial, 2-3 rows deep in the true lamina, less well developed in the wings; the spongy tissue composed of strongly-lobed cells.

**Air cavities**: none obvious apart from small substomatal cavities. **Vascular bundles** c. 23 in each half of true lamina plus c. 17 in each wing (i.e. c. 81 altogether in T/S) oval or rounded, those opposite adaxial ribs much larger than remainder, orientation of v.b's in true lamina normal, with phloem pole abaxial, except for v.b. nearest the true margin which is oblique; orientation of v.b's in wing various, some normal, some inverted and some oblique. **Bundle sheaths**: inner sheaths fibrous; outer sheaths parenchymatous, those of major v.b's extending to epidermis as sheaths to sclerenchyma girders. **Secretory cells** numerous in chlorenchyma.
4.3.3. Key to the Southern African species of Scleria
based on anatomy of lamina

1. Bulliform cells of epidermis
   restricted to median adaxial
   groove .......................................................... 2

1. Bulliform cells of epidermis
   not restricted to median
   adaxial groove ............................................. 5

2. Lamina V-shaped in profile ...... S. woodii

2. Lamina flanged V-shaped in profile .............. 3

3. Stellate cells absent from
   mesophyll ............................................. S. welwitschii

3. Stellate cells present in
   mesophyll ...................................................... 4

4. Trabeculae of translucent cells
   traversing lamina transversely;
   vascular bundles on both sides
   of lamina and in trabeculae...... S. poaeformis

4. Trabeculae of translucent cells
   absent; vascular bundles in a
   single series midway between
   adaxial and abaxial surfaces .... S. greigiifolia
5. Adaxial epidermis from median groove to major vascular bundle of true margin uninterrupted by stomata; all cells bulliform except those overlying sclerenchyma strand in angle region ...................... 6

5. Adaxial epidermis from median groove to major marginal vascular bundle interrupted by stomata; some bulliform cells present intercostally ......................... 8

6. Abaxial epidermis with bulliform cells near true margin of lamina .. S. angusta

6. Abaxial epidermis without bulliform cells ................................. 7

7. Lamina thickest at angle; major vascular bundle of angle region with adaxial sclerenchyma strand remote from adaxial sclerenchyma cap ................................. S. achtienii
S. unguiculata
S. lagoensis
S. natalensis
S. transvaalensis

7. Lamina not noticeably thicker at angle; major vascular bundle of angle region usually with adaxial sclerenchyma girder .............. S. melanomphala
8. Bulliform cells restricted to median groove and angle region .... *S. lacustris*

8. Bulliform cells not thus restricted ........................................... 9

9. Hypodermis of large translucent cells present, subjacent median adaxial bulliform and adaxial intercostal epidermal cells ...... *S. aterrima*

9. Hypodermis of large translucent cells absent ..................................... 10

10. Lamina widely V-shaped in profile . *S. per gracilis var. brachystachys*

10. Lamina flanged V-shaped in profile ............................ 11

11. Major vascular bundle of angle
   with abaxial sclerenchyma girder;
   adaxial sclerenchyma strand
   remote from bundle ........................................ 15

11. Major vascular bundle of angle
   with abaxial and adaxial sclerenchyma girders .......................... 12

12. Palisade absent or poorly differentiated .................... *S. drègeana*

12. Palisade present ................................................................. 13
13. Palisade adaxial and abaxial .......... *S. nutans*  
* S. rehmannii

13. Palisade adaxial only ................................. 14

14. Minor vascular bundle mostly with  
both abaxial and adaxial sclerenchyma  
girders ........................................... *S. longispiculata*  
with

14. Minor vascular bundles mostly abaxial  
girders; adaxial caps or strands ... *S. bulbifera*

15. Length of arm of V less than length  
of flange; number of minor bundles  
in flange between major bundle of  
angle and major bundle of margin 6–7  
(8); palisade present; substellate  
cells present ................................... *S. veseyfitzgeraldii*

15. Length of arm of V exceeding or  
equalling length of flange; number  
of minor bundles in flange between  
major bundle of angle and major  
bundle of margin 1–3 (4) .............................. 16

16. Stellate cells present in mesophyll;  
palisade present ............................... *S. foliosa*

16. Stellate cells absent from  
mesophyll; palisade present ...... *S. dieterlenii*  
* S. sobolifer*
Fig. 51. Plan of L/S ovary of Scleria natalensis (Hennessy 410) with single, basal, anatropous, bitegmic ovule.

**OP** outer, multilayered zone of pericarp: isolated cell shown in surface view and in L/S view

**MP** middle, few-layered, secretory and vascularised zone of pericarp: isolated cells shown in surface view and in L/S view

**IP** inner, single-layered zone of pericarp: isolated cells shown in surface view and in L/S view.

**S** stipe

**P** pedicel
Fig. 52. Photomicrographs of ovary of *Scleria natalensis* (Hennessy 410)

A. L/S ovary, ovule, hypogynium, stipe and pedicel (X 20)

B. L/S pericarp showing three zones, outer multilayered zone, inner, single-layered zone of translucent cells and middle, few-layered zone comprising secretory cells and vascular strands (X 128)

C. L/S solitary basal bitegmic crassinucellate anatropous ovule with curved micropyle (X 52)

D. Tangential section of part of pericarp showing cells of outer zone (right) and middle zone (left) (X 320)

E. Tangential section of part of pericarp showing secretory cells of middle zone (X 320)

F. Tangential section of part of pericarp showing cells of inner zone (X 320)
Fig. 53. Photomicrographs of T/S stipe and base of ovary of *Scleria natalensis* (Hennessy 410) (all X 52)

A. proximal part of stipe with numerous vascular traces

B. stipe shortly above base showing vascular traces converging

C. distal part of stipe with vascular traces organised in six strands, three large and three small, and silicification apparent towards centre of stipe

D. section through base of ovary with hypogynium lobe on right (unsilicified) and ovule in centre with its single vascular strand on right.
4.4. Flowers

4.4.1. Staminate flowers

Flowers reduced to 3, 2 or 1 stamen; each stamen receiving one vascular strand receptacle with two vascular bundles, one of which branches to produce a third strand if three stamens present, or with a single vascular bundle in species with a single stamen per flower.

4.4.2. Pistillate flowers (Fig. 51; Fig. 52 A-F)

Flower reduced to a stipitate ovary with a terminal, three-branched style; the stipe trigonous without hypogynous disc or lobes, or obpyramidal with hypogynous disc or lobes elaborated distally. Stipe parenchymatous except for vascular strands (see vasculature); placenta in median axile position deeply seated within tissue of stipe (interpreted by Blaser, 1941, as a perigynous tendency). Pericarp of three clearly-defined zones; outer zone multilayered, of parenchyma cells with wavy radial walls, the cells flat and shallow, without air-spaces, with chloroplasts when young; middle
zone of 2- few layers of thin-walled cells morphologically like cells of outer zone but densely packed with secretory products, the zone traversed longitudinally by vascular strands (3), the dorsal carpel bundles (Blaser, 1941); inner zone of a single layer of deep, thin-walled cells which are elongate in the plane of the circumference of the ovary, with tapered ends. Vasculature; proximal part of stipe with numerous small traces (Fig. 53 A,B) which converge in groups as they pass upwards to form three large and three smaller vascular strands (Fig. 53 C); the three large (dorsal carpel bundles, Blaser, 1941) passing upwards in the angles of the stipe, dipping once towards the junction of the stipe with the body of the achene before ascending through the pericarp into the style; the three smaller vascular strands (ventral carpel bundles, Blaser, 1941) passing upwards through the stipe to the placenta where they converge to form the single vascular strand of the solitary ovule (Fig. 53 D).
Fig. 54. Scanning Electron Micrographs of silicified achene shells of *Scleria* spp. after removal of organic matter by maceration. A-E. *S. woodii* (Henne s sy 409); F. *S. melanomphala* (Ward 5077)

A. Shell of mature achene with inner layer of pericarp intact and outer layers of pericarp removed from viewing side revealing the silicified outer tangential walls of cells of the inner pericarp and silicified radial and tangential walls of cells of the multi-layered middle and outer pericarp and stipe (X 30)

B. Shell of mature achene broken more-or-less in half to reveal the silicified inner tangential walls of cells of the inner pericarp (X 40)

C. Outer surface of outermost layer of pericarp of immature achene showing thinly silicified outer tangential walls of cells and wavy cell-outline (X 450)

D. The same layer viewed from inside, showing proud-standing silicified, wavy radial walls, with inner tangential walls absent or partially present as very thin siliceous layers with pitting evident (X 450)

E. Inner surface of inner layer of pericarp of mature achene showing silicified inner tangential cell walls and cell outlines (X 220)

F. Portion of pericarp of immature achene showing proud-standing silicified radial walls of remaining cells of inner layer of pericarp, their tangential walls removed by maceration because not silicified, and underlying cells of middle zone of pericarp with silicified radial walls, their tangential walls also absent because not yet silicified (X 100)
4.5. Fruit

4.5.1. Induration of the Fruit (Fig. 54 A-F)

When the achenes has attained its full size the style is shed and induration commences at the distal end and proceeds progressively until finally the stipe becomes silicified and the attachment of the achene to its pedicel is severed. Silica is deposited in and on the outer periclinal walls of the epidermal cells and on their radial walls and the radial walls of the cells of the underlying pericarp layers. Silicification of the inner tangential wall of the cells of the outermost layer and of outer and inner tangential walls of more deeply seated cells proceeds progressively. In the early stages unsilicified areas in these walls appear as "pits" (Fig. 54 D).

The only cells of the achene (excluding the seed) which remain unsilicified at maturity are those of the free margin or lobes of the hypogynium when one is present (Fig. 10 A-C).
Silica deposition in epidermal cells may be even (Fig. 10 A,C,E), or there may be nodular accretions standing proud as papillate protrusions from the outer surface of the achene (Fig. 10 G,H).

4.5.2. Trichomes

Achenes of some species are hirsute (see Chapter 4). A hair is an unicellular derivative of an enlarged epidermal cell, the outer tangential wall forming the hair-shaft. At maturity only the radial walls and inner tangential wall of a hair cell become silicified (Franklin, 1979, Figs. 2-20). In some species inflated epidermal cells may occur the outer tangential walls of which are not produced as hair-shafts. The outer tangential walls of such cells are either not silicified, or thinly silicified and collapse inwards at maturity (Fig. 10 H).

4.6. Discussion

Among the diagnostic anatomical characters listed by Metcalfe (1969) as being of importance and significance were those to be seen in surface-view preparations of the leaf epidermis and in
transverse sections of the lamina taken midway between its apex and the position where the lower end of the lamina joins the sheathing base of the leaf. Some useful characters were also revealed in transverse sections of the culm, while the rhizome and the root provided few characters of diagnostic value.

In this study, transverse sections of the lamina have proved to be most useful in revealing characters of diagnostic value at supraspecific and specific levels and culm anatomy has contributed some information of value, but root and rhizome anatomy, except in certain species, have provided little useful information, and features of sobole anatomy appear to be of value only at the species level.

Certain anatomical features of laminas and culms which have diagnostic value at the species level, are associated with ecological conditions, and may not be constant. In particular this is true of the type of mesophyll/ground tissue present. Stellate achlorophyllous cells in mesophyll tissue are present only in hydrophytes and are always associated with actual or potential schizogenous air cavities. In one species examined, *S. melanomphala*, plants collected from drier
habitats and those from wet habitats showed differences in the type of mesophyll present. Similarly, hypodermal translucent cells and trabeculae or partial trabeculae of translucent cells have been found only in plants from wet habitats. The occurrence of palisade chlorenchyma in addition to spongy chlorenchyma may be an advanced condition.

Another tendency seen in laminas of large hydrophilous plants in which the thickness of the lamina is greatly increased by the development of aerenchyma and air cavities, is the arrangement of vascular bundles in more than one horizontal row. In *S. lacustris* the tendency is apparent (Fig. 43 16); in *S. melanomphala* (wet form only, Fig. 45 5) it is incipient, and in *S. poaeformis* (Fig. 43 2) it is very well developed.

In culms, the chlorenchyma is invariably of the same type as in the lamina of the same plant. Hydrophytes may have what has been described by Metcalfe (1971) as "net-type" translucent ground tissue. This type of tissue breaks down to form large central air cavities, but the ground tissue of some species which is not of the net-type may do the same if the plant is growing in wet conditions.
Great caution should, therefore be employed in attributing taxonomic value to those anatomical characters which may vary with ecological conditions.

Certain anatomical characters have greater constancy and these, used in conjunction with evidence from other, such as morphological, sources, are a valuable aid in classification.

Among the characters with reliable diagnostic value among Southern African species of *Scleria* are:-

1. the mid-lamina profile.
2. the relative cell sizes in different parts of the epidermis, particularly on the adaxial as compared with the abaxial surface.
3. the occurrence of stomata in both upper and lower epidermes or their restriction to the lower epidermis.
4. the continuity or otherwise of the outer, parenchymatous bundle-sheath around the associated sclerenchyma.
5. the development, in otherwise dorsiventral leaves, of a pseudodorsiventral extension beyond the true margin.
6. the occurrence, in culms, of a sub-peripheral ring of sclerenchyma linking adjacent vascular bundles.

The shape of sclerenchyma girders/strands as a means of distinguishing taxa among Southern African representatives of the genus is of limited value, since the same basic shapes occur among all the taxa, and there may be variation even in the two halves of the same lamina in the same transverse section (Fig. 43). The repetition of similar shapes of sclerenchyma girders/strands among many species of diverse habit and habitat points to the essential homogeneity of the genus. Even the sub-T-shaped and subtriangular girders thought by Metcalfe (l.c.) to be characteristic of Scleria greigiifolia which was treated as a separate, monotypic genus, Acriulus greigiifoliu.s, can be found among other species of Scleria (Fig. 43 3,4,18,20,21,23).

Other indications of homogeneity are the occurrence in all species examined of paracytic stomata with broadly-triangular to dome-shaped cells, and of a range of the same types of silica bodies in all species.
Epidermal prickles, although varying in size and number from species to species, are structurally alike, consisting of an inflated base with a short antrorse barb. Epidermal hairs, in the species in which they occur, are also alike, being thick-walled, unicellular, with an inflated base.

Despite morphological differences, achene structure in all species examined is fundamentally alike. Whether the manner of induration of the pericarp is unique to the genus I am unable to say. Survey of literature has not yielded any reports of similar types of silicified achenes in other genera. If the wholly silicified pericarp of *Scleria* (excluding the lobes of the hypogynium in those species which possess one) is unique, its occurrence serves to emphasise the homogeneity of the genus, including *S. greigiifolia*.

Difficulties in obtaining fresh material for fixation have prevented systematic survey of ultrastructural features which provide evidence of photosynthetic pathways. The laminas of only two species, *S. sobolifer* and *S. natalensis*, have been investigated by TEM, and the mestome sheath of both specimens suggested $C_3$ type ultrastructure. At light microscope level, no evidence of a radiate arrangement of chlorenchyma such as may indicate $C_4$ metabolism was observed in any species.
On the basis of anatomical structure, it is postulated that from an ancestral stock of hygrophilous herbs with slender culms having little mechanical tissue, possessing dorsiventral leaves with narrow laminae with a V-shaped profile, with spongy mesophyll of slightly lobed cells, with the cells of the adaxial and abaxial epidermes more-or-less equal except for bulliform cells which were restricted to the median adaxial groove, with stomata more-or-less equally distributed in both surfaces, two major evolutionary lines have developed, one of which comprises more-or-less hygrophilous taxa which have retained the ancestral slender structure and narrow leaves, (Line A), and the other, (Line B), which culminates in hydrophilous taxa some of which have attained stout stature and broad laminae. Within both lines some taxa have retained some primitive characters.

Twelve of the twenty-three species of *Scleria* recorded from Southern Africa can be assigned to Line A, which comprises slender, hygrophilous forms, usually of open, grassland habitats. All are amphistomatic. Two, *S. woodii* and *S. pergracilis*, have V-shaped lamina profiles and ten have flanged-V-shaped lamina profiles. Two, *S. woodii* and *S. welwitschii*, have ad- and abaxial epidermal cells more-or-less equal with bulliform cells.
restricted to the median adaxial groove. All others have at least some intercostal adaxial epidermal cells bulliform. One, *S. aterrima*, which is more-or-less hydrophilous, has hypodermal translucent cells subjacent to the adaxial epidermis. Although most species have mesophyll at least slightly differentiated as palisade and spongy tissue, some or all specimens of four species examined, *S. welwitschii*, *S. pergracilis*, *S. drègeana* and *S. dieterlenii*, lacked palisade.

Of the eleven species which comprise Line B, all have flanged-V-shaped lamina profiles. Four, *S. lacustris*, *S. foliosa*, *S. poaeformis* and *S. greigiifolia*, are amphistomatic. Two of these, *S. poaeformis* and *S. greigiifolia*, have bulliform cells restricted to the median adaxial groove whereas *S. lacustris* has additional adaxial bulliform cells in the angle region and *S. foliosa* has at least some intercostal adaxial bulliform cells. A striking feature of seven species, *S. melanomphala*, *S. transvaalensis*, *S. natalensis*, *S. unguiculata*, *S. achtienii*, *S. lagoensis* and *S. angusta*, is that all the adaxial epidermal cells from the median groove to the major marginal v.b., except those overlying the sclerenchyma strand/girder in the angle,
region, are bulliform. Such laminas are effectively hypostomatic. The thickness of the lamina of this group of species is greatest in the angle region, giving the lamina profile a distinctive form (Fig. 43). *Scleria angusta* differs from the other members of this group in having an extension beyond the true margin, of laminar tissue which is pseudodorsiventral, a feature which by increasing the surface area and the volume of the lamina is likely to increase the photosynthetic capacity of the plant. I consider this to be an advanced condition. All species in Line B have clearly differentiated palisade and spongy mesophyll, and in most, the cells of the spongy tissue are strongly lobed, with four species, *S. lacustris*, *S. foliosa*, *S. poaeformis* and *S. greigiifolia*, having stellate chlorophyllous cells and one, *S. poaeformis*, also having stellate achorophyllous cells with silicified walls. Among the species in Line B the occurrence of translucent hypodermal cells is not infrequent and trabeculae or partial trabeculae of translucent cells occur in *S. poaeformis*, *S. lacustris* and some specimens of *S. melanomphala* and *S. transvaalensis*.

Three species, *S. poaeformis*, *S. greigiifolia* and *S. angusta*, all of them robust, have a sub-peripheral ring of sclerenchyma linking adjacent v.b's in the culm. One other, *S. lacustris*,
has very heavy sclerenchyma sheaths around the major peripheral culm bundles which although not quite confluent, closely approach such a condition. Net-type translucent ground tissue is present in culms of *S. unguiculata*, *S. poaeformis*, *S. greigiifolia* and *S. angusta*. One species *S. greigiifolia* has some amphivasal v.b's in the culm, the only character which is not shared with any of the other species examined.

Although there is a greater range of diversity of features in line B then in Line A, members of Line B have many characters in common. Their leaves all have clearly differentiated palisade and strongly lobed spongy mesophyll, which is considered to be an advanced condition. All have the outer, parenchymatous bundle-sheath continuous around the sclerenchyma girders associated with the vascular bundles, a condition rarely seen in members of Line A. Many show anatomical features of leaves and culms associated with hydrophily, which is a specialised state. The development of increased amounts of mechanical tissue in the culm has allowed some species to attain considerable height without having recourse to a semi-scandent habit.
Among Southern African members of Line A there are fewer anatomically advanced characters than among members of Line B, yet the taxa in Line A are as well adapted to their habitats as are the taxa of Line B to theirs.

Anatomical evidence therefore corroborates morphological evidence that within Scleria, evolution has been diphyletic from a common source. Line A comprises species assigned on the basis of morphological evidence to subgenus Hypoporum and Line B, to subgenus Scleria. Of the two, subgenus Hypoporum has retained a greater number of primitive morphological and anatomical characters than subgenus Scleria.
5. Distribution

The approximately 200 species (Core, 1936; Cronquist, 1981) of *Scleria* are distributed in the tropical, subtropical and warm temperate regions of both hemispheres in a zone extending from c. 40°N (except for more northerly incursions in Japan and Southeast Canada) to c. 35°S. *Scleria* is absent from Europe and Asia north of the Himalayas. Within the tropics and subtropics the genus is absent from desert areas such as the Arabian peninsula, the Sahara, the Namib and the Great Australian desert (see Fig. 1).

Members of sections Hypoporum (Nees) Endl. and *Scleria* (Berg.) Endl. are widely distributed in the Americas, Africa, Madagascar, Indomalaysia, China, Korea, Japan and Australia. The single species, *S. greigiifolia* (Ridl.) C.B.Cl. of section Acriulus (Ridl.) C.B.Cl. is recorded from Africa and Madagascar. Section Schizolepis (Nees) C.B.Cl. is represented in tropical America and Madagascar, with a single species, *S. angusta* Nees ex Kunth recorded from the African continent. A Representatives of section Ophryoscleria (Nees) C.B.Cl. are recorded from tropical America, Africa and Madagascar. Section Hymenolytrum (Nees) Core is endemic in tropical South America.

The recorded distribution of species represented in Southern Africa is shown in Table VI.
TABLE VI. Summary of recorded geographical range of the species of *Scleria* represented in Southern Africa.

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5.1. Distribution of Scleria in Africa

The genus is absent from the coast of Africa bordering the Mediterranean basin, from the Sahara and Namib deserts, and in Southern Africa from the arid west coast, the karroid regions and the south-west Cape Province.

The greatest number and diversity of species occurs in tropical latitudes (Nelmes, 1955; 1956) and within the tropics relatively few species (Napper, 1971) are present at high (and therefore temperate) altitudes.

5.2. Distribution of Scleria in Southern Africa

5.2.1. Definition of Southern Africa

Geographical limits of Southern Africa territory for the Flora of Southern Africa (F.S.A.) include the Republic of South Africa, South West Africa/Namibia, Swaziland, Lesotho, Transkei and Botswana (Ross et al., 1977).
5.2.2. Distribution of Scleria

Of the twenty-three species recorded from this region to date, fifteen have been found only in the summer-rainfall area east of the twenty-seventh parallel, and of these, six, *S. angusta* Nees ex Kunth, *S. poaeformis* Retz., *S. achtenii* De Wild., *S. natalensis* C.B.Cl., *S. greigiifolia* (Ridl.) C.B.Cl. and *S. sobolifer* E.F. Franklin are known in the region only from the subtropical, high-rainfall areas of the coastbelt as far as 32°S.

Four species, *S. woodii* C.B.Cl., *S. drègeana* Kunth, *S. rehmannii* C.B.Cl. and *S. melanomphala* Kunth have been found in the eastern summer-rainfall area and also in damp, or seasonally damp habitats in the northern Cape (*S. drègeana*), north-central Botswana (*S. woodii, S. drègeana and S. melanomphala*) and north-eastern Namibia (*S. rehmannii*). Four other species *S. lacustris* Wright ex Sauvalle, *S. longispiculata* Nelmes, *S. unguiculata* E.A. Robinson and *S. veseyfitzgeraldii* E.A. Robinson are known for our region only from north-central Botswana or north-eastern Namibia. Of
these, the distribution of *S. longispiculata* may be controlled as much by edaphic as by climatic factors. It occurs only in Kalahari sands.

It is likely that when the area is better known botanically, north-central Botswana, in particular the region around the Okavango swamp, will prove to be far richer in species of *Scleria* with both east- and west-tropical African affinities than present records indicate.

All but three of the species recorded from Southern Africa are wide-ranging on the African continent and in some cases, beyond it (Table VI). The endemic species are *S. natalensis*, *S. transvaalensis*, E.F. Franklin and *S. sobolifer*. The other twenty reach the southern limits of their distribution in Southern Africa. Robinson (1966) stated categorically that *S. welwitschii* C.B.Cl. and *S. drègeana*, both widespread in west, central and east tropical Africa, are of southern African origin, but whether this is indeed the case is a question which, in view of the present fragmentary state of knowledge of the biological history of these and
in Southern Africa.

Fig. 55. Recorded distribution of *S. woodii* C. B. C. L.
in Southern Africa.

Fig. 56. Recorded distribution of S. welwitschii C. B. Cl.
The type locality of species in southern Africa.

Fig. 57. Recorded distribution of S. rehmannii C.B.Cl.
Fig. 58. Recorded distribution of S. longispiculata Nelmes in Southern Africa.
FIG. 59. Recorded distribution of S. bulbifera Hochst.

ex A. Rich. in southern Africa.
Type locality of species

in Southern Africa.

Fig. 64. Recorded distribution of S. dieterlenii Turill.
Scleria aterrima (Ridley) Napper

Fig. 66. Recorded distribution of S. aterrima (Ridley) in Southern Africa.
ex Sauvalle in Southern Africa.

Fig. 67. Recorded distribution of S. lacustris Wright ex Sauvalle.
E. F. Franklin in Southern Africa.

Fig. 68. Recorded distribution of S. transvaalensis.
In Southern Africa, Figure 69. Recorded distribution of S. natalensis C. B. Cl.

Scleria natalensis C. B. Cl.
Fig. 70. Recorded distribution of *S. foliosa* Hochst. ex A. Rich. in Southern Africa.
E.A. Robinson in Southern Africa.

Fig. 71. Recorded distribution of S. unguiculata.
Scleria achtenii De Wild.
Fig. 75. Recorded distribution of *S. paeformis* Retz. in Southern Africa.

*Scleria paeformis* Retzius
Fig. 76. Recorded distribution of *Scleria griseifolia* (Ridl.) C.B.Cr.
related taxa, must remain open.

Distribution maps of Scleria spp. in Southern Africa are presented as Figs. 55-77.

5.3. Habit and Habitat of Southern African species of Scleria

There is considerable diversity of form and of habitat preference among the species represented in the region.

Analysis (Table VII) has shown that on the basis of habit and habitat these taxa may be grouped into eight categories, five of which contain all the Southern African representatives of section Scleria, together with S. angusta (section Schizolepis) and S. greigiiifolia (section Acriulus) (categories A - E), while members of section Hypoporum fall into three categories (F - H). Members of categories A - E are all stout herbs of frost free habitats (except S. transvaalensis), whereas members of categories F - H are slender herbs with a wider range of temperature tolerance. There is anatomical and morphological similarity (see Chapter 3 and 4) among the taxa in A - E which suggests that they
E. Perennial, stout plants with annual aerial parts, of open or semi-shaded, seasonally damp areas.

<table>
<thead>
<tr>
<th>Species</th>
<th>Characteristics</th>
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<tbody>
<tr>
<td>S. <strong>transvaalensis</strong></td>
<td>(Scleria) (partly sheltered among rocks in damp grassland or damp slopes near streambanks)</td>
</tr>
</tbody>
</table>

F. Perennial, slender plants with annual aerial parts, of open, permanently wet areas.

<table>
<thead>
<tr>
<th>Species</th>
<th>Characteristics</th>
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</thead>
<tbody>
<tr>
<td>S. aterrima (Hypoporum)</td>
<td>(perennially wet sandy areas)</td>
</tr>
<tr>
<td>S. drègeana (Hypoporum)</td>
<td>(permanent bogs and wet streambanks)</td>
</tr>
<tr>
<td>S. nutans (Hypoporum)</td>
<td>(permanent bogs)</td>
</tr>
<tr>
<td>S. welwitschii (Hypoporum)</td>
<td>(permanent bogs)</td>
</tr>
</tbody>
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G. Perennial, slender plants with annual aerial parts, of open, seasonally damp areas.

<table>
<thead>
<tr>
<th>Species</th>
<th>Characteristics</th>
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<tbody>
<tr>
<td>S. veseyfitzgeraldii</td>
<td>(Hypoporum) (flood plains, seasonally inundated or saturated)</td>
</tr>
<tr>
<td>S. bulbifera (Hypoporum)</td>
<td>(wide range of tolerance)</td>
</tr>
<tr>
<td>S. longispiculata (Hypoporum)</td>
<td>(well-drained sandy soil bordering wet grassland on Kalahari sands)</td>
</tr>
<tr>
<td>S. woodii (Hypoporum)</td>
<td>(seasonally boggy areas and damp woodland in partial shade)</td>
</tr>
<tr>
<td>S. rehmannii (Hypoporum)</td>
<td>(seasonally wet bogs but also tolerant of permanent wetness)</td>
</tr>
<tr>
<td>S. sobolifer (Hypoporum)</td>
<td>(strictly coastal, in sandy soil)</td>
</tr>
<tr>
<td>S. dieterlenii (Hypoporum)</td>
<td>(strictly montane in seasonal bogs)</td>
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H. Annual, slender plants of open, seasonally damp areas.

<table>
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<tr>
<th>Species</th>
<th>Characteristics</th>
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<tbody>
<tr>
<td>S. <em>pergracilis</em> var. brachystachys (Hypoporum)</td>
<td>(seasonal bogs in neutral or acid soil)</td>
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constitute a natural series. Likewise there is close anatomical and morphological similarity among taxa in F - H, which form a natural assemblage.
6. Taxonomy

The distinctiveness of Scleria within Cyperaceae has been recognised since its placement in the tribe Sclerieae by Nees (1834). Bentham (1883), by his placement of the tribe in series Diclines drew attention to the unisexuality of its flowers. Although Pax (1886, 1887) and Eiten (1976) both placed Scleria in sub-family Caricoideae, their diagnoses of the sub-family differed markedly because of their diametrically opposite views of the interpretation of the position of the female flower in the androgynaeceous spikelet. Eiten's opinion favouring a lateral positioning of the female flower is supported by the findings made in this study of species from Southern Africa.

The tribe Sclerieae comprising the genera Becquerelia, Bisboeckelera, Calyptrocarya, Diplacrum (including Pteroscleria), and Scleria (including Acriulus), was not upheld by Eiten, on the grounds that whereas the ultimate inflorescence unit of four of these genera is a compound axis system in which the main axis which bears lateral, true, racemosely-branched spikelets of true, male flowers, terminates (apparently) in a pistil, the ultimate inflorescence unit of Scleria is a simple axis which comprises a true, racemosely-branched spikelet of true, unisexual
flowers, that is, in Scleria no branch system terminates in a pistil. Accordingly, Scleria was excluded from the assemblage and the tribe Bisboeckelereae was proposed for the other four genera.

Scleria was not assigned by Eiten to any tribe since, although two tribes, Rhynchosporeae and Cariceae have spikelets with a branching pattern similar to that of Scleria, the former has bisexual flowers and the latter has the female flower included in an utricle or a seminutricular prophyll.

Since the findings of this study support Eiten's view of the interpretation of spikelet morphology in Scleria, it is proposed that this genus be assigned to a tribe, Sclerieae and that the tribal limits be re-defined accordingly.

Thus in sub-family Caricoideae, diagnosed by Eiten (l.c.) as having true, always unisexual flowers in true, racemosely-branched spikelets, it is proposed to distinguish the tribes Bisboeckelereae and Sclerieae as follows:

Ultimate inflorescence unit compound, comprising an axis apparently terminating in a pistil, and lateral, true, racemosely-branched spikelets of true male flowers ................. Bisboeckelereae
Ultimate inflorescence unit simple, 
comprising a true, racemosely-branched 
spikelet of true, unisexual 
flowers....................... Sclerieae 
(Scleria).

It has long been recognised that Scleria 
comprises more than one infrageneric (supra- 
specific) group. Discounting Nees von 
Esenbeck's segregation of the genus into eleven 
small genera (1834-1842), the earliest sub- 
division of Scleria was that of Endlicher (1836) 
who recognised three sections, Scleria, 
Becquerela and Hypoporum. Many other treatments 
followed (see Chapter 1).

The scope of the present investigation 
has indicated that the separation proposed by 
Clarke (1894) of the genus into two subgenera, 
Hypoporum and Scleria, in which Hypoporum 
was diagnosed as comprising species with many 
bisexual spikelets and Scleria comprising 
species with bisexual spikelets few or none, 
is the most natural system proposed to date, 
since morphological and anatomical evidence 
suggests that evolution within the genus has
been diphyletic, one line comprising taxa with glomerate-spicate inflorescences, many bisexual spikelets and achenes without hypogynia, and the other, taxa with terminal and lateral panicles, bisexual spikelets few or none, and achenes with hypogynia (Fig. 78).

In later publications Clarke (1898, 1900, 1902, 1908) successively modified his concepts of infra-generic limits, without, in my opinion, improving on his original concept. In his final, posthumous publication (1908), polyphyletic descent was implied by according subgeneric rank to six groups and Becquerelia and generic rank to Acriulus.

The majority of workers since Clarke's day have assumed a monophyletic course of evolution within the genus (if Diplacrum is excluded from synonymy and Acriulus is included).

Little consensus in diagnosis of infrageneric limits, and concepts of what constitute primitive and advanced characters has been reached, largely on account of the on-going conflict in interpretation of the structure of the inflorescence, in particular of the position of the female flower in the androgynaeceous spikelet, and in interpretation of the hypogynium.
Subgenus Scleria

Ophryoscleria

Schizolepis

Acriulus

Inflorescence of terminal and lateral panicles;
bracts foliaceous; spikelets pedicillate, solitary and/or sessile, clustered; mostly unisexual; achenes hypogyniate

Elongation of proximal internodes of primary and some higher order branches;
loss of female flower from some spikelets;
loss of male flowers from some spikelets;
achene stipe elaborated distally to form hypogynium

Subgenus Hypoporum

Inflorescence simply glomerate-spicate; glomerules of many + sessile spikelets; bracts glumaceous; spikelets androgynaeceous and male; achenes without hypogynia

Shortening of internodes of primary and higher order branches; reduction of bracts; loss of female flower from some spikelets

S. lacustris

S. woodii
Inflorescence many-branched, each branch glomerate-spicate; glomerules of few, shortly-pedicillate or sessile spikelets; bracts foliaceous; spikelets androgynaeceous; achenes without hypogynia

Inflorescence a loose panicle with foliaceous bracts: spikelets solitary, pedicillate, androgynaeceous; achenes without hypogynia

Shortening of internodes of high order branches resulting in aggregation of spikelets in tight glomerules with few spikelets in each.

Fig. 38. Putative evolution, a relationship with size.
Often too much reliance has been placed as indicators of taxonomic relationships, on characters such as the annual or perennial habit which may have resulted from evolutionary convergence brought about as a result of ecological adaptation. Too little attention has been given to sources of evidence other than morphology, and far more emphasis has been placed on differences rather than on similarities between taxa.

Based on two main sources of evidence, morphology and anatomy, and a limited number of species (23 + 1), from a single geographic region (southern Africa), the following conclusions are offered:

1. The fundamental branching pattern of the inflorescence of all species of *Scleria* including *Acriulus*, is alike.

2. Modification of the fundamental type of lax panicle has occurred in two ways, each independently of the other:
   (a) by progressive contraction of all or most ramuli leading to a "glomerate-spicate" type of inflorescence
   (b) by progressive contraction of some ramuli and progressive elongation of others, leading to an "interrupted-paniculate" type of inflorescence.
3. The extremes of both types of inflorescence are highly specialised, the "interrupted-paniculate" type with progressively maturing achenes possibly being more advanced than the "glomerate-spicate" type in which achenes mature more-or-less simultaneously.

4. The androgynaecous (bisexual) spikelet is primitive.

5. Unisexual spikelets have been derived from androgynaecous spikelets by loss of:

(a) the basal female flower resulting in male spikelets

(b) male flowers resulting in:
   i) subandrogynaecous spikelets with sterile male glumes
   ii) female spikelets without male rudiments.

6. An achene with a trigonous stipe and lacking an hypogynium, is primitive.

7. An achene with an obpyramidal stipe elaborated distally as an hypogynium, is derivative.
8. An hypogynium which is elaborated to function as a flotation device to effect dispersal of the achene by water is more highly specialised than one which does not serve this function.

9. Leaves with praemorse tips are derived from leaves with their apices tapering smoothly towards the tips.

10. Use of anatomical features as diagnostic characters must be made judiciously as some anatomical characters vary with ecological conditions.

11. In leaves, the amphistomatic condition is primitive and the hypostomatic condition is derivative.

12. In leaves, a parenchyma bundle-sheath which is continuous around the sclerenchyma associated with a v.b. is more highly specialised than one which is not continuous around the associated sclerenchyma.

13. In culms, the absence of a peripheral ring of mechanical tissue linking adjacent vascular bundles is primitive and the presence of such a ring is advanced.
The occurrence of taxonomically useful characters among Southern African species of *Scleria* together with *S. racemosa* Poir. which has not been recorded from the F.S.A. region but which occurs in Mozambique, is shown in Table VIII.

It is immediately apparent from this table that Southern African species fall naturally into two categories, which are equivalent to Clarke's two subgenera, *Hypoporum* and *Scleria* (1894).

The twelve locally represented species of subgenus *Hypoporum* have provisionally been placed in a single section, *Hypoporum*. The species with the least-contracted inflorescence, *S. woodii* is undoubtedly the least specialised, and those with the most-contracted inflorescences, *S. nutans* and *S. aterrima* are probably the most specialised in this regard. Until all members of the subgenus over the whole range of their distribution have been analysed, I am of the opinion that further delimitation of sections in the sub-genus is impossible.
The eleven locally represented species of subgenus Scleria and a twelfth species, *S. racemosa* from Mozambique, have provisionally been placed in four sections. In section Scleria have been placed all species which usually have at least some subandrogyneceous spikelets in the inflorescence. Sections Acriulus, Schizolepis and Ophryoscleria comprise those species which lack any distal male rudiments in the female spikelets and are therefore more advanced than members of section Scleria.

The hypogynia of members of sections Scleria and Acriulus have smooth margins, those of section Schizolepis have fimbriate margins and those of section Ophryoscleria have ciliate margins.

The leaves of local representatives of sections Schizolepis and Ophryoscleria are praemorse whereas those of local species belonging to other sections are not. However, there are members of section Scleria and some specimens of *Scleria greigiifolia* from other regions which may have praemorse leaves. Such leaves occur only among more highly specialised members of subgenus Scleria, never in Hypoporum.

The member of section Scleria with the least-specialised inflorescence and the least-developed hypogynium is *S. lacustris*. It is also the only
local representative of the subgenus which invariably has some fully androgynaeceous spikelets. To cyperologists who believe that evolution in Scleria has been monophyletic, the placement of this species, and others which have a similar constellation of morphological characters such as the Malaysian S. junghuhniana, has been problematical. In a diphyletic scheme such as I propose, its placement poses no problems (Fig. 78).

The line between sections Scleria and Acriulus is a thin one. Were it not for the strictly female spikelets, the strongly beaked achene, the presence of amphivasal vascular bundles in the culm, and the hirsute adaxial surface of the glumes of S. greigiifolia, it would fall naturally into section Scleria. The zoniform hypogynium with its smooth margin very closely resembles that of S. melanomphala, although its panicles are much more lax than are those of this species. Although S. greigiifolia is provisionally placed in section Acriulus, future analysis of other species from other regions may show that the characters enumerated above are shared, in which event S. greigiifolia would have to be placed in section Scleria and the diagnosis of the section amended slightly.
Sections Schizolepis and Ophryoscleria are distinguished by the form of their hypogynia. In both sections the hypogynium is elaborate, that of section Schizolepis being superficially papillose at high resolutions and having a deeply fimbriate margin, and that of section Ophryoscleria being greatly enlarged, cupuliform, exceeding the achene in width and conferring buoyancy on the fruit which may be advantageous in an aquatic habitat. The highest level of specialisation has been attained in Ophryoscleria.
6.1. Description of Genus


**Habit:** monoecious annual herbs with fibrous roots or stout or slender monoecious perennial herbs with short or long, horizontal, oblique or descending, fleshy or woody rhizomes or with more-or-less horizontal subterranean soboles, or with both rhizomes and soboles. **Culms** solitary or more-or-less tufted, erect or scandent, trigonous or triquetrous, leafy towards the base or throughout, smooth or more usually scabrid on the angles, glabrous or hairy. **Leaves** 3-ranked, narrowly to broadly linear with sheathing bases, more-or-less smooth to scabrid on the margins and the 3-5 principal ribs, glabrous or hairy, the lowermost represented by almost bladeless or bladeless sheaths; **laminas** tapering smoothly towards apex or suddenly narrowed at unequal distances on each side from the apex ("praemorse"); profile more-or-less V-shaped, flanged V-shaped, or in the praemorse species flanged V-shaped distally and with additional lateral wings to the flange proximally; **sheaths** closed, sometimes shortly 3-winged, the mouth truncate, concave, convex or produced into a short tongue. **Inflorescence** paniculate with a lax or compact terminal panicle and usually one or more lateral panicles, with (rarely without) foliaceous bracts, or branched or simply glomerate-spicate with more-or-less glumaceous bracts. **Spikelets** androgynaeceous and male, or female and male, the functionally female spikelets sometimes subandrogynaeceous; **androgynaeceous spikelets** with one basal or sub-basal, lateral female floret and 1 - several upper male florets some of which may be sterile; functionally
female spikelets with 2-4 empty glumes proximally, one sub-basal lateral female floret and 1-several empty glumes (sterile male florets) distally. (subandrogyneceous), or lacking sterile distal glumes; male spikelets with (usually) 1-2 sterile glumes proximally and several to many male florets of which the distal few may be sterile. Flowers unisexual, solitary in axils of spirally arranged glumes. Male flowers consisting of 1-3 free stamens; anthers bithecate, linear, often apiculate. Female flowers consisting of a tricarpellary, unilocular ovary with a terminal style branched above into 3 filiform stigmas, deciduous, or, rarely, the base persistent. Achenes ovoid, ellipsoid or subglobose and obscurely or obtusely trigonous, or strongly trigonous, smooth or variously sculptured, glabrous or hairy, with silicified pericarp, whitish, grey, brown, purple or violet, lustrous or dull, borne on a trigonous or obpyramidal gynophore (stipe) which is sometimes expanded at the apex into a persistent, triangular, trilobed, zoniform or cupulate hypogynium with entire, fimbriate, or ciliate margin.

6.2. Descriptions of subgenera and sections represented in Southern Africa

6.2.1. Subgenus Hypoporum (Nees) C.B. Clarke in Hooker f., Fl. Brit. Ind. 6 : 685 (1894)

Habit: medium sized to small, sometimes very slender, annual or perennial herbs, the perennial species rhizomatous or soboliferous or with both rhizomes and soboles. Leaves evenly spaced along length of culm or crowded towards base of culm,
narrow (2 mm) or broad (to 9 mm) tapering evenly towards apex, glabrous or hairy, the ribs and margins scaberulous or smooth. Inflorescence terminal, glomerate-spicate, branched or unbranched, with more-or-less glumaceous bracts. Spikelets all bisexual (androgyneceous) or bisexual and male. Achenes smooth or variously sculptured, glabrous, the stipe trigonous. Hypogynium absent.

6.2.1.1. Section Hypoporum (Nees) Endlicher, Gen. PI. 112 (1836).

Characters of sub-genus

6.2.1.1.1. Species recorded from Southern Africa (twelve)

S. woodii C.B.Cl.
S. welwitschii C.B.Cl.
S. rehmannii C.B.Cl.
S. longispiculata Nelmes
S. bulbifera Hochst. ex A. Rich.
S. veseyfitzgeraldii E.A. Robinson
S. drègeana Kunth.
S. sobolifer E.F. Franklin
S. pergracilis (Nees) Kuntz var. brachystachys Nelmes
S. dieterlenii Turrill.
S. nutans Willd. ex Kunth
S. aterritma (Ridl.) Napper
6.2.2. Subgenus Scleria (Bergius) C.B. Clarke in Hooker f., Fl. Brit. Ind. 6: 686 (1894)

Habit: tall, (to 2.5 m) stout, rhizomatous perennial herbs, or medium-sized rhizomatous perennial herbs, or medium-sized annual herbs. Leaves evenly spaced along length of culm or crowded towards base of culm, narrow, broad or very broad (to 4 cm), tapering evenly towards apex or abruptly and unequally narrowed in the distal part (praemorse), glabrous or hairy, the ribs and margins scabrid or scaberulous. Inflorescence paniculate, the panicles lax or contracted, terminal and lateral, with foliaceous bracts. Spikelets androgynaeceous (rarely), subandrogynaceous, female and male. Achenes smooth or variously sculptured, glabrous or hairy, the stipe obpyramidal. Hypogynium present.

6.2.2.1. Section Scleria (Bergius) Endlicher, Gen. Pl. 112 (1836)

Habit: tall, (to 2 m), stout, rhizomatous perennial herbs (S. poaeformis) or medium-sized rhizomatous perennial herbs, or medium sized annual herbs. Leaves evenly spaced along length of culm or crowded towards base of culm (S. poaeformis), very broad (to 4 cm) (S. poaeformis), broad, or narrow (S. unguiculata), usually tapering smoothly towards apex. Inflorescence paniculate, the panicles lax or contracted, terminal, and lateral, with foliaceous bracts, or in S. poaeformis, terminal, usually without foliaceous bracts. Spikelets androgynaeceous (rarely,
380.

S. lacustris), subandrogynaeceous, female and male. Achenes smooth or variously sculptured, glabrous or hairy; beakless or almost so, the stipe obpyramidal. Hypogynium strongly or obscurely trilobed, rarely zoniform, (S. melanomphala), the margin entire, glabrous.

6.2.2.1.1. Species recorded from Southern Africa (nine)

S. lacustris Wright ex Sauv.
S. transvaalensis E.F. Frank.
S. natalensis C.B.Cl.
S. foliosa Hochst. ex A. Rich.
S. unguiculata E.A. Robinson
S. achtenii De Wild.
S. lagoensis Boeck.
S. melanomphala Kunth
S. poaeformis Retz.

6.2.2.2. Section Acriulus (Ridley) C.B. Clarke in Thisdt.-Dyer, Fl. Trop. Afr. 5: 496 (1902)

Habit: tall (to 2 m), stout, rhizomatous perennial herbs. Leaves crowded towards base of culm, broad, tapering smoothly towards apex, or, rarely, abruptly and unequally narrow in the distal part, glabrescent or hispidulous, the ribs and margins smooth or scabrid. Inflorescence paniculate, lax, terminal and lateral with foliaceous bracts. Spikelets female and male. Female glumes densely hirsute on adaxial surface. Achenes smooth, glabrous, strongly
beaked. Hypogynium zoniform, the margin entire, glabrous.

6.2.2.2.1. Species one: present in Southern Africa.

S. greigiifolia (Ridl.) C.B.Clarke in Hooker f., Fl. Brit. Ind. 6 : 694 (1894)

Habit: tall (to 2.5 m), stout, rhizomatous, perennial herbs. Leaves evenly spaced along length of culm, broad, usually abruptly and unequally narrowed in the distal part, glabrous, the ribs and margins scabrid. Inflorescence paniculate, terminal and lateral, with foliaceous bracts. Spikelets female and male. Achenes smooth, glabrous, beakless. Hypogynium trilobed, the margin fimbriate, the fimbriae papillose.

6.2.2.3.1. Species recorded from Southern Africa (one)

S. angusta Nees ex Kunth

6.2.2.4. Section Ophryoscleria (Nees) C.B. Clarke in Urban, Symb. Antill. 2 : 138 (1900)

Habit: tall (to 2.5 m), stout, rhizomatous perennial herbs. Leaves
evenly spaced along length of culm, broad, usually abruptly and unequally narrowed in the distal part, glabrous or, rarely, hispidulous, the ribs and margins scabrid. Inflorescence paniculate, lax, terminal and lateral, with foliaceous bracts. Spikelets female and male. Achenes smooth or various, sculptured, glabrous or sparsely hairy, shortly beaked; with persistent style-base. Hypogynium cupulate, broader than the achene, the margin ciliate.

6.2.2.4.1. Species recorded from Southern Africa (F.S.A. region) none, but section represented in Mozambique S. racemosa Poir.
6.3.1. Artificial Key to the Southern African species of *Scleria*

1. Fertile spikelets predominantly unisexual; hypogynium present ..................................... 2

1. Fertile spikelets predominantly androgynaeceous; hypogynium absent or poorly developed ........................................ 11

2. Lamina usually abruptly narrowed towards apex (praemorse); hypogynium margin fimbriate ........ 23. *S. angusta*

2. Lamina tapering smoothly towards apex; hypogynium margin entire ................................ 3

3. Leaves (1) - 2 - 4 cm broad; inflorescence terminal, without foliaceous bracts; hypogynium obscurly 3-lobed; achene more-or-less globose, smooth, glabrous, greyish-white ............... 21. *S. poaeformis*

3. Leaves less than 2 cm broad; inflorescence terminal and lateral, with foliaceous bracts; hypogynium 3-lobed or collar-like without defined lobes; achene smooth or patterned, glabrous or hairy .......................................................... 7

4. Achene hairy (at least proximally) .................................... 5

4. Achene glabrous ............................................................ 7
5. Achene hairy proximally, glabrous
distally, smooth or faintly
striate-lacunose; female glumes
glabrous .......................... 19. S. lagoensis

5. Achene hairy distally and
proximally, patterned; female
glumes glabrous ................................

6. Achene very faintly reticulate-
lacunose, male spikelets 7-9 mm
long; lateral panicles single at
the nodes ............................. 18. S. achtenii

6. Achene distinctly tesselate-
lacunose, male spikelets 3-5 mm
long; lateral panicles 2-4(5) at
the nodes ............................. 17. S. unguiculata

7. Achene patterned ..................................

7. Achene smooth ..................................

8. Plant caespitose, without rhizome,
annual; achene alveolate-
lacunose .................................. 16. S. foliosa

8. Plant rhizomatous, perennial;
achene reticulate-lacunose to
tuberculate-lacunose ........................
9. Culm bases not or hardly swollen, 3-4 mm in diameter; foliaceous bract of terminal panicle ensiform, 3-4 mm broad 20 mm behind apex, exceeding inflorescence .............. 15. S. natalensis

9. Culm bases swollen, 9-10 mm in diameter; foliaceous bract of terminal panicle subulate, 1-2 mm broad 10 mm behind apex, sometimes exceeding inflorescence 14. S. transvaalensis

10. Panicles compact, 1 - 2 -(4); female glumes 7-11 mm long, glabrous adaxially; achene ovoid, beakless, greyish-white proximally, blackish around style-base........ 20. S. melanomphala

10. Panicles lax, many; female glumes 6-7 mm long, densely villous adaxially in distal half; achene broadly ovoid, distinctly beaked, pinkish brown, sometimes with violet blotches ............ 22. S. greigiifolia

11. Plants without any subterranean propagative stem; adventitious roots present at base of culm and sometimes from several of the nodes above the base (S. lacustris) ..................

11. Plants with long or very short rhizomes, or soboles ("stolons"), or both ........................................
12. Inflorescence of terminal and lateral panicles, the branches glomerate-spicate, subtended by foliaceous bracts; leaves 10 mm or more wide .......... 13. S. lacustris

12. Inflorescence simply glomerate-spicate or very shortly branched towards the base; bracts more-or-less glumaceous ..................

13. Leaves 1-2 mm wide; achene sub-globose, obscurely trigonous, trabeculate-tuberculate .......... 9. S. pergracilis var. brachystachys

13. Leaves 2-7 mm wide; achene obovoid, acutely trigonous strongly reticulate-trabeculate .......... 6. S. veseyfitzgerald

14. Culms distinctly bulbous and more-or-less woody at the base ........ 5. S. bulbifera

14. Culms not, or only very slightly bulbous at the base ....................

15. Culms arising in a more-or-less straight series from a hard horizontal rhizome at least 2 mm thick ................................

15. Culms and rhizomes not as above ................................

16. Glumes hairy ................................

16. Glumes glabrous or glabrescent ................................

17. Glomerules reflexed at maturity; hairs on glumes blackish; achene stipe pale .............. 11. S. nutans

17. Glomerules not reflexed at maturity; hairs on glumes pale; achene stipe black .............. 4. S. longispiculata
18. Inflorescence rhachis 6-25 cm long, flexuous; spikelets 5-8 mm long; glumes fulvous to castaneous at maturity, glabrous or glabrescent ................. 2. S. welwitschii

18. Inflorescence rhachis less than 15 cm long, stiffly erect, spikelets 4-5 mm long; glumes reddish-brown to dark brown at maturity, glabrous ............. 3. S. rehmannii

19. Lower glumes hairy .................................................

19. Lower glumes glabrous or sparsely ciliate on margin and keel distally.............................

20. Glomerules reflexed at maturity;
achene smooth .................... 12. S. aterrima

20. Glomerules not reflexed at maturity;
achene trabeculate-verrucose .... 10. S. dieterlenii

21. Plant without true rhizome, spreading by means of long, hard, horizontal, culm-like soboles with internodes 8-47 mm long; achene with a series of deep horizontal troughs separated by horizontal and vertical ridges at junction of stipe and body ........ 8. S. sobolifer

21. Plant not as above ....................................................
22. Plant caespitose or sometimes with rhizome with very short internodes and more-or-less contiguous culms, or with one or a few soft, slender, spreading soboles; inflorescence unbranched or with few basal branches; achene smooth at junction of stipe and body........7. S. drègeana

22. Plant usually with a single, soft, fleshy, strongly scented tuberous rhizome which shrinks markedly soon after removal from soil; inflorescence profusely branched, branches delicate ..... 1. S. woodii
6.3.2. Key to the Southern African species of Scleria for use in the field

1. Plants tall (to 2.5 m) and stout, or medium-sized; inflorescence paniculate .................................................. 2

1. Plants medium-sized to small (0.5 m), sometimes very slender; inflorescence glomerate-spicate, branched or unbranched ............................................. 11

2. Leaves abruptly and unequally narrowed towards the apices; shade-dwelling in coastal swamp-forest; Transkei, Natal ........ 23. S. angusta

2. Leaves tapering smoothly towards apices .......................................................... 3

3. Inflorescence terminal, without foliaceous bract; leaves more-or-less 4 cm broad, thick and spongy proximally; forming dense stands in open coastal pans; Natal, north of Tugela River ........... 21. S. poaeformis

3. Inflorescence terminal, or terminal and lateral, with foliaceous bracts ................................. 4

4. Achene hairy .......................................................... 5

4. Achene glabrous .......................................................... 7
5. Achene hairy proximally, glabrous towards and on top; open damp habitats; known for our area from a single gathering made in Swaziland .................. 19. S. lagoensis

5. Achene hairy proximally and on top .................................................. 6

6. Lateral panicles single at each node; male spikelets 7-9 mm long; achene hairs white; open damp habitats on Natal coastbelt ...... 18. S. achtenii

6. Lateral panicles 1-3 or more at each node; male spikelets 3-5 mm long; achene hairs golden; open wet habitats; known for our area only from northern Botswana ...... 17. S. unguiculata

7. Achene patterned ................................................................. 8

7. Achene smooth ................................................................. 10

8. Plants caespitose, without rhizome; achene smooth on top, patterned proximally; annual in open, seasonally wet habitats inland; Swaziland, Transvaal and northern Namibia ......................... 16. S. foliosa

8. Plants rhizomatous, perennial ................................. 9
9. Panicles lax, pale greenish-yellow; bracts broad, over-arching their panicles; culm bases not or hardly swollen; partly shaded streambanks in margins of coastal forest; Natal and Transkei .......... 15. S. natalensis

9. Panicles dense, golden or reddish; bracts narrowed towards apices, not conspicuously overarchig their panicles; culm bases swollen to c. 1 cm diameter; open, damp habitats or semi-sheltered by banks or among rocks; northern and eastern Transvaal, Swaziland and known from one locality (Nkandla) in Natal ....................... 14. S. transvaalensis

10. Leaves evenly spaced along length of culm; panicles very compact, spike-like, dark reddish-brown; achene ovoid, beakless, grey with black apex; in, or on periphery of open, wet, frost-free habitats in Transkei, Natal, Transvaal, Swaziland and northern Botswana ......................... 20. S. melanomphala

10. Leaves crowded towards base of culm; panicles lax, very copiously branched, dark reddish-brown; achene ovoid, strongly beaked, pale brown sometimes with violet blotches; in, or on periphery of open, wet, frost-free coastal habitats in Southern Natal and known from one locality near Lake St. Lucia .................. 22. S. greigiifolia
11. Plants with subterranean propagative stems .................................................. 1:

11. Plants without propagative stems: annual .................................................. 1:

12. Plants medium sized, aquatic, with floating roots at several basal nodes of culm; inflorescence stiffly branched, the branches glomerate-spicate; bracts subfoliaceous; in rivers or lakes; northern Botswana .... 13. *S. lacustris*

12. Plants slender, caesitose; leaf profile very flattened V-shaped without lateral flanges, margins slightly recurved; inflorescence simply glomerate-spicate or with one short basal branch; in seasonally wet areas; recorded only once from our area near Dundee in Natal ..................... 9. *S. pergracilis var. brachystachys*

13. Achene acutely trigonous, rhizome very short, more-or-less vertical and difficult to discern; culm bases thickly invested with numerous dry leaf-sheaths; leaves mostly short-bladed, crowded towards base of culm; seasonal flood-plains in Caprivi Strip ............... 6. *S. vesevfitzgeraldii*

14. Culm bases distinctly bulbous and woody; leaves subequally spaced along length of culm; inflorescence simply glomerate-spicate or with 1-several basal branches; widespread in open, seasonally damp grassland; Transkei, Natal, Transvaal, Swaziland .......................... 5. S. bulbifera

14. Culm bases not, or only very slightly bulbous .................................................. 1

15. Rhizome woody, at least 2 mm thick, elongate, more-or-less horizontal, with culms arising at intervals from it .................................................. 10

15. Rhizome and culms not as above ........................................ 10

16. Glumes densely hairy .......................................................... 11

16. Glumes glabrous or very sparsely hairy .................................................. 13

17. Glomerules reflexed at maturity; hairs on glumes mostly reddish-black; leaves more-or-less evenly spaced along length of culm; open, permanent bogs; Transkei, Natal, Transvaal ...... 11. S. nutans

17. Glomerules not reflexed at maturity; hairs on glumes pale; achene stipe black; open, damp grassland in sandy soil; northern Namibia and northern Botswana ... 4. S. longispiculata
18. Inflorescence simply glomerate-spicate or sparingly branched, usually drooping, spikelets dull straw coloured, large (5-8 mm long); open, permanent bogs; Natal midlands and uplands, Transvaal, Swaziland .............. 2. S. welwitschii

18. Inflorescence simply glomerate-spicate or sparingly branched, stiffly erect, spikelets reddish-brown, small (4-5 mm long); open, seasonally or permanently wet grassland; Transvaal, northeastern Namibia ................. 3. S. rehmannii

19. Glomerules reflexed at maturity, glumes densely hairy, the hairs purplish-black; leaves crowded towards base of culm; plant apparently caespitose because rhizome very short; sometimes with one or more soft fleshy soboles arising from culm-cluster; open, permanently wet areas in sandy soil; Transkei, Natal, Transvaal ......................... 12. S. aterrima

19. Glomerules not reflexed at maturity .................................................. 20

20. Perennating stem wholly or partly softly tuberous, swollen ...................... 2

20. Perennating stem not swollen and tuberous ...................................... 2
21. Rhizome descending, very slender becoming swollen and softly tuberous towards the tip; slender, delicate, caespitose, strictly montane plants of open, seasonally wet habitats; Cape, Transvaal, Natal, Lesotho .......................... 10. *S. dieterlenii*

21. Rhizome horizontal or oblique, the internodes of young rhizomes pearly-white or pink, swollen and softly tuberous, very strongly scented; lamina profile V-shaped without lateral flanges; inflorescence copiously branched, branches delicate; glomerules of few spikelets; open seasonally wet habitats or damp woodland in partial shade; Transkei, Natal, O.F.S., Transvaal, Lesotho, Swaziland .......................... 1. *S. woodii*

22. Culms clustered, sometimes with one or more soft, terete soboles from base of culm-cluster; true rhizome very short, linking closely-clustered culm bases; inflorescence simply glomerate-spicate or sparing branched towards base; open, permanently wet habitats; northern and eastern Cape, Transkei, Natal, Transvaal, Lesotho, Swaziland, northern Botswana .... 7. *S. drègeana*

22. Culms usually solitary, widely spaced, linked by hard, trigonous, red-speckled soboles with internodes at least 8 and up to 47 mm long; inflorescence simply glomerate-spicate; strictly coastal in open, seasonally wet habitats in sandy soil; Natal .............. 8. *S. sobolifer*
6.4. Descriptions of species


Type: South Africa, Zululand, Wood 3994 (K, Lectotype; NH, BOL, isotypes)

Habit; slender rhizomatous perennial.
Rhizome 2 - 4 mm thick, soft, fleshy, brittle, pearl white or pink, strongly scented, the swollen internodes 2 - 8 mm long; scales pink. Culms usually solitary, 25 - 75 cm tall, glabrous or sparsely hairy. Leaves 1 - 3 mm wide, glabrous or sparsely hairy; sheaths glabrous or sparsely hairy, the mouth truncate or concave, densely hirsute to glabrescent. Inflorescence branched, 8 - 20 cm long; branches simple or compound, short and rigid or up to 10 cm long and nodding, each branch bearing 1 - 3 (4) sessile glomerules of 1 - 6 spikelets, the upper glomerules subcontiguous, the lower up to 5 cm apart, erect; bracts shortly glumiform at the base, glabrous or sparsely scaberulous-ciliate, the midrib excurrent into a scabrid awn 1 - 10 mm long, straight or curved. Spikelets 3.5 - 5 mm long. Female glumes 2.5 - 3 mm long, glabrous, the midrib excurrent into a smooth or sparsely scaberulous awn up to 2 mm long, pale with fine red striae. Male glumes 3.5 - 4.5 mm long, glabrous, muticous or midrib excurrent into a very short awn, reddish-brown with darker striae. Achene 1.5 - 1.8 mm long, 1 - 1.5 mm broad, ovoid to subglobose, obscurely trigonous, glabrous, smooth, tuberculate or
transversely verrucose (even on the same plant), pale grey.

**Distinguishing Characters**

- **Rhizome**: soft, fleshy, tuberous, pearly-white or pink, strongly scented.
- **Culms**: usually solitary, slender.
- **Lamina**: profile V-shaped, without flange.
- **Inflorescence**: profusely branched, the branches delicate.
- **Glumes**: glabrous.
- **Achene**: glabrous, smooth or tuberculate-trabeculate, pale grey.

The delicate, branched inflorescence and strongly scented tuberous rhizome make this species easy to recognise.

**Specimens Examined**

**BOTSWANA**

- **1824** (Kachikau) (-CB) N district, Zwezwe flats, v. 1977 P.A. Smith 2033 (PRE).

**SOUTH AFRICA, TRANSVAAL**

- **2428** (Nylstroom) (-CB) Waterberg district, Nooitgedacht 699, ii. 1942, Acocks and Naudé 76 (PRE).
- **2528** (Pretoria) (-CA) Rietvallei 221, N position, margin of seepage in NW corner, 1500 m, iii. 1945, Acocks 11340 (K, PRE).
- **2530** (Lydenburg) (-BD) Witklip, i. 1974, J.P. Kluge 403 (PRE).
(Komatipoot) (-CA) Rhenosterkop, 6 km SE of Nelspruit, iii. 1980, J. Onderstall 388 (PRE).

(Johannesburg) (-AA) Houghton Estate, ii. 1923, Moss s.n. (K); Birchleigh, iv. 1925, Moss 11207 (J); Frankenwald, iv. 1934, D. Weintraub s.n (J); ii. 1951, H.B. Gilliland 25046 (PRE, J); Bryanston, iii. 1955, T.M. Pellatt s.n. (J).

SWAZILAND

(Mbabane) (-AD) Manzini (Bremersdorp) district, i. 1944, Mogg A7 (K, PRE).

(-DB) marshy bank of Usutu R. 10 miles above Banya, ii. 1979, R.W. Haines 7031 (PRE).

NATAL

(Ubombo) (-DA) West side Mbazwane/Mkuze swamps, 15 m, i. 1974, Ward 8494 (PRE).

(Harrismith) (-CB) Bergville district 8 miles from Bergville on Rustenburg road, xii. 1958, Edwards 2405 (PRE, NU).

(-CC) Cathedral Peak Forest Reserve station, xii. 1950, Killil 1222 (K, PRE, NH, NU); i. 1951, Killick 1254 (K, NH, NU).

(Dundee) (-AA) near Glencoe, i. 1893, Wood 4757 (NH).

(-DD) Kranskop district between Kranskop and Jameson’s Drift near old mill, i. 1959, K.D. Gordon-Gray (NU, UD-W).
2832  (Mtubatuba)  (-AD) Dukuduku Forest area, xi. 1976, Ward 9071 (PRE).

2929  (Underberg)  (-AB) Cathkin Park Estate, i. 1982, E.F. Hennessy 431 (UD-W); 438 (UD-W).

(-BA) Estcourt district Tabamhlope Research Station, xii. 1943, Acocks 10007 (PRE, NH).

(-BB) Highlands, Station ix. 1894, O. Kuntze s.n. (K); near Mooi River, 4000 ft, xii. 1898, Mason 64 (NH). 


(-DB) Impendle district farm Tillietudlum, iii. 1955, K.D. Hunt 910 (NU); upper Umkomaas, i. 1966, Killick and Vahrmeijer 3683 (K, PRE).

2930  (Pietermaritzburg)  (-AC) Lions River district, Lidgetton, undated, Mogg 896 (PRE).


(-DB) Inanda Game Park xii. 1974, Ward 8738 (PRE).
2931

(Stanger)  (-AB) Zululand, near Inyoni River, iv. 1888, Wood 3994
(K, lectotype, NH, BOL, isotypes).

3028

(Matatiele)  (-DA) Mount Fletcher, 4700 ft, i. 1962, Acocks 21929 (K, PRE).

LESOTHO

2828

(Bethlehem)  (-CC) Leribe slopes, received 1919, Dieterlen 766 b (PRE).

SOUTH AFRICA, ORANGE FREE STATE

2828

(Bethlehem)  (-DA) Golden Gate National Park, i. 1965, B.R. Roberts 3087 (PRE).

(-DB) Bester's vlei, near Witsieshoek, xii. 1893, Bolus 8274 (PRE, BOL); 1894, Flanagan 2035 (PRE).

CAPE

3227

(Stutterheim)  (-AD) Fort Cunynghame, xii. 1900. Sim 2705 (NU).

(-CB) Dohne Hill, iii. 1891, Sim 197 (PRE).

(-DB) grassy valleys near Komgha, xii. 1891, Flanagan 954 (PRE, BOL).

TRANSKEI

3228

(Butterworth)  (-AD) Kentani district, 360 m, ii. 1907, Alice Pegler 1421 (K); ii. 1901, 1498 (K).


*S. junciformis* Welw. in Ridl. in Trans. Linn. Soc., ser. 2, Bot. 2: 168 (1884), non Thwaites (1864), nom. illegit.


**Habit**, tall, slender, rhizomatous perennial. **Rhizome** 3 - 4 mm thick, woody, red, straight or sinuous, scales stramineous-reddish. **Culms** 30 - 100 cm tall, 1 - 2 mm thick, villous to glabrescent, arising at intervals of 5 - 7 mm from the rhizome. **Leaves** 2 - 3 mm wide, glabrous to densely villous, lowermost reduced to almost bladeless sheaths; **sheaths** glabrous to densely villous, the mouth produced into a triangular or rounded, densely villous or glabrescent tongue 1 - 2 mm long. **Inflorescence** (6) - 15 - 25 cm long, simply branched with branches up to 10 cm long, lax and drooping; rarely unbranched. **Glomerules** 3 - 8, of 1 - 2 (-6) erect, sessile spikelets, the upper from contiguous to twice their own length apart, the lower 3 - 5 (-10) cm apart. **Spikelets** 5 - 8 mm long. **Bracts** inconspicuous, glumiform, shortly awned, glabrous to minutely scaberulous distally, much shorter than the glomerule. **Glumes** 3 - 5 mm long, usually with midrib excurrent into an awn 0.25 - 0.5 mm long, glabrous or minutely hispidulous distally, pale stramineous with a few faint reddish streaks or wholly castaneous.
Achene 1.5 - 1.8 mm long, 1 - 1.2 mm broad, ellipsoid to ovoid, glabrous, smooth, grey.

**Distinguishing Characters**

<table>
<thead>
<tr>
<th>Character</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>Rhizome</td>
<td>horizontal, woody.</td>
</tr>
<tr>
<td>Inflorescence</td>
<td>sparingly long-branched glomerate-spicate or simply glomerate-spicate, flexuous.</td>
</tr>
<tr>
<td>Spikelets</td>
<td>5 - 8 mm long.</td>
</tr>
<tr>
<td>Glumes</td>
<td>glabrous or glabrescent, fulvous pale stramineous.</td>
</tr>
<tr>
<td>Achene</td>
<td>smooth or tuberculate, grey, light brown or chestnut-coloured, the stipe pale.</td>
</tr>
</tbody>
</table>

This species may be confused with *S. rehmannii* from which it is distinguished by its flexuous, often long-branched inflorescence its longer spikelets and its differently coloured glumes.

**Specimens Examined**

**ANGOLA**

+ 1413 Huilla, deep grass-grown wooded meadows near Catumba, iii. 1860, *Welwitsch* 7138 (BM, lectotype*)

**MALAWI**

1036 (-BA?) Nyika Plateau, Lake Kaulime, i. 1959, Robinson 3027 (NU).

**ZIMBABWE**

1832 (-CA) Inyanga district, Inyanga Mountains, i. 1961, H. Wild 5467 (NU).
SOUTH AFRICA, TRANSVAAL

2529  (Witbank) (-CB) Middelburg, vlei W of Eerstekamp, x. 1968, C.J. du Plessis 880 (PRE).

2627  (Potchefstroom) (-BB) Witwatersrand division, Witpoortje Kloof, ii. 1922, Moss 6583 (K, J).

SWAZILAND

2631  (Mbabane) (-AA) Forbes Reef swamp, xi. 1961, Compton 30964 (PRE); Forbes Reef, vlei alongside main road to Mbabane, i. 1965, K.D. Gordon-Gray 6096 (PRE, NU).

(-AC) Black Umbuluzi valley swamp, xii. 1963, Compton 31872 (PRE).

SOUTH, AFRICA, NATAL

2829  (Harrismith) (-BA) Glencoe, Biggarsberg 1200-1500 m, ii. 1893 Wood 4757 (K).

2929  (Underberg) (-BC) Highmoor Forest station S of Giant's Station, i. 1978, L. Smook 1058 (PRE).

(-CB) Cobham Forest Reserve near Sani Pass road, iii. 1975, E.F. Hennessy 408 (NU, UD-W); Bamboo Mountain, N face, 6000 ft, iv. 1977, Hilliard and Burtt 1089 (NU).

(-CC) Bergville district, Cathedral Peak Forest Station, 1815 m, xii. 1950, Killick 1233 (K, PRE, NH, NU); Garden Castle Forest Reserve, xii. 1980, Hilliard and Burtt 13843 (NU).
(-CD) 11 miles WNW of Underberg, c. 5300 ft, iii. 1962, Acocks 22171 (PRE).

(-DB) Impendle district, Impendle, iii. 1966, M. Hancox s.n. (NU).

2930 (Pietermaritzburg) (-AC) Lions River district, Nottingham Road, i. 1956, Edwards 1127 (K, PRE, NU).

(-CA) Impendle district, 6 miles along Everglades-Boston road, iii. 1964, Moll 704 (PRE, NU).

3029 (Kokstad) (-AD) Mount Currie, ii. 1962, Acocks 22049 (K, PRE).

Type: South Africa, Rehmann 5626 (K, holotype; BOL, isotype).


Type: Central African Republic (Ubangi Shari), Tisserant 2922 (P).

**Habit**, slender, erect, rhizomatous, perennial. Rhizome pale stramineous, 3 – 6 mm thick, woody, straight; **scales** light brown. **Culms** 30 – 150 cm tall, glabrous including the rachis, borne at intervals of 5 – 10 mm along the rhizome. **Leaves** 1 – 3.5 mm wide, very sparsely to densely villous, minutely scabrid on margins towards apex, the lowermost reduced to almost bladeless sheaths; **sheaths** very sparsely to densely villous, mouth of at least lower sheaths produced into a triangular tongue 1 – 2 mm long. **Inflorescence** 4 – 12 (17) cm long, simply glomerate-spicate with 4 – 12 glomerules each of 1 – 6 sessile spikelets, the upper glomerules from contiguous to up to their own length apart, the lower 1 – 2 (4) cm apart, erect; or inflorescence with simple glomerate-spicate branches from the lower 1 – 7 glomerules. **Spikelets** 4 – 5 mm long. **Bracts** inconspicuous, shortly glumiform, awned, glabrous to minutely scaberulous distally, shorter than or as long as the glomerules. **Glumes** 2 – 4.5 mm long, usually with midrib excurrent into an awn up to 1 mm long, glabrous,
blackish-red or pale red with darker red streaks and blotches. Achene 1.25 - 2 mm long, 1 - 1.6 mm broadly ovoid or globose, glabrous, smooth to tuberculate, grey or light brown.

**Distinguishing Characters**

<table>
<thead>
<tr>
<th><strong>Rhizome</strong></th>
<th>horizontal, woody, stout.</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Inflorescence</strong></td>
<td>sparingly short-branched glomerate-spicate or simply glomerate-spicate, stiffly erect.</td>
</tr>
<tr>
<td><strong>Spikelets</strong></td>
<td>4 - 5 mm long.</td>
</tr>
<tr>
<td><strong>Glumes</strong></td>
<td>glabrous or glabrescent, blackish-red or red with darker streaks.</td>
</tr>
<tr>
<td><strong>Achene</strong></td>
<td>smooth or tuberculate, grey or light brown, the stipe pale.</td>
</tr>
</tbody>
</table>

This species may be confused with *S. welwitschii* from which it is distinguished by its stiffly-erect, usually simply glomerate-spicate inflorescence which are rarely shortly branched, its shorter spikelets and its differently-coloured glumes.

**Specimens Examined**

**ZAMBIA**

1032 (-CA) Chinsali, Nashinga, xi. 1955, Vesey-Fitzgerald 1007 (NU).

1227 (-DB) Chingola, iii. 1960, Robinson 3405 (NU).
ZIMBABWE

1931 (Buhera) (-CC) Gutu, x.
1969, A. Johnston 17 (NU).

SOUTH AFRICA, TRANSVAAL

2329 (Pietersburg) (-DD) Houtbosch,
1857 - 1880, Rehmann 5626 (K, holotype, BOL, isotype*).

NAMIBIA

1819 (Karakuwisa) (-BD) Okavango,
Omuramba Omatoko, 41.8 miles S of Runtu, iii. 1956, B. de Winter
and W. Marais 5049 (K, PRE).

**Type:** Tanzania Milne-Redhead and Taylor 9739 (K, *lectotype, sheet 1*).

**Habit**, rhizomatous perennial. **Rhizome** 4 - 6 mm thick, woody, horizontal, producing culms at intervals of 0.5 - 2 cm. **Culms** 45 - 105 cm tall, glabrous or sparsely villous, scaberulous on the angles. **Leaves** 2 - 4 (5) mm wide, glabrous or villous, especially on margins and abaxially on midrib, scaberulous especially towards apex, usually shorter than the culms; **sheaths** glabrous or villous, particularly on the angles, minutely scaberulous; mouth produced into a triangular or rounded, glabrous or villous tongue 0.5 - 5 mm long. **Inflorescence** 4 - 13 cm long, simply glomerate-spicate of 4 - 8 sessile glomerules each of 1 - 5 spikelets, upper glomerules up to their own length apart, lower c. 1.7 cm apart, erect. **Spikelets** 8 - 9 mm long. **Bracts** glumiform, awned, shorter than or exceeding the glomerules. **Glumes** hispidulous - pubescent, light castaneous, 4 - 7 mm long with midrib excurrent into an awn 0.75 - 2 mm long. **Achene** 4 - 4.5 mm long, 2 - 2.75 mm broad, ovoid to broadly ovoid, glabrous, smooth, light brown with three interangular stripes of darker brown, the stipe black.
Distinguishing Characters

Rhizome : horizontal, woody.

Inflorescence : simply glomerate-spicate.

Spikelets : 8 - 9 mm long.

Glumes : hairy.

Achene : smooth, light brown with three darker interangular stripes, the stipe black.

This species is unlikely to be confused with any other. It is allied to S. welwitschii and S. rehmannii but differs from both these species in having invariably simply glomerate-spicate inflorescences, hairy glumes, and a darker achene with a black stipe. It differs from S. rehmannii in having very much longer spikelets.

Specimens Examined

TANZANIA

1035 (-CA) Songea district, near R. Mtanda about 9 km SW of Songea, iii. 1965, Milne-Redhead and Taylor 9739 (K, lectotype, sheet I; isolectotypes, sheets II × III)

NAMIBIA

1920 (Tsumkwe) (-DC) 30 miles N of Gautscha Pan, ii. 1968, Story 6467 (K, PRE).

1818 (.Tsitsib ) (-AB) mixed forest in deep white sand 3 miles S of Omuramba on road to Tsinsabis, xii. 1955, de Winter 3915 (K, PRE).

Syntypes: Ethiopia, Schimper 1557 (BM, K); Quartin-Dillon and Petit s.n. (BM, K).


Type: Ethiopia, *Schimper* 327 (K, BM).

*S. schweinfurthiana* Boeck. in Flora 62: 570 (1879)

Type: Sudan, *Schweinfurth* 2193 (K).

*S. buchanani* Boeck., Cyper. Nov. 1: 33 (1888)

Type: Malawi, *Buchanan* 32, 1272 (K).


Type: Congo, *Verdick* 398 (BR).


Type: Tanzania, *Schlieben* 782 (B, not seen by me)


Habit, rhizomatous perennial with bulbous, woody, culm-bases. Rhizome 1 - 2 mm thick, usually little more than the connection between contiguous culm bases but internodes sometimes longer and culm bases intervallate; scales light brown. Culms 12 - 110 cm tall; bases woody, swollen, up to 12 mm thick; aerial part glabrous or hairy, smooth or with scaberulous angles above. Leaves 1 - 5 (9) mm wide, glabrous or hairy, few, subequally spaced in the middle of the culm, the lowest reduced to almost bladeless light brown sheaths; sheaths glabrous to densely villous, the mouth concave, truncate or rarely produced into a short, membranous tongue. Inflorescence 2 - 20 cm long, simply glomerate-spicate with 3 - 17 erect glomerules each of 1 - 12 sessile spikelets, the upper glomerules from contiguous to up to twice their own length apart, the lower from their own length to 4 cm apart; or inflorescences with simple glomerate-spicate branches from the lowermost glomerules. Spikelets 4 - 6.5 mm long. Bracts shortly glumiform, awned, glabrous or hairy, as long as to twice as long as the glomerules, the awn straight or curved; lowest bract sometimes subfoliaceous, up to 3 cm long. Glumes 2 - 5 mm long, glabrous or hairy, the midrib usually excurrent into a smooth, scabrid or ciliate awn 1 - 3 mm long, castaneous or dark reddish-brown. Achene 1.6 - 2 mm long, 1 - 1.8 mm broad, obovoid to subglobose, glabrous, smooth to lightly or strongly tuberculate or trabeculate (even on the same plant), grey or pale brown.
Distinguishing Characters

Rhizome: more-or-less horizontal, internodes very short between swollen culm-bases.

Culm bases: distinctly bulbous and woody, invested with few leaf-sheaths.

Leaves: subequally spaced towards middle of culm, a few of the basal leaves short-bladed or bladeless.

Inflorescence: branched or simply glomerate-spicate.

Achene: obovoid to subglobose, obscurely trigonous, smooth, tuberculate or trabeculate; grey or light brown.

This species can be confused with several species with a similar type of inflorescence only if the rhizome and culm-bases are not examined. It is essential to have the base of the plant if confusion is to be avoided.

Specimens Examined

ETHIOPIA

(N) meadows in upper region of Scholoda mountains, x. 1837, Schimper 1557 (K, syntype^x^); x. 1837, Schimper 327 (K, type of S. atrosanguinea^x^).

TANZANIA

0830 Msanzi, Ufipa, Sumbewanga, i. 1958, Vesey-Fitzgerald 1353 (NU); Ufipa Mbisi, ii. 1958, Vesey-Fitzgerald 1507 (NU); Ilemba Gap, Ufipa, iii. 1958, Vesey-Fitzgerald 2260 (NU).
0833 (-CD) Mbeya mountain, Impinde, ii. 1959, Vesey-Fitzgerald 2347 (NU).

ZAMBIA

0831 (-CD) Abercorn, i. 1954, W. Siame 289 (NU); Nsizye Hill, ii. 1956, D. Kafuli 88 (NU); Senga Hill, i. 1958, Vesey-Fitzgerald 1323 (NU); Abercorn, ii. 1958, Vesey-Fitzgerald 1447 (NU).

0928 (-DD) Luapula district, Mbereshi, i. 1960, M. Richards 12383 (NU).

1332 (-DA) Fort Jameson, Kamkulo dambo, xii. 1963, V.J. Wilson s.n. (NU).

1626 Kalomo district, xii. 1963, B.L. Mitchell 23/26 (NU).

MALAWI

1534 (-BA?) Shire Highlands, undated, Buchanan 32 (K, type of S. buchanani); 1891, Buchanan 1272 (K).

ZIMBABWE

1828 (Gokwe) (-AD) Charama road fly gate, i. 1963, M.G. Bingham s.n. (NU).

1928 (Nyamandhlovo) (-DC) Bubi district, 40 miles N of Bulawayo, xii. 1963, D.H.M. Clark 334 (NU).

2030 (Fort Victoria) (-BA?) Victoria, 1908, C.F.H. Monro 633 (BOL).
2132 (Massangena) (-AC?) Gorhua Native Reserve, Seagrief 3158 (RUH).

SOUTH AFRICA, TRANSVAAL

2329 (Pietersburg) (-BB) Louis Trichardt, xii. 1921, Breyer 24236 24236 (PRE).

(-CD) xii. 1917 C.E. Moss and F.A. Rogers 452 (BOL).


2527 (Rustenburg) (-DD) farm Uitkomst 499 JQ, xi. 1970, B.J. Coetzee 499 (PRE).

2528 (Pretoria) (-CA) Malan's farm, Hartebeesthoek, xi. 1908, Burtt Davy 767 (PRE); Pretoria, x. 1908, M. Collin 26 (PRE); Fairy Glen, xi. 1908, R. Leendertz 1623 (PRE); Rietfontein, xii. 1921, Venter s.n. (PRE); Fountains Valley, xi. 1922, Moss 7207 (K); 8343 (J); Ashburg Station, xi. 1925, C.A. Smith 1341 (PRE); Fountains Valley x. 1929, Cecil Sandwith (K); Pretoria, 1931, Mogg 16575 (PRE); Meintjies Kop, xi. 1931, H. Forbes 803 (NH); Hornsnek, xi. 1937, J.E. Repton 1113 (PRE, NH, BOL); Rietvallei 221, N portion, xi. 1944, Acocks 10745 (PRE).

2529 (Witbank) (-BA) 1,2 miles S by W of Monsterslus Post Office, Groblersdal, xi. 1959, Acocks 20882 (PRE).


(-CA) Belfast, xii. 1900 R. Leendertz 16233 (PRI).

2627 (Potchefstroom) (-BA) 4 miles NE of Krugersdorp, ii. 1956, Acocks 18794 (PRE).

2628 (Johannesburg) (-AA) Windsor Park, xii. 1952, H.B. Gilliland s.n. (J.)

(-AD) Hoogeveld near Heidelberg, xi. 1883, F. Wilms 1646 (K).

2630 (Carolina) (-CA) Mavriestad, xi. 1915, R. Pott 15253 (PRE, BOL).

SWAZILAND

2631 (Mbabane) (-AA) Komati Bridge, iv. 1958, Compton (PRE); Hlatikulu district, Goedgegun, ix. 1965, Compton 32441 (PRE).

(-AC) Evelyn Baring Bridge, x. 1961, Compton 32221 (PRE).

(-CA) Malkerns swamp, xii. 1957, Compton 27364 (PRE).

SOUTH AFRICA, NATAL

2828 (Bethlehem) (-DB) Bergville district, Royal Natal National Park, iii. 1976, R. Physick 78 (NU).
(Harrismith) (-CB) Bergville district
Cathedral Peak, ix. 1960, M. Ruch 2034 (PRE).

(-CC) Cathedral Peak
Forest Reserve Station, xi. 1950,
Killick 1063 (K, PRE, NH); xi. 1951,
Killick 1579 (K, NU); x. 1978,
R.P. Ellis 3279 (PRE).

(Underberg) (-AB) with S. woodii
in meadows above Cathkin Park Hotel, i.
1982, E.F. Hennessy 433 (PRE, NH, NU,
UD-W); in grassland with Pteridium
aquilinum on hills above Cathkin Park
Hotel, i. 1982, E.F. Hennessy 437 (UD-W)
beside road to Champagne Castle, c. 2 km
from turn-off to Cathkin Park, i. 1982,
E.F. Hennessy 440 (UD-W).

(-BB) Weenen County,
top of Griffin's Hill, x. 1944, Acocks
10735 (NH); above New Formosa station
near Estcourt, xi. 1944, Acocks 10758
(PRE, NH).

(-BC) Impendle district
Loteni Nature Reserve, x. 1978,
A.J. Phelan 148 (NU).

(-CB) Cobham Forest
Reserve, near Sani Pass road, iii. 1975,
E.F. Hennessy 407 (NU, UD-W); Cobham
Forest Station, x. 1980, Hilliard and
Burtt 13394 (NU).

(-DC) Giant's Castle
Game Reserve, i. 1969, H.J. McAllister
99 (PRE).
(Pietermaritzburg) (-AC) Lions River district, Lidgetton, undated, Mogg 897 (PRE).

(-CA) St Ives, Dargle Road, x. 1919, Mogg 5543 (PRE).

(-CB) Pietermaritzburg, Claridge, xi. 1948, Killick 706 (NU); Pietermaritzburg, Town Hill, xi. 1949, K.D. Huntley 567 (K, NU).

(-DD) Pinetown district, New Germany, x. 1973, T.A. Coleman 691 (PRE, NH).

(Matatiele) (-DC) between Maclear and Mount Fletcher, x. 1958, E. Werdmal and H.D. Oberdieck 1152 (K, PRE).

(Kokstad) (-AD) Mount Currie, ii. 1962, Acocks 22048 (PRE).

(-CB) East Griqualand near Kokstad, xii. 1883, W. Tyson 1825 (PRE, BOL).

(Port Shepstone) (-BC) Alexandra County, c. 600 m, Umgayi, x. 1909, Rudatis 528 (STE).


TRANSKEI

(Umtata) (-CB) Tembuland, Umyolo, undated, R. Baur 759 (K).
Photographs/Photostats Examined

SUDAN : no locality given, vii. 1869, Schweinfurth 2193 (K, type of S. schweinfurthiana*).

Zaire : no locality given, 1900, Verdick 398 (BR, type of S. verdickii*).

+ 1027 (S) : Katanga, Kundelungu Plateau, v. 1923, R.X.I. Thomas 1202 (BR, type of S. thomasii*).

Holotype : Zambia, Robinson 4220 (K).

Habit, caespitose perennial. Culms 1 - many forming a dense cluster, to 100 cm tall, 1 - 3 mm broad, the bases slightly swollen, invested with many dry leaf-sheaths. Leaves 2 - 7 mm broad, glabrescent to densely hirsute, mostly crowded at base of culm, the majority reduced to shortly bladed light brown sheaths; sheaths glabrescent to densely hirsute, the mouths of the distal sheaths deeply and narrowly concave, of the proximal sheaths invariably split. Inflorescence 5 - 15 cm long, simply glomerate-spicate with 4 - 8 erect, sessile glomerules, the upper glomerules more-or-less contiguous, the lower up to 4 cm apart; rarely inflorescence with simple glomerate-spicate branches up to 2 cm long from lower-most glomerules. Glomerules dense, multispiculate. Spikelets 4 - 6.5 mm long. Bracts shortly glumiform, aristate, hairy, as long as to twice as long as the glomerules, straight or curved; lowest bract sometimes subfoliaceous up to 3 cm long. Glumes 4 - 6 mm long, glabrescent or hairy, the midrib usually excurrent into a scabro-ciliate awn 1 - 3 mm long, castaneous or blackish-brown with green keels, hairs black or pale. Achene 2 mm long, 1.3 - 1.6 mm broad, acutely trigonous, broadly obovoid, glabrous, distinctly reticulate-trabeculate, grey.
Distinguishing Characters

Rhizome : very short, descending, not apparent without sectioning.

Culm-bases : not bulbous and woody, thickly invested with numerous dry leaf-sheaths.

Leaves : mostly crowded towards the base of the culm, mostly short-bladed or bladeless.

Inflorescence : simply glomerate-spicate, rarely with a basal branch.

Achene : acutely trigonous, reticulate-trabeculate, grey.

This species can be distinguished from S. bulbifera by its descending rhizome, the absence of swollen culm bases, the crowding of leaves towards the base of the plant and its acutely trigonous achenes. No other Southern African species has acutely trigonous achenes.

Specimens Examined

ZAMBIA

1227 (-DB) Banks of Kafue river, 11 km N of Chingola in seasonally damp ground, i. 1961, Robinson 4220 (NU, isotype^X).

NAMIBIA

1723 (Singalamwe) (-CB) E. Caprivi Zipfel, in marsh, common, xii. 1958, Killick and Leistner 3218 (PRL).

_Type_: Cap B. spei; Drège legit (? B).

_Lectotype_: South Africa, Drège (3934) (K).

*S. meyeriana* Kunth l.c. : 354 (1837)
_Type_: Cap. b. spei, ad oram orientalem; Drège legit (? B).

_Lectotype_: South Africa, Drège s.n (4364) of C.B.Cl. not seen by me.

*S. holcoides* Kunth l.c. : 354 (1837)
_Type_: Cap. b. spei, ad oram orientalem; Drège legit (? B).

_Lectotype_: South Africa, Drège s.n. (4381) of C.B.Cl. (K).

_Type_: Angola, Welwitsch 7135 (K, BM).

*S. setulosa* Boeck., Cyper. Nov. 1 : 33 (1888)
_Type_: Malawi, Buchanan 36 (K).

**Habit**, perennial with two different kinds of horizontal subterranean stem; both kinds not always present on the same plant; _true rhizome_ with very short internodes, sometimes little more than the connective between more-or-less contiguous culm-bases, with amphivasal vascular bundles; rarely plants with one or more slender propagative stems with collateral vascular bundles arising from the culm cluster; _scales_
reddish-brown. **Culms** 25 - 100 cm tall, glabrous or glabrescent, smooth or with scaberulous or scabro-ciliate angles above. **Leaves** 1 - 3 mm wide, glabrescent or hairy, scaberulous on margins and major veins distally, few, subequally spaced in the middle of the culm, the lowest reduced to almost bladeless reddish sheaths; sheaths sparsely to densely villous especially near the truncate mouth. **Inflorescence** 1 - 10 cm long, simply glomerate-spicate with 1-11 erect glomerules each of 1-8 sessile or subsessile spikelets, the upper glomerules more-or-less contiguous, the lower from their own length to 3.8 cm apart, or inflorescence with simple glomerate-spicate branches from the lowermost glomerules. **Spikelets** 4.5 - 6 mm long. **Bracts** aristate from a very shortly glumiform base, glabrous or ciliate on the scabrid keel and margins, straight or curved, the lowest up to 3.5 cm long, the upper as long as or shortly exceeding the glomerule. **Glumes** 2.25 - 5 mm long, glabrous or sparsely ciliate, blackish-red, red-brown or pale with red-brown streaks especially near the margins, usually with green midrib, the midrib of the female glumes and lowest male glumes excurrent into a smooth or minutely scaberulous awn. **Achene** 1.5 - 2 mm long, c. 1.2 mm broad, ovoid, ellipsoid or subglobose, obscurely trigonous, glabrous, smooth, smooth and lightly or strongly tuberculate towards the apex, or trabeculate and strongly tuberculate towards the apex, dirty-grey, smooth at junction of stipe and body.
Distinguishing Characters

**Rhizome**: present, very short, woody, usually little more than the connective between clustered culm-bases.

**Soboles**: one or more sometimes present, soft, short, pale.

**Culms**: slender, clustered.

**Leaves**: glabrescent or hairy.

**Inflorescence**: branched or simply glomerate-spicate.

**Achene**: smooth or variously tuberculate-trabeculate, the tubercles best developed towards the apex, smooth at junction of stipe and body, grey

This species is likely to be confused with *S. sobolifer* if the underground organs are not present. It differs from this species mainly in having a rhizome, in sometimes having a branched inflorescence, and in the absence of horizontal grooves and ridges at the junction of achene-stipe and body.

Specimens Examined

**ZAMBIA**

1528 (AD) Lusaka, v. 1958, Robinson 2870 (NU).

**MALAWI**

1535 (CA?) Shire Highlands, received Edinburgh vii. 1885, Buchanan 36 (K, type of *S. setulosa*).
ZIMBABWE

1832 (Umtali) (-BD) Inyanga district, Inyangombi River, i. 1961, H. Wild 5468 (NU).

BOTSWANA

1923 (Maun) (-AA) Okavango Swamp, Moremi Wildlife Reserve, Island in Gobega Lagoon, iii. 1972, H. Biegel and C. Russell 3889 (PRE, NU).

(-AB) Ngamiland, Okavango Delta, near Mboma camp, i. 1973, P.A. Smith 341 (PRE).

(-AC) off edge of Dassakao Island on Moanachira River, ii. 1979, P.A. Smith 2635 (PRE).

SOUTH AFRICA, TRANSVAAL

2429 (Zebediela) (-AA) Pyramid Estate near Potgietersrust, 1650 m, iii. 1921, Galpin 9104 (PRE).


2528 (Pretoria) (-CA) near Pretoria, 1410 m, xi. 1893, Schlchter 3705 (K, PRE, BOL); Fairy Glen, xi. 1908, Leendertz 6213 (PRE); Donkerspoort, 20 miles E of Pretoria, iii. 1938, Doidge and Bottomley s.n. (PRE); Rietvlei Reserve, S. end, 1500 m, ii. 1974, Repton 3295 (PRE).
2627  (-DA) Rayton, iii. 1918, F.A. Rogers s.n. (PRE 39045, 57235, J).

Potchefstroom) (-BB) about 9 miles W of Krugersdorp on Gladysvale farm, ii. 1948, Rodin 3922 (K, PRE).

2628  (Johannesburg)  (-BB) Bronkhorstspruit, i. 1962, R.A. Lubke 181 (PRE); Klip River, iii. 1963, P. Hancock s.n. (J).

(-CC?) Am Vaalfluss, Kloete's farm, x. 1888, Wilms 1586 (K).

2730  (Vryheid)  (-AD) Wakkerstroom, Oshoek, xii. 1962, Devenish 970 (K, PRE).

SWAZILAND

2630  (Carolina)  (-DB) open grassy marsh just outside Usutu Forest Sect. C 15 at exit of road iii, ii. 1979, R.W. Haines 7009 (PRE).

2631  (Mbabane)  (-CA) edge of Typha swamp near Usutu Pulp Mill, ii. 1979, R.W. Haines 7010 (PRE).

LESOTHO

no precise locality, 1861, T. Cooper 3355 (K).

2828  (Bethlehem)  (-CC) Leribe Plateau, received 1919, Dieterlen 889 (PRE).
SOUTH AFRICA, NATAL

no precise locality given, received xi. 1875, Buchanan 349 (K, as S. holcoides).

2829 between Greytown (2930BA) and Newcastle (2729DD), xi. 1883, Wilms 2327 (K).

2929 (Harrismith) (-CC) Bergville district, Cathedral Peak Forest Reserve Station, xi. 1950, Killick 1084 (K, PRE, NH, NU).

(-DD) Weenen County, Brakfontein near Frere, xii. 1944, Acocks 10850 (PRE, NH).

2929 (Underberg) (-AB) Estcourt district, Giant's Castle Game Reserve, xii. 1960, D.M. Skead 66 (NU).

(-BB) Weenen County, top of Griffin's Hill, x. 1944, Acocks 10738 (PRE, NH); Estcourt district, xi. 1964, B. Downing 233 (PRE); Estcourt district, Kamberg, xii. 1974, F.B. Wright 2063 (NU).

(-BC) Lions River district, Kamberg, xii. 1974, F.B. Wright 1946 (NU); Highmoor Forest Station S of Giant's Castle, i. 1978, L. Smook 1055 (PRE).

(-CC) Garden Castle Forest Reserve, xii. 1980, Hilliard and Burt 13795 (NU).

(-DB) Impendle district, farm Tilietudlum, xii. 1948, K.D. Huntley 425 (K, NU).
2930  (Pietermaritzburg) (-AA) Mooi River, 4000 ft, xii. 1898, Mason 30 (NH).

(-AC) Balgowan, Glen Arum, x. 1919, Mogg 5637 (PRE).

(-CA) Lions River district, Umgeni Poort, xii. 1964, Moll 1424 (PRE, NU).

(-DD) Durban flat, received vi. 1874, Buchanan 3 (K, as S. holcoides).

3030  (Port Shepstone) (-AD) Alexandra County, 800 m, Campbelltown, Dumisa, x. 1914, Rudatis 1803 (STE, as S. holcoides).

TRANSKEI

3128  (Umtata) (-CB) Tembuland, Baziya, 600-750 m, undated, R. Baur 311

3130  (Port Edward) (-AA) between Umtentu and Umzimkulu River below 150 m, received xi. 1840 Drège [4381] (K, lectotype of S. holcoides; PRE, fragment of type).

CAPE

2723  (Kuruman) (-CB) Bechuanaland, near source of Kuruman River, xi. 1812, Burchell 2463 (K, as S. meyeriana; PRE, fragment).

3226  (Fort Beaufort) (-DA) Stockenstrom division, Kat Berg, 1200-1500 m, received xi. 1840, Drège [3934] (K, lectotype*).

3227  (Stutterheim) (-D3) marshy places near Komgha, ii. 1892, H.G. Flanagan 1260 (K 3934, same Clarke number as Drège lectotype of S. drègeana; BOL).

Type: South Africa, Natal, *Ward* 5128 (K, holotype; PRE, NH, NU, UD-W, isotypes).

Habit; slender, soboliferous perennial. Soboles 1 - 1.5 mm thick rooting at the nodes, the internodes whitish with wine-red blotches, 8 - 47 mm long; scales purple-red. Culms 18 - 101 cm tall, glabrous or sparsely hairy. Leaves 1.1 - 2.6 mm wide, glabrous adaxially, sparsely hairy on major veins adaxially; sheaths sparsely hairy, the mouths truncate, densely pilose. Inflorescence simply glomerate-spicate, 2 - 6.5 cm long, of 2 - 6 sessile glomerules; glomerules of 2 - 6 spikelets, 2.5 - 5 mm broad, the upper contiguous, the lower from contiguous to 20 mm apart, erect; bracts shortly glumiform at the base which is 2 mm long, the midrib excurrent into an awn 4.5 - 8 mm long, glabrous with proximal margins sparsely hairy, distal margins and midrib of awn scabrid, pale straw-yellow with fine red striae, the awn reddish-brown; spikelets c. 4 mm long. Female glumes 2 - 2.5 mm long, the midrib excurrent in an awn up to 1.6 mm long, glabrous or sparsely hairy on the midrib distally, pale straw-yellow with fine reddish striae except the keel which is green, becoming reddish-brown with age. Male glumes 1.7 - 2.6 mm long, the midrib excurrent in an awn up to 1.5 mm long, glabrous or sparsely hairy on the midrib distally, pale straw-yellow with fine reddish striae except the keel which is green becoming straw-yellow. Achene 1.5 - 1.8 mm long, 1 - 1.2 mm broad, subglobose, obscurely
Specimens Examined

SOUTH AFRICA, NATAL

2632 (Bela Vista) (-DD) Ingwavuma district 2 miles from Kosi Nature Reserve on Maputa road, ix. 1961, Edwards 2563 (K); Lower Umfolosi district, Kosi Bay on hill in Nature Reserve, ix. 1961, M.A. Meyer s.n. (NU); Ubombo district, Bazwana sand flats, i. 1964, Strey 5136 (PRE, NH); Ingwavuma district, Kosi Bay Estuary, Bela Vista, xi. 1969, Moll 4534 (K, PRE, NU).

2732 (Ubombo) (-BA) E of Vasi Swamp, Mazengwenya, ix. 1969, Moll 4778 (NH, NU)

(-DA) source of Sordwana River near Mhlambanyati Pan, iii. 1941, A.P.G. Michelmore 44 (K, PRE)


2831 (Nkandla) (-CD) Eshowe, iii. 1950, J.G. Lawn 1665 (NH)


2832 (Mtubatuba) (-AB) Hlabisa district, W of Charter's Creek, xi. 1955, Ward 2784 (PRE, NH).

(-AC) E of Mtubatuba, i. 1941, A.P.G. Michelmore 9 (PRE).
trigonous, glabrous, undulate-tuberculate, white or dirty-grey with three darker grey interangular lines, with a series of deep horizontal troughs separated by horizontal and vertical ridges at junction of stipe and body.

Distinguishing Characters

<table>
<thead>
<tr>
<th>Character</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>Rhizome</td>
<td>none.</td>
</tr>
<tr>
<td>Sobole</td>
<td>long, slender, hard, pale with vinaceous blotches.</td>
</tr>
<tr>
<td>Culms</td>
<td>slender, rarely clustered.</td>
</tr>
<tr>
<td>Leaves</td>
<td>glabrescent.</td>
</tr>
<tr>
<td>Inflorescence</td>
<td>simply glomerate-spicate</td>
</tr>
<tr>
<td>Achene</td>
<td>undulate-tuberculate all over with a series of deep horizontal troughs separated by horizontal and vertical ridges at junction of stipe and body, grey.</td>
</tr>
</tbody>
</table>

This species differs from *S. drègeana* mainly in lacking a rhizome, in its long, hard, red-blotched soboles, in its simply glomerate-spicate inflorescence, and in having horizontal grooves and ridges at the junction of achene-stipe and body.
Specimens Examined

SOUTH AFRICA, NATAL

2632
(Bela Vista) (-DD) Ingwavuma district, 2 miles from Kosi Nature Reserve on Maputa road, ix. 1961, Edwards 2563 (K); Lower Umfolosi district, Kosi Bay on hill in Nature Reserve, ix. 1961, M.A. Meyer s.n. (NU); Ubombo district, Bazwana sand flats, i. 1964, Strey 5136 (PRE, NH); Ingwavuma district, Kosi Bay Estuary, Bela Vista, xi. 1969, Moll 4534 (K, PRE, NU).

2732
(Ubombo) (-BA) E of Vasi Swamp, Mazengwenya, ix. 1969, Moll 4778 (NH, NU)

(-DA) source of Sordwana River near Mhlambanyati Pan, iii. 1941, A.P.G. Michelmore 44 (K, PRE)


2831
(Nkandla) (-CD) Eshowe, iii. 1950, J.G. Lawn 1665 (NH).


2832
(Mtubatuba) (-AB) Hlabisa district, W of Charter's Creek, xi. 1955, Ward 2784 (PRE, NH).

(-AC) E of Mtubatuba, i. 1941, A.P.G. Michelmore 9 (PRE).
(-AD) Hlabisa district, Dukuduku, i. 1965, Strey 5711 (K, PRE, NH, UD-W); Mpathe Forestry Plantation, x. 1971, Ward 7242 (PRE, UD-W). 4 km from St. Lucia Estuary on road to Cape Vidal, ix. 1973, T.H. Arnold 467 (PRE); Eastern Shore Lake St Lucia, ii. 1974, R.H. Taylor 142 (NU); St Lucia Estuary, v. 1976, Ward 8870 (K, PRE, NU, UD-W); St Lucia Estuary, game park E of Cape Vidal road, xi. 1977, E.S. Pooley 1967 (UD-W).

(-CC) Lower Umfolosi district, near Richards Bay, i. 1949, Ward 723 (PRE, NU); Richards Bay, vi. 1963, Robinson 5524 (NU); Richards Bay, iv. 1964, Ward 4935 (NU, UD-W).


(-DD) Clairmont, x. 1898, Wood 12022 (NH); Durban district, Merebank East, ix. 1965, Ward 5128 (K, holotype; PRE, NH, NU, UD-W isotypes); ix. 1965, Ward 5172 (PRE, NH, NU, UD-W); iii. 1966, Ward 5172 (PRE, NH, NU, UD-W); iii. 1966, Ward 5435 (K, PRE, NH, NU, UD-W); iii. 1976, Ward 8851 (PRE, NH, NU, UD-W); Merebank West, ii. 1967, H. Baijnath 126 (PRE, NU, UD-W).

(Port Shepstone) (-BC) Umzinto district, Umgayi, iii. 1966, Ward 5470 (K, PRE, NH, NU, UD-W).

(-CC) Alfred district, cliffs near Otterburn on Paddock – Izingolweni road, i. 1969, K.D. Gordon-Gray 6251 (NU); Highlands farm, Paddock
(cont.)


(-CD) Uvongo Beach, x. 1963, Ward 4737 (NH, NU, UD-W).


Type: India, Wallich 3406 (K).


Type: Zimbabwe, Brain 3710 (K, PRE, SRGH).

**Habit** slender caespitose annual. **Culms** 13 - 38 cm tall, 0.25 - 1 mm thick, glabrous. **Leaves** 1 - 2 mm wide, glabrous; sheaths glabrous or sparsely and minutely pilose towards mouth, mouth truncate or concave. **Inflorescence** simply glomerate-spicate or rarely with a short branch bearing a single glomerule from the lower glomerules, 2 - 6.5 cm long of 2 - 13(18) glomerules each of 1 - 7 sessile or subsessile erect spikelets, the upper glomerules more-or-less contiguous, lower up to 1.5 cm apart. **Spikelets** 4 - 5 mm long. **Bracts** glumiform, glabrous, shorter than or slightly exceeding the spikelets, acuminate with scaberulous keel. **Glumes** 2.5 - 3.5 mm long, glabrous, pale with numerous red-brown streaks proximally becoming almost
wholly red-brown distally, shortly mucronulate. 
Achene 1.4 - 1.8 mm long, 1.2 - 1.6 mm broad, 
mcre-or-less globose, glabrous. tuberculate- 
verrucose, grey with brown stipe (only 
immature achenes seen).

**Distinguishing Characters**

<table>
<thead>
<tr>
<th>Character</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>Rhizome</td>
<td>none.</td>
</tr>
<tr>
<td>Culms</td>
<td>clustered, forming a small clump, very slender.</td>
</tr>
<tr>
<td>Lamina</td>
<td>profile very flat V-shaped, without flange.</td>
</tr>
<tr>
<td>Inflorescence</td>
<td>simply glomerate-spicate, rarely with one basal branch.</td>
</tr>
<tr>
<td>Glumes</td>
<td>glabrous.</td>
</tr>
<tr>
<td>Achene</td>
<td>tuberculate-verrucose, grey, the tubercles grey.</td>
</tr>
</tbody>
</table>

This species may be confused with S. dieterlenii from which it differs in lacking a 
rhizome, in its V-shaped lamina-profile, in its 
glabrous glumes, in the patterning of its achene-
surface and in the colour of the achene.

This species is known in Southern Africa 
from a single gathering (Pentz and Acocke 10277) 
made near Dundee in Natal in 1944. Robinson 
(1966) expressed reservations about the validity 
of maintaining the variety brachystachys Nelmes. 
Since the species is unknown to me in the field, 
and I have examined very little material, I am 
unable to express an opinion, and have 
provisionally accepted Nelmes' judgement in 
the matter.
Specimens Examined

SOUTH AFRICA, NATAL

2830 (Dundee) (AC) near Waschbank, c. 3000 ft., iii. 1964, Pentz and Acocks 10277 (PRE, det. E. Nelmes, 1955; NH).

Photographs Examined

ZIMBABWE

1731 (Salisbury) (-CC) Salisbury (Harare), 4800 ft., iv. 1931, Brain 3710 (K, type of S. pergracilis var. brachystachys).

Type: Lesotho, Dieterlen 749 (K, holotype; PRE, NH, isotypes).


*S. flexuosa* sensu E.A. Robinson in Kew Bull. 18 : 3 : 505 (1966), pro parte, non Boeck.

**Habit:** slender, rhizomatous perennial. **Rhizome** curved-descending, 0.5 - 1 mm thick, terminating in a swollen tuber up to 1 cm long, 3 - 4 mm thick; **scales** pale reddish striate. **Culms** closely clustered, 15 - 37 (45) cm tall, 0.5 - 0.8 mm thick, glabrous or very sparsely villous; **rhachis** scabrociliate. **Leaves** 1 - 2.5 mm wide, glabrous or more often sparsely villous, the lower shortly bladed or reduced to almost bladeless reddish sheaths; **sheaths** glabrous to villous, mouth truncate or concave, villous. **Inflorescence** simply glomerate-spicate or rarely with a single branch from lowermost glomerule, 2 - 8 cm long, of 3 - 8 glomerules, the upper glomerules from contiguous to up to their own length apart, the lower up to 2 cm apart; **glomerules** of 1 - 8 sessile, erect spikelets. **Spikelets** 4 - 5 mm long. **Bract** of lowest glomerules often subfoliaceous, 2.5 - 4 cm long; **bracts** shortly glumiform, awned, villous, the awn more-or-less densely ciliate proximally, scabro-ciliate distally,
straight or curved, shorter than or exceeding the glomerule. **Glumes** 2.5 - 4.5 mm long, sparsely to densely villous, the upper male glumes glabrous, orange-brown with darker red streaks, the midrib usually very shortly excurrent. **Achene** 1.3 - 1.8 mm long, 1 - 1.25 mm broad, glabrous, subglobose, whitish or cinereous, transversely light to bright reddish-brown trabeculate-verrucose.

**Distinguishing Characters**

<table>
<thead>
<tr>
<th>Character</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>Rhizome</td>
<td>descending, very slender with swollen tuberous tip.</td>
</tr>
<tr>
<td>Culms</td>
<td>clustered, forming a small clump, very slender.</td>
</tr>
<tr>
<td>Lamina</td>
<td>profile shortly-flanged V-shaped.</td>
</tr>
<tr>
<td>Inflorescence</td>
<td>simply glomerate-spicate, rarely with one short basal branch.</td>
</tr>
<tr>
<td>Glumes</td>
<td>hairy.</td>
</tr>
<tr>
<td>Achene</td>
<td>trabeculate-<strong>verrucose</strong>, grey, the trabeculae light to bright reddish-brown.</td>
</tr>
</tbody>
</table>

This species differs from *S. pergracilis* with which it might be confused in having a rhizome, in having a flanged V-shaped lamina profile, in the patterning of its achene surface and in the colour of the achene.
Specimens Examined

SOUTH AFRICA, TRANSVAAL

2328  (Baltimore)  (-CD) Palala River, i. 1918, H.G. Breyer 18070 (PRE).

2530  (Lydenburg)  (-DB) Kaapsche Hoop, ix. 1915, Wager s.n. (PRE).

NATAL

2730  (Vryheid)  (-AD) farm Oshoek near Wakkerstroom, ii. 1978, L. Smook 1186 (PRE).

2829  (Harrismith)  (-AD) Van Reenen, i. 1914, Bews 471 (NU).

2929  (Underberg)  (-BC) Estcourt district Highmoor Forest Station, i. 1966, Killick and Vahrmeijer 3663 (K, PRE).

LESOTHO

2828  (Bethlehem)  (-CC) Leribe plateau, received viii. 1911, A. Dieterlen 749 (K, holotype : PRE, NH, isotypes ).

2929  (Underberg)  (-CC) Sehlabathebe National Park, Matsa a Mafikeng, ii. 1978, F.K. Hoener 2014 (NU, UD-W).

SOUTH AFRICA, CAPE

3028  (Matatiele)  (-DC) Maclear, 3 miles SW of Katkop Post Office, 5200 ft, i. 1962, Acocks 2196 (K, PRE).

Holotype: Venezuela, Cumana, Humboldt s.n. in Herb. Willd. 17336 (B - W) (not seen by me).

Hypoporum humile Nees in Linnaca 2 : 303 (1834) nomen nudum.

Scleria mollis Kunth, l.c. : 352 (1837)
Type: Brazil. Sellow s.n. (K).

S. cenchroides Kunth, l.c. : 352 (1837)
Type: South Africa, Drège s.n. (K)

Hypoporum nutans (Willd. ex Kunth) Nees in Mart., Fl. Bras. 2 (1) : 170 (1842).


S. hirtella Sw. var. tuberculata C.B.Cl. in Thisd.-Dyer, Fl. Cap. 7 : 294 (1898); Schenland, Mem. Bot. Surv. S. Afr. 3 : 44; Fig 73 (1933).
Type: South Africa, Burke 62 (K).

Type: Uganda, A.S. Thomas 95 (K).

[S. hirtella auctores permulti, non Sw.]
Habit, slender rhizomatous perennial. Rhizome woody, more-or-less horizontal, 2 - 4 mm thick; scales brown. Culms 16 - 50 cm tall, glabrous or very sparsely hairy on the angles, borne at intervals of 2 - 15 mm along the rhizome, the bases sometimes slightly thickened. Leaves 1.5 - 5 mm wide, glabrous, sparsely hairy or densely hairy on margins and major veins, the lowermost reduced to almost bladeless reddish-brown sheaths; sheaths glabrous, sparsely or densely hairy, villous near the truncate or convex mouth. Inflorescence 2.5 - 8.5 cm long, simply glomerate-spicate, of 3 - 6 (7) glomerules, the upper erect, the lower reflexed, the upper glomerules from contiguous to up to their own length apart, the lower up to 5 cm apart; glomerules of 2 - 7 sessile or very shortly pedicillate spikelets. Spikelets 4 - 5 mm long. Bracts shortly glumiform below, awned, densely pale-, reddish- or blackish-ciliate, 4 - 12 mm long, straight or curved. Glumes 2 - 5 mm long, mucronate, muticous or with the midrib excurrent into a densely ciliate awn, pale with faint reddish streaks, densely pale-, reddish- or blackish-ciliate except the male glumes sometimes glabrous. Achene 1.2 - 1.5 mm long, c. 1 mm broad, broadly ovoid to globose, glabrous, smooth or lightly tuberculate, pale grey or grey-brown.
Distinguishing Characters

Rhizome: straight, woody, horizontal.
Culms: arising at intervals from rhizome.
Leaves: more-or-less evenly spaced along length of culm.
Inflorescence: simply glomerate-spicate.
Glomerules: reflexed.
Glumes: thickly invested with pale-, reddish or reddish-black hair.
Achene: smooth or lightly tuberculate, grey or grey-brown.

The feature which most easily distinguishes this species from *S. aterrima* is its woody, often long, horizontal rhizome. It is also distinguished from this species by its leaves being more-or-less evenly spaced along the culm, by the colour of the hairs on its glumes and by the absence of hypodermal translucent cells in the intercostal region of the lamina.

Specimens Examined

SOUTH AMERICA, BRAZIL

no precise locality given, undated, Sellow s.n. (K, ex B, type of *S. mollis*).

AFRICA, ZAIRE

Mvasi marais et savanes humides, ii. 1953, Devred 1287 (NU).
0624 (-BC) Gandajika, i. 1957, Lieben 2409 (NU).

UGANDA

Kalangala, Bugala, vi. 1932, Thomas 95 (K, type of S. hirtella var. chondrocarpa).

ZAMBIA

0831 (CD?) Abercorn district, Chianga River dambo, vi. 1956, Robinson 1724 (NU); edge of Lake Chila, ii. 1959, M. McCallum-Webster s.n. (NU); Chila, iii. 1959, Vesey-Fitzgerald 230 (NU).

SOUTH AFRICA, TRANSVAAL

2430 (Pilgrim's Rest) (-DD) Pilgrim's Rest, xi. 1958, Killick and Stacey 2506 (PRE).

2527 (Rustenburg) (sic), undated, Burke 62 (K, type of S. hirtella var. tuberculata).

2528 (Pretoria) (-CD) Bronkhorstspruit district, vlei source of Pienaar's R., 4 km E of Lynnwood Drive-in, xii. 1980, C. Reid 423 (PRE).

NATAL

2831 (Nkandla) (-DC) Mtunzini district, Ngoye forest, xii. 1968, K.D. Gordon-Gra 6182 (NU).


2832 (Mtubatuba) (-AD) Hlabisa district, W of St. Lucia Estuary, xi. 1959 Feeley and Ward 7 (PRE, NH); Dukuduku, E corne of U 175, xi. 1964, Ward 5057 (PRE, NH, NU, UD-W).
(Pietermaritzburg) (-DA) Table Mountain, i. 1949, Killick 249 (K, PRE, NU).

(Port Shepstone) (-BC) Umzinto district Pennington, near Liebenberg's cottage, i. 1969, K.D. Gordon-Gray 6210 (NU); Umgayi, x. 1909, Rudatis 736 (K, PRE, STE as 517).

(-CD) Umtamvuna Coast, i. 1941, D. Thompson 29 (NU); Uvongo grassland, xii. 1963 Strey 4894 (K, PRE, NH); wet situation in garden of cottage owned by D.G. Basel, Uvongo, xii. 1982, R.I'ons and D.G. Basel 129/82 (NU).

(Port Edward) (-AA) vlei near Post Office, vi. 1951, K.D. Huntley 705 (K, NU); x. 1975, C.H. Stirton 5649 (PRE).

TRANSKEI

(Port St Johns) (-BD) mountainous grassland, Port St Johns, 11. 1919 Moss 2358 (K, J).

(Port Edward) (-AA) Natal or Pondolant (sic), between Umtentu and Umzimkulu rivers below 500 ft, received at K v. 1840, Drège s.n. (K, as S. cenchroides); Pondoland, Sea View, xii. 1949, Ward 1106 (NU); 1 km before Mzamba river mouth, x. 1973, T.H. Arnold 796 (PRE).

(Butterworth) (-CB) Komgha, near Kei Mouth, xi. 1894, Flanagan 2363 (K, PRE).

*S. hirtella* Sw. sensu Boeckeler in Linnaca 38 : 439 (1874) excl. synon., quoad Barter 1561.


Type: Angola, Welwitsch 7143 (K; isotype).


Type: Nigeria, Barter 1561 (K).

Habit, perennial with two different kinds of horizontal subterranean stem, both kinds not always present on the same plant; **true rhizome** if present little more than the connective between more-or-less contiguous culm-bases, with amphivasal vascular bundles; more often culms solitary with slightly swollen bases 2 - 3 mm thick producing 1 - 4 slender, soft horizontal stems 1 - 2 (3) mm thick with collateral vascular bundles; **scales** castaneous. **Culms** 25 - 70 cm tall, villous, rarely glabrescent. **Leaves** 2 - 3 mm wide, villous especially on the margins and midrib abaxially, rarely glabrescent, shorter than or exceeding the culms, mostly produced toward the base of the culm, the lowermost represented by almost bladeless sheaths; **sheaths**
villous or glabrescent, densely hirsute near the truncate or concave mouth which is usually split. Inflorescence simply glomerate-spicate, 4 - 18 cm long, the upper glomerules from contiguous to up to their own length apart, the lower up to 3 cm apart; glomerules of 1 - 7 reflexed sessile spikelets. Spikelets c. 6 mm long. Bracts 6 - 7 mm long, shortly glumiform, awned, densely hairy, the hairs pale or purple-black, the awn usually curved. Glumes 2.5 - 4.5 mm long, densely hairy, the hairs purple-black. Achene 1.2 - 1.5 mm long, c. 1 mm broad, broadly ovoid to globose, glabrous, smooth, pale grey or grey-brown.

Distinguishing Characters

<table>
<thead>
<tr>
<th>Rhizome</th>
<th>: little more than the connective between crowded culm-bases.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sobole</td>
<td>: one or more sometimes present, soft.</td>
</tr>
<tr>
<td>Culms</td>
<td>: clustered.</td>
</tr>
<tr>
<td>Leaves</td>
<td>: mostly crowded towards base of culm.</td>
</tr>
<tr>
<td>Inflorescence</td>
<td>: simply glomerate-spicate.</td>
</tr>
<tr>
<td>Glomerules</td>
<td>: reflexed.</td>
</tr>
<tr>
<td>Glumes</td>
<td>: very thickly invested with black hairs.</td>
</tr>
<tr>
<td>Achene</td>
<td>: smooth, grey or grey-brown.</td>
</tr>
</tbody>
</table>

This species is distinguished from _S. mutans_ mainly by the absence of an elongated horizontal rhizome, by its leaves being crowded towards the base of the culm, by the black hairs on its glumes and by the presence of hypodermal translucent cells in the intercostal region of the lamina.
Specimens Examined

NGERIA

Nupe in a swamp near Lom, not seen elsewhere, undated, Barter 1561 (K, type of S. catophylla*).

ANGOLA

+ 1413 Huilla; plentiful on the higher spongy slopes in the mixed woods of Moora de Lopollo, but only seen in this place, iii–iv. 1860, Welwitsch 7143 (K, isotype of S. hirtella var. aterrima*).

ZAMBIA

0831 (-CD) Abercorn district, Lake Chila, ii. 1959, M. McCallum-Webster s.n. (NU).

1031 (-AA) Kasama district, Mungwi, iii. 1962, Robinson 5055 (NU).

1150 (-BB) Chipili, 38 miles N of Forest Rosebery, iv. 1956, Robinson 1748 (NU).

1528 (-CA) Kafue National Park, xi. 1963, C.D. Simpson 16/60 (NU).

MOZAMBIQUE


ZIMBABWE

2032 (Chipinga) (-AC) Chipinga, ii. 1962, Moll 255 (NU).
SOUTH AFRICA, TRANSVAAL

2428 (Nylstroom) (-AD) Waterberg, Nooitgedacht, ii. 1942, Acocks and Naude 34 (PRE).

2430 (Pilgrim's Rest) (-DD) Graskop, i. 1921, Pole-Evans s.n. (PRE, 39049).

2528 (Pretoria) (-CA) 25 miles E of Pretoria, ii. 1952, Schweickerdt 2344 (K, PRE, NU).

2529 (Witbank) (-CC) in marsh near Brug Spruit, i. 1894, Schlechter (7, 2120; PRE, 5155; BOL, 4120).

NATAL

2732 (Umbombo) (-BA) Mazengwenya, E of Vasi Swamp, xi. 1969, Moll 4759 (K, PRE, NH, NU).

2832 (Mrubatubba) (-AB) Hlabisa district, W of Charter's Creek, xii. 1955, Ward 2924 (NH, NU).

2930 (Pietermaritzburg) (-DD) Clairmont, xii. 1881, Wood 1428 (K, NH).

3030 (Port Shepstone) (-CD) St Michaels on Sea, xii. 1966, Steyn 7035 (K, PRE, NH, UD-W); x. 1971, H.B. Nicholson 1103 (PRE).

TRANSKEI


Holotype: Cuba, Wright s.n. (K).


Type: Gabon, Le Testu 5845 (P).

Habit: stout, erect, glabrous aquatic annual (?), with numerous slender, finely branched adventitious roots at one to several submerged lower nodes of culm, basal roots stouter, 2 mm thick. Culms up to 180 cm tall, 7 - 12 mm thick, angles spinulose, including inflorescence rachis and rachillae. Leaves 10 - 15 mm wide, glabrous, scabrid on margins, midrib abaxially and major lateral veins adaxially; sheath glabrous, scabrid on angles and major veins; the mouth produced into an oval membranous tongue 5 - 10 mm long with a narrow hispid zone in the angles at its base, often blackish. Inflorescence branched paniculate 19 - 20 - (100) cm long, the branches subtended by leafy bracts; branches glomerate-spicate, many with subsidiary glomerate-spicate branches from their lower glomerules; glomerules of 1 - 4 sessile, erect spikelets, the upper of each branch more-or-less contiguous, the lower up to 5 cm apart. Spikelets 4 - 6 mm long. Bracts setaceous from auriculate base, scabrid on margins and midvein with a few stiff blackish hairs on the blackish auricles, from
twice as long as the glomerule to 2.5 cm long. Glumes 3 - 5 mm long, glabrous, dark red-brown, mucronulate or the female sometimes with the midrib excurrent into an awn up to 1 mm long. Achene ovoid, 3 - 3.5 mm long, 2 - 2.5 mm broad, smooth, glabrous, grey or brown with darker interangular stripes; hypogynium small, with three very small triangular lobes, brown.

Distinguishing Characters

Rhizome : none.

Roots : basal, anchoring and free-floating from several nodes above culm-base.

Inflorescence : large, from several nodes, much-branched, the branches glomerate-spicate.

Spikelets : androgynaecous, subandrogynaecous and male.

Glumes : glabrous

Achene : glabrous, smooth, brown.

Hypogynium : very small, obscurely 3-lobed, pale brown.

This species cannot be confused with any other from the region, being distinguished by its finely-divided floating roots, its androgynaecous and subandrogynaecous spikelets and by the very small hypogynium. The only species which has a similar type of hypogynium is S. poaeformis.
Specimens Examined

GABON

0010 ( ) Mare de lac plassie Ndolo pris Ste. Croix des Echiras, xii. 1925, Le Testu 5845 (P, type of S. aquatică*).

ZAMBIA

1129 ( ) Lawinga district, Nsombo, at N end of Lake Bangweulu, in shallow stagnant water with more-or-less muddy bottom; probably an annual as no rhizomes recoverable from mud, v. 1961, Robinson 4700 (NU).

BOTSWANA

1822 (Kangara) (-AC) in water meadow alongside Okavango River, in water 0,6 m deep, very slow-flowing, ii. 1979 P.A. Smith 2718 (PRE).

1923 (Maun) (-AA) in 70 cm deep flood plain off the Mboroga River, vi. 1979, P.A. Smith 2796 (PRE).

Photograph Examined

CUBA

received K i. 1869, Wright s.n. (K, isotype*).

**Type:** South Africa, Transvaal, T.H. Arnold 336 (K, holotype; PRE, isotype).

**Habit:** Rhizomatous perennial. **Rhizome** little more than the connective between contiguous, woody, swollen culm-bases; **scales** reddish-brown. **Culms** 50 - 125 cm tall, swollen base 8 - 10 mm thick, glabrous, reddish toward the base. **Leaves** 4 - 10 mm wide, glabrous, distally scaberulous on margins and principal ribs; the lowest reduced to almost bladeless reddish-sheaths; **sheaths** glabrous or minutely hispidulous, densely hispidulous near the mouth; **mouth** produced into a deltoid-rounded tongue 2 - 5 mm long, with a membranous extension up to 1 mm long. **Inflorescence** terminal and lateral; **terminal panicle** more dense than the laterals, 4.5 - 9 cm long, 2 - 4.5 cm broad; **lateral panicles** 1.5 - 5.5 cm long at 1 - 2 (3) distantly spaced nodes, borne on (0) 1 - 2 narrowly winged glabrous or distally hispidulous peduncles exserted 2 - 12 mm from their sheaths. **Bracts** foliaceous, longer than their panicles, subulate. **Male spikelets** 4 - 6 mm long, sessile or shortly pedicillate; **glumes** glabrous or minutely hispidulous, reddish-brown with green midrib or wholly reddish-brown. **Female glumes** 4 - 5 mm long, broadly ovate with the midrib excurrent in an awn to 1 mm long, glabrous, reddish-brown with paler greenish midrib. **Achene** oblong-subglobose, glabrous, 2.5 - 3 mm long, c. 2 mm broad, tessellate-lacunose to tuberculate-lacunose, brownish-white; **hypogynium** obtusely 3-lobed, stramineous.
Distinguishing Characters

Rhizome : usually with very short internodes.

Culm : base swollen, 9 - 10 mm thick.

Inflorescence : of terminal and lateral panicles, laterals at (0) 1 - 2 nodes, (0) 1 - 2 per node on inconspicuously winged peduncles.

Bracts and leaves : subulate.

Achene : glabrous, oblong-subglobose, tessellate-lacunose, light brown.

Hypogynium : with three rounded lobes, stramineous.

This species has hitherto been confused with *S. natalensis*, from which it differs in having swollen culm-bases, a smaller number of more copious panicles, markedly subulate leaves and bracts and a barrel-shaped achene.

Specimens Examined

SOUTH AFRICA, TRANSVAAL

2230 (Messina) (-CC) Zoutpansberg, Entabeni, xi. 1931, Obermeyer 3095 (PRE)

(-CD) Zoutpansberg, N of Pepiti, xii. 1935, Smuts and Gillett 3260 (PRE); Sibasa district, Tate Vondo Forest Reserve, iii. 1978 G. Hemm 563 (PRE, J).
(Pilgrim's Rest) (-AA) Letaba district on top of mountain opposite Metz Mission Hospital; xi. 1976, F. Venter 1150 (PRE).


(-DC) Mount Sheba Forest v. 1973, Mogg 36608 (J).

(-DD) Pilgrim's Rest, ix. 1966, Davidson and Mogg 32901 (PRE); 15 km from Sabie at Mac Mac Pools, iii. 1973, T.U. Arnold 336 (K, holotype; PRE, isotype x).

(Komatipoort) (-CC) Kaapsche Hoop, i. 1929, Phillips 3550 (K, PRE); Ida Doyer Nature Reserve, 38 km SE of Barberton, xii. 1971, P.J. Muller 2031 (K).

SWAZILAND

2631 (Mbabane) (-AC) 1917, F.A. Rogers 11623 (K); Ukutula, edge of forest, iii. 1955, Compton 24985 (PRE); Forbes Reef, granite crevices, xi. 1963, Compton 31805 (PRE); hillside above Mbabane near wireless masts among granite boulders, i, 1965, K.D. Grodon-Gray 6020 (NU).

SOUTH, AFRICA, NATAL

2831 (Nkandla) (-CA) Nkandla forest, v. 1956, Seagrief 18; 23 (NU).

Type: South Africa, Natal, Buchanan 352 (K, holotype; NH, isotype).

Habit, rhizomatous perennial. Rhizome c. 5 mm thick with very short internodes, usually little more than the connective between almost contiguous culm-bases; scales reddish-brown. Culms 50 – 85 cm tall, 2 – 3 mm thick at the base, glabrous, reddish towards the base. Leaves 4 – 11 mm wide, glabrous, distally scaberulous on margins and principal ribs, the lowest reduced to almost bladeless reddish sheaths; sheaths glabrous or sparsely and minutely hispidulous, densely hispidulous near the mouth; mouth produced into a deltoid-rounded tongue 2 – 5 mm long with a membranous extension 1 mm long. Inflorescence terminal and lateral; terminal panicle more dense than the laterals, 2.5 – 6.5 cm long, 1.5 – 2 cm broad; lateral panicles 1.0 – 4 cm long at 2 – 3 distantly spaced nodes, borne on 1 – 4 distally conspicuously winged, glabrous or minutely hispidulous unequally exserted pendulous peduncles 3 – 23 cm long. Bracts foliaceous, longer than their panicles, ensiform, the upper overarching the terminal panicle. Male spikelets 4 – 6 mm long, sessile or pedicillate; glumes glabrous or hispidulous, stramineous with fine reddish streaks. Female glumes 4 – 5 mm long, broadly ovate, glabrous or hispidulous, stramineous with fine reddish streaks which are more numerous near the
margins, midrib excurrent into an awn up to 1 mm long. Achene subglobose, obtusely trigonous, 2.5 mm long, 2 mm broad, glabrous, reticulate lacunose to tuberculate lacunose, brownish-white; hypogynium distinctly 3-lobed, the lobes rounded, stramineous.

**Distinguishing Characters**

<table>
<thead>
<tr>
<th>Character</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>Rhizome</td>
<td>usually with very short internodes.</td>
</tr>
<tr>
<td>Culm</td>
<td>base not or only very slightly swollen, 3 - 4 mm thick.</td>
</tr>
<tr>
<td>Inflorescence</td>
<td>of terminal and lateral panicles; laterals at 2 - 3 nodes, (1) 2 - 4 per node on conspicuously winged peduncles.</td>
</tr>
<tr>
<td>Bracts and leaves</td>
<td>ensiform.</td>
</tr>
<tr>
<td>Achene</td>
<td>glabrous, subglobose, obtusely trigonous, reticulate-lacunose, light brown.</td>
</tr>
<tr>
<td>Hypogynium</td>
<td>with three rounded lobes, stramineous.</td>
</tr>
</tbody>
</table>

This species is distinguished from the closely allied S. transvaalensis mainly by its culm-bases which are not swollen, by its ensiform leaves and bracts, by its greater number of less dense panicles borne on conspicuously winged peduncles and its obtusely trigonous to subglobose achene.
Specimens Examined

**SOUTH AFRICA, NATAL**

no precise locality given, received xi. 1857, Buchanan 352 (K, holotype, NH, isotype*).

2831

(Nkandla) (-DD) Hlabisa valley, xi. 1962, H.J.T. Venter 733 (NH); Mtunzini, Twostreams farm, ix. 2973 T.H. Arnold 435 (K, PRE).

2930


(-DD) near Durban, 190; Wood 8875 (NH); Westville, Palmiet valley, iv. 1964, Ward 4935 (PRE, UD-W); Gillitts, Everton, ii. 1968, K.D. Gordon Gray s.n. (NU); Pinetown, Umbilo river valley, i. 1972, Ward 7518 (PRE, UD-W).

3030

(Port Shepstone) (-BC) Umzinto district, Umgayi, Mgoro river, ix. 1964, Ward 5043 (NH, NU, UD-W); Umzinto district, Umdoni Park, ix. 1969, Jarman and Guy 404 (NU).


(-CC) Alfred district, cliffs near Otterburn on Paddock - Izingolweni road, i. 1969, K.D. Gordon-Gray 6245 (NU).

(-CD) Uvongo kloof, xi. 1969, Strey 9464 (PRE, NH).
TRANSKEI


3129 (Port St Johns) (-BC) Lusikisiki, Egossa forest, ii. 1929, Galpin 10988 (PRE).

(-DA) Forests, Port St. Johns, i. 1919 Moss 5515 (K, J).

Syntypes: Ethiopia, Schimper 1232 (K, BM); Quartin Dillon & Petit s.n. (K, P).


Type: Angola, Welwitsch 7122 (BM).


Type: Madagascar, Perrier de la Bathie 12704 (P).

**Habit**: caespitose annual. **Culms** 20 - 60 (200) cm tall, glabrous, smooth or scabrid on the angles. **Leaves** borne at subequal intervals along the length of the culm, 2 - 7 mm wide, glabrous, scabrid on the margins, on midrib abaxially and on principal lateral veins adaxially, the lowest reduced to almost bladeless sheaths; **sheaths** glabrous or glabrescent except at the mouth which is densely villous; mouth truncate or produced into a dark reddish-brown tongue 1 - 2 mm long.

**Inflorescence** terminal and lateral; terminal **panicle sessile**, 2.5 - 6 cm long; lateral **panicles** pedunculate, 1.5 - 6 cm long, single at 1 - 3 nodes, erect or pendulous at maturity, shortly exserted from bract sheaths. **Bracts** foliaceous, longer than their panicles.
Male spikelets 4 - 5 mm long, sessile to shortly pedicillate, glumes glabrous, reddish-brown. Female glumes c. 5 mm long, glabrous, pale reddish-brown or dark brown distally, paler proximally, the midrib greenish, excurrent into a scaberulous awn c. 1 mm long. Achene 3 - 4 mm long, 2 - 2.5 mm broad, glabrous, strongly alveolate-lacunose except near apex which is smooth and rounded, light or dark grey, the interlacunar ridges paler than the lacunae; hypogynium distinctly 3-lobed, the lobes rounded, pale yellow.

Distinguishing Characters

Rhizome : none.
Culms : clustered.
Inflorescence : of terminal and lateral panicles, laterals single at 1 - 3 nodes.
Achene : glabrous, strongly alveolate-lacunose proximally, more-or-less smooth distally, grey.
Hypogynium : with three rounded lobes, ochreous.

This species is distinguished from all other local representatives of subgenus Scleria by the absence of a rhizome and by the patterning of its achene.
Specimens Examined

ETHIOPIA

Near Gafta, ix. 1838, Schimper 1232 (K, syntype x); Chiré Plain, x-xi. 1840, Quartin Dillon and Petit s.n. in part (K, syntype x).

ZAMBIA

Kabulamwanda, 70 miles N of Choma, ii. 1955. Robinson 1102 (K).

ZIMBABWE

1725 (Livingstone) (-DD) Victoria Falls in rain forest, iii. 1932, Brain 8788 (K).

SWAZILAND

2031 (Mbabane) (-CA) bank of Usutu River, 5 miles below Benya, ii. 1979, R.W. Haines 7034 (PRE).

SOUTH AFRICA, TRANSVAAL


2431 (Acornhoek) (-CA) iii. 1967, P. van Wyk 4786 (PRE).

NAMIBIA

1820  (Tarikora)  (-BB) 1 km SE of Kandatora School in dry Jossa pan, iv. 1977, M. Müller and W. Giess 489 (K, PRE).

1917  (Tsumeb)  (-BA) Tsumeb, Nossib Pan, iv. 1934, Dinter s.n. (K).

1918  (Grootfontein)  (-AC) Abenab Gurneb, v. 1934 Schoenfelder 808 (K, PRE).

(-CA) farm Keibeb, iv. 1950, Schweickerdt 2189 (K, PRE, NU); Grootfontein north, iii. 1958, Merxmüller and Giess 2081 (PRE).

Photographs/Photostats Examined

ANGOLA

0915  Pundo Andongo district, 2400 - 3800 ft., i. 1857, Welwitsch 7122 (BM. type of S. dumicola)

MADAGASCAR

Bencnitsa, undated, Perrier de la Bâthie 12704 (P, type of S. perrieri).
Habit, rhizomatous perennial. Rhizome 2.5 - 5 mm thick, red, little more than the connective between contiguous swollen culm bases which form a more-or-less irregular clump, scales pale brown. Culm 45 - 100 (135) cm tall, glabrous. Leaves spaced throughout the middle part of the culm, 1.4 - 5 mm wide, glabrous or sparsely pilose, the lowest represented by almost bladeless reddish sheaths; sheaths glabrous or sparsely pilose towards the mouth; mouth truncate or produced into a very short rounded tongue. Inflorescence terminal and lateral, elongated; terminal panicle solitary, up to 3 cm long; lateral panicles shorter, 2 - 4 (5) at 2 - 3 nodes on slender, unequally exserted, glabrous or glabrescent, pendulous peduncles. Male spikelets 4 - 5 mm long, pedicillate, the pedicels sparsely pilose, 1 - 8 (10) mm long. Glumes 3.5 - 5 mm long, glabrous, stramineous or light reddish-brown with green keels, the midrib of the female glumes sometimes excurrent in an awn up to 1 mm long. Achene ovoid or subglobose, 2.7 - 2.8 mm long, 1.7 - 1.9 mm broad, lightly tessellate-lacunose, grey or light brown with 3 darker longitudinal stripes, hairy, the hairs white or golden; hypogynium zoniform proximally with three acutely triangular lobes clasping the base of the achene, light brown.
Distinguishing Characters

Rhizome: with very short internodes so that culm form an irregular clump.

Inflorescence: of terminal and lateral panicles, laterals at 2 - 3 nodes, 1 - 3 (5) per node.

Achene: hairy distally and proximally, tessellate-lacunose, grey or light brown, the hairs often golden.

Hypogynium: small, with three unguiculate lobes, brown.

This species is easily confused with *S. nyasensis* C.B.Cl., a species which has not been recorded from the F.S.A. area. It differs from this species mainly in having narrower laminas, in having the lobes of the hypogynium strongly unguiculate and in often having the achene hairs golden whereas those of *S. nyasensis* are white. Of the species recorded from the F.S.A. area it comes closest to *S. achtenii*, but differs in having much narrower leaves and a more strongly patterned achene surface with very many more hairs. The hairs of *S. achtenii*, like those of *S. nyasensis*, are white, and the lobes of the hypogynium, although acute, are not unguiculate. The hypogynium of *S. unguiculata* is brown whereas that of *S. achtenii* is white.

Specimens Examined

ZAMBIA

1150 (-BB) 35 miles N of Fort Rosebery, vi.
1957, Robinson 2267 (NU).
1258 (-DC) 16 miles NW of Ndola, vi. 1957, Robinson 2228 (NU).

BOTSWANA

1923 (Maun) (-AA) near island on Mboroga River headwaters, vi. 1979, P.A. Smith 2790 (PRE); near a minor tributary of the Mboroga R. at Qwa Island, vi. 1979, P.A. Smith 2799 (PRE).

(-CA), between Xoroko and Xhorokaé Islands, iv. 1977 P.A. Smith 1980 (PRE); sides of Central Boro River, xi. 1977 P.A. Smith 1994 (PRE).

Photographs Examined

ZAMBIA

1030 (-AA?) Luwingu district, iii. 1962, Robinson 5056 (K, holotype*).

Type: Congo, Achten 97 B (BR, holotype)

Achten 97 A (BR, isotype, no rhizome)


Syntypes: Congo, Vanderyst 1060, 8190 & s.n. (BR)

S. subintegrioloba De Wild. in Pl. Bequaert. 4: 238 (1927); as S. achtenii var. subintegrioloba (De Wild.) Pierart in Lejeunia, Méém. 13: 47 (1951)

Type: Congo, Vanderyst 2839 (BR).

S. nyasensis sensu E. Nelmes in Kew Bull. 11: 1: 86 (1956), pro parte, non C.B.CI.7

Habit, rhizomatous perennial. Rhizome 3 - 5 mm thick, sometimes more-or-less straight with culms arising from it at intervals of up to 1.5 cm, or more often little more than the connective between swollen culm-bases, red; scales pale reddish brown. Culm 70 - 110 cm long, glabrescent or sparsely villous-hispidulous. Leaves spaced throughout the middle part of the culm, 2.5 - 5 mm wide, glabrous adaxially, villous on principal ribs abaxially, the lowest reduced to almost bladeless sheaths; sheaths villous but always glabrous immediately below the mouth; mouth usually produced into a reddish, rounded tongue with a pale, membranous margin, the margin-base villous. Inflorescence terminal and lateral, much elongated so that the distance from the lowest panicle-bearing node to the apex of the terminal panicle is up to 85 cm; terminal panicle up to 9 cm long; lateral panicles 2.5 - 4 (5) cm long, single at
2 - 3 nodes, on pendulous, villous peduncles exserted up to 18 cm from the sheaths. Male spikelets 7 - 9 mm long, glumes glabrous, stramineous or reddish, sessile or on pedicels shorter than themselves. Female glumes glabrous, partly or wholly reddish. Achene 2.5 - 3 mm long, 1.8 - 2 mm broad, obovoid to subglobose, lightly and obscurely lacunose, hairy, grey, brownish-grey or violet-grey at maturity, white when immature; hypogynium small, 3-lobed, the lobes terminating in ligulate extensions up to 1 mm long which may be 2 - 3 fdd, white.

**Distinguishing Characters**

**Rhizome** : sometimes with very short internodes but often elongate with culms arising at intervals of up to 1.5 cm.

**Inflorescence** : of terminal and lateral panicles, laterals single at 2 - 3 nodes.

**Achene** : hairy distally and proximally, very faintly reticulate-lacunose, grey or brownish-grey, the hairs white, sparse.

**Hypogynium** : small with three acuminate to acute lobes, white.

The distinguishing features which separate this species from *S. unguiculata* and *S. nyasensis* are discussed under *S. unguiculata*. 


Specimens Examined

ZAMBIA

1150 (-BB) Chipili, 35 miles N. of Fort Rosebery, vi. 1957, Robinson 2270 (NU).

MOZAMBIQUE


SOUTH AFRICA, NATAL

2632 (Bela Vista) (-DD) Kosi area, Lakeside Amanzimnyama forest, xii. 1958, Tinley 361 (PRE, NH, NU); Kosi Bay estuary, xi. 1969 Moll 4534 (NH).

2831 (Nkandla) (-DD) Mnunzini, vi. 1976, Ward 8887 (PRE, NH).

2832 (Mtubatuba) (-CA) Lower Umfolosi district, Richards Bay, vi. 1963, Robinson 5523 (K).


(-DD) Durban district, Merebank East, iii. 1966 Ward 5437 (NH, NU, UD-W).

(-BC) Umzinto district, Pennington, below Liebenberg's cottage, i. 1969, K.D. Gordon-Gray 6215 (NU).

Photographs Examined

ZAIRE

0415 (AC?) Lower Congo, Leopoldville, 1915, Achten 97 (BR, holotype of S. achtenii);
1913, Vanderyst 1060 (BR, type of S. substriato-alveolata); Katchaka, xii.
1913, Vanderyst 2839 (BR, type of S. subintegriloba).

Lectotype: Brazil, 2. iii. 1864, Warming s.n. (C).

S. moritziana Boeck. in Linnaea 38 : 460 (1874).

Type: Venezuela, Moritz 645 a (BM) not seen by me.


Type: Sudan, Schweinfurth 2474 (K).

S. diurensis Boeckeler in Flora 62 : 573 (1879)

Type: Sudan, Schweinfurth 2389 (K, P) pro parte.


Type: Angola, Welwitsch 7127 (BM).


Type: Madagascar, Mayotte, Boivin 3043 (P).


Type: Five syntypes including Vanderyst 3471 (BR), not seen by me.


Type: Ten syntypes including Mullenders 159 and 672 (K) not seen by me.
Habit: rhizomatous perennial. Rhizome 3 - 4 mm thick with very short internodes obscured by thickened culm-bases; scales pale brown. Culms 50 - 200 cm tall, slender, smooth and glabrous. Leaves, evenly spaced throughout the lower part of the culm, 5 - 12 mm wide, glabrous, scabrid on margins and major veins adaxially and sometimes scaberulous over the whole adaxial surface towards the leaf apex; sheaths glabrous or scaberulous on the angles, often villous near the mouth, mouth truncate or produced into a short membranous tongue which may be glabrous or villous. Inflorescence terminal and lateral; terminal panicle 3 - 12 cm long; lateral panicles 3 - 8 cm long, 1 - 3 at 2 - 3 nodes on unequally exserted pendulous peduncles which are scaberulous on the angles. Male spikelets 4 - 6 mm long, sessile or nearly so, their glumes pale with fine reddish-brown striae, glabrous, scaberulous on midrib distally. Female glumes 4 - 5 mm long, glabrous, pale with fine reddish-brown striae, midrib scaberulous, excurrent into a scabrid awn up to 1 mm long. Achenes 3 - 4 mm long, 2 - 2.5 mm broad, ovoid to sub-globose, smooth or lightly striate-lacunose, hairy towards the base, glabrous on the top, grey or brown at maturity; hypogynium 3-lobed the lobes narrowly lanceolate - acuminate, 0.5 - 1 mm long, creamy-white.

Distinguishing Characters

Rhizome : with very short internodes so that culms form an irregular clump.

Culm : base slightly swollen.
Inflorescence: of terminal and lateral panicles; laterals at 2 - 3 nodes, 1 - 3 per node.

Female glumes: glabrous.

Achene: glabrous distally, hairy proximally, smooth or lightly striate-lacunose, grey or brown.

Hypogynium: with three narrowly acuminate lobes, cream-coloured.

This species is distinguished from _S. unguiculata_ and _S. achtenii_, the other two species recorded from the area which have hairy achenes, by the absence of hairs from the top of the achene, the absence of patterning on the achene surface or its faintness and by a tendency for the achene of _S. lagoensis_ to be more nearly globose than the achenes of the other two species which are usually more ovoid. It is distinguished from _S. adpresso-hirta_ (Kük) E.A. Robinson by its glabrous female glumes in particular. The last species has not been recorded from the F.S.A. region.

Specimens Examined

SOUTH AMERICA, BRAZIL

Mato Grosso, Barra do Garças - Xavantina road, about 77 km from Barra do Garças, wet camp sedge, nuts, white, vi. 1966, D.R. Hunt and J.F. Ramos 6067 (K).
AFRICA, SUDAN

0728 ( ) Bahr el Ghazal Province, ix. 1869, Schweinfurth 2389 partly (K); x. 1869, Schweinfurth 2474 (K, type of S. canaliculata-triquetra*).

ZAMBIA

1528 (-CC?) 40 miles S of Ndola, iii. 1960, Robinson 3368 (NU).

SWAZILAND

2631 (Mbabane) (-AA) near top of Komati Pass, xii. 1950, Compton 29644 (K, PRE).

Photographs/Photostats Examined

BRAZIL

Lagoa Santa, iii. 1864, Warming s.n. (C, lectotype*); M. Dec., Warming s.n. (C).

ANGOLA

0915 Pundo Andongo district, iii. 1857, Welwitsch 7127 (BM, type of S. cervina*).

MADAGASCAR

Mayotte, 1849, Boivin 3043 (P, type of S. mayottensis*).
6.4.20. Scleria melanomphala Kunth, Enum. Pl. 2 : 345 (1837)

Type: Cap. b. spei; in ora orientali legit Drège (?B).

Lectotype: South Africa, Drège s.n. [4360 of C.B. Cl.] (K; isolectotype, OXF).

S. macrantha Boeckeler in Flora 62 : 572 (1879)
non S. macrantha Boeck. (1859), nom illegit.

Type: Sudan, Schweinfurth 3746 (K).


Type: Brazil, Ule 8066 (formerly at B, not seen).


Syntypes: Central African Republic, Le Testu 2436 (P), Tisserant 1233 (P).

Habit, robust, rhizomatous perennial.
Rhizome 4 - 5 (7) mm thick; scales purplish-red or reddish-brown. Culms 80 - 200 cm tall, smooth and glabrous or scabrid on the angles, glabrescent on the sides, either more-or-less contiguous or arising at intervals of 1 - 2.5 cm
from the rhizome. Leaves spaced throughout the middle part of the culm, 7 - 15 (20) mm wide, glabrescent or sparsely villous, scaberulous on the margins and principal ribs, the lowest reduced to almost bladeless sheaths; sheaths glabrescent or villous, the mouth produced into a rounded tongue with pale membranous margin. Inflorescence terminal and lateral, much elongated, the panicles very shortly branched or more-or-less spicate; terminal panicle 3 - 9 (11) cm long; lateral panicles 2 - 5 (6) cm long, single or 2 - 3 at 1 - 3 nodes, on pendulous peduncles exserted up to 30 cm from the sheaths. Male spikelets 8 - 12 mm long, more-or-less sessile, their glumes hispidulous or villous on the midrib. Female glumes 10 - 12 mm long, hispidulous or villous on the keels and towards the awned tip, keel pale green, sides reddish or blackish. Achenes 4 - 5.25 mm long, 2.5 - 3.5 mm broad, obtusely trigonous, ovoid, smooth, glabrous, or with sparse hairs in a narrow zone adjacent the hypogynium proximally, grey or brown at maturity; the apex usually black; hypogynium obscurely 3-lobed or unlobed, zoniform, pale brown.

Distinguishing Characters

Rhizome : stout, horizontal, internodes long or short.

Leaves : more-or-less evenly spaced along length of culm.

Inflorescence : of terminal and lateral, very compact, almost spiciform panicles; laterals 0 - 2 (3) at 2 - 3 nodes.
Female glumes: glabrous adaxially.

Achene: glabrous or rarely with very few tiny hairs proximally, ovoid, beakless, grey with black apex.

Hypogynium: more-or-less zoniform, brown.

This species may be confused with S. greigiifolia, from which it is distinguished by the even spacing of leaves along the length of the culm, by its very compact, spiciform panicles, by its adaxially glabrous female glumes, by its beakless achene and by the black apex of the achene. Both species have brown, zoniform hypogynia.

Specimens Examined

SUDAN

0930 (N) Bahr el Ghazal, Niamniam swamps at Huuh or Hoo River, v. 1870, Schweinfurth 3746 (K, type of S. macrantha Boeckeler, nom. illegit.).

ZAMBIA

0831 (-CD) Abercorn, undated, Seagrief 2286 (RUH); Chianga river dambo, vi. 1956, Robinson 1715 (NU); Abercorn, ix. 1957, Vesey-Fitzgerald 1258 (NU); settlement by road near Kiwimbe, ii. 1959, M. McCallum-Webster s.n. (NU).

1131 (-BD) Nkondwe plain, Lukulu drainage, Mpika, iv. 1959, Vesey-Fitzgerald 2488 (NU).

Munshiwenta, iii. 1941, F. Stohr 570 (BOL).

BOTSWANA

1923 (Maun) (-AA) river headwaters near Dindinga Island, iv. 1979, P.A. Smith 2789 (PRE).

(-AB), northern district Mboma Harbour, 1. 1973, P.A. Smith 2789 (PRE).

ZIMBABWE

2032 (Chipinga) (-BC) Chipinga farm, ii. 1962, Moll 257 (NU).

SOUTH AFRICA, TRANSVAAL

2230 (Messina) (-CD) Tate Vondo Forest Reserve, ii. 1978, G. Hemm 556 (PRE, J).

2430 (Pilgrim's Rest) (-DB) Mariepskop, xii. 1963, H.P. van der Schiff 6384 (PRE).

2530 (Lydenburg) (-BD) i. 1974, J.P. Kluge 435 (PRE).

SWAZILAND

2031 (Mbabane) (-CA) Malkerns, iii. 1975, Compton 27369 (PRE); Black Umbuluzi Valley swamp, xii. 1963, Compton 31862 (PRE).
SOUTH AFRICA, NATAL

costlands, Isikane, ii–iv. 1855, Sutherland s.n. (K); no precise locality given, received xi. 1857 at K, Buchanan 351 (K, NH); Zululand, no precise locality given, xii. 1898, Jenkinson 8 (Wood 7313) (K); no precise locality given, x. 1909, Galpin 8581 (Wood 11513) (PRE, STE).

2632 (Bela Vista) (-DD) Ingwavuma district Kosi system, xi. 1958, Tinley 303 (PRE, NU).

2831 (Nkandla) (-CD) Isilwa, near reservoir, x. 1949, J.G. Lawn 1213 (NH).

(-DC) Mtunzini district slopes of Ongoye above Ongoye Mission, xi. 1956, E. Bayer s.n. (NU); Ongoye Forest Reserve, xii. 1963, B.J. Huntley 696 (NU); xii. 1964, B.J. Huntley 789 (NU); Ongoye Mountain, xi. 1968, Strey 8304 (PRE, NH); Mtunzini district Ongoye Reserve, xii. 1968, K.D. Gordon-Gray 6188 (NU).

(-DD) Mtunzini district Umlalazi Nature Reserve, ix. 1962, Ward 4327 (PRE); Mtunzini, KwaDlangezwa University College, Zululand, xi. 1962, H.J.T. Venter 842 (NH); Mtunzini district, xii. 1963, B.J. Huntley 638 (PRE); KwaDlangezwa on edge of Inkonjane Creek, xi. 1966, P.J. Mtombeni 32 (PRE).

2832 (Mtubatuba) (-AB) Hlabisa district, W of Charter's Creek, xii.
1955, Ward 2856 (PRE, NH, NU); Inhlawat Active Mission, xii. 1960, Ward 3648 (PRE, NU).

(-AC) east of Mtubatuba, iii. 1941, A.P.G. Michelmore 10 (K, PRE).

(-AD) Hlabisa district, Dukuduku, E corner of U 175, iv. 1964, Ward 5077 (K, PRE, NH, NU, UD-W); St Lucia Estuary, v. 1976, Ward 8872 (PRE, NU, UD-W); v. 1976 Ward 8874 (NU, UD-W).

(-CC) Zululand, near Richards Bay, i. 1949, Ward 724 (NU); Lower Umfolosi district, Richards Bay, iv. 1964, Ward 4936 (NH, UD-W).

2930 (Pietermaritzburg) (-DB) Inanda, xii. 1881, Wood 1597 (NH, BOL).

(-DD?) near Umlaas River, vi. 1890, Krauss 42 (K).

3030 (Port Shepstone) (-BB) Umbogintwini, x. 1913, Moggs 4318 (PRE, J).

(-BC) Umzinto district, Pennington, below Liebenberg's cottage, i. 1969, K.D. Gordon-Gray 6217 (NU).

(-CB) Oribi Flats, iv. 1937, A.P.D. McClean 387 (PRE, NH).

(-CD) Uvongo Beach, x. 1964, Ward 4740 (NU); Uvongo South, xii. 1975, Ward 8837 (PRE, NH, NU); St Michaels, iii. 1966, H.B. Nicholson 317 (NH).
3130 (Port Edward) (-AA) Beacon Hill East, i. 1967, Strey 7251 (NH).

**TRANSKEI**

3129 (Port St Johns) (-BD) Port St Johns, i. 1921, Schonland 4189 (PRE); i. 1933, Mogg 17070 (PRE); upper grassland: ii. 1965 Moss 4001 (K, J).

3228 (Butterworth) (-AD - CB) Kentani district, iii. 1904, Alice Pegler 322 (BOL); (-CB?) Between Bashee river and Morley, Tembuland, ii. 1840, Drège [4369] (K, lectotype,)

(-CB) near Kei Mouth, i. 1892, H.G. Flanagan 988 (PRE, BOL).

**Photographs/Photostat Examined**

+0535 (N) Oubangi - Chari, ii. 1921, Le Testu 2.436 (P, syntype of *S. centralis*);

Oubangi Plateau, Bambari district, ix. 1923, Tisserant 1233 (P, syntype of *S. centralis*).

Type: India Or., Koenig s.n. (LD, duplicate at LZ).


Type: Philippines, Haenke s.n. (PR, duplicate at K).
**Habit**: robust rhizomatous perennial. Rhizome 5 - 17 mm thick; scales brown. Culms 130 - 180 (200) cm tall arising at intervals of c. 10 cm from the rhizome, glabrous, smooth or scaberulous above. Leaves mostly crowded towards the base, up to 5 cm wide, tough, sometimes corky in texture towards the base and up to 5 mm thick, glabrous with smooth or distally scabrid margins, red towards the base; sheaths usually split almost to base from the concave mouth, red towards mouth. **Inflorescence** a single terminal panicle usually without foliaceous bracts, the compound branches scabrid, bearing very numerous spikelets, 10 - 20 cm long, 5 - 12 cm broad. Male spikelets 3.5 - 4.5 mm long, sessile, their glumes glabrous or hispidulous, reddish-brown. Female glumes 3.5 - 5 mm long, glabrous or hispidulous, reddish-brown. Achenes 3 - 3.5 mm long, 2.5 - 2.8 mm broad, obscurely and obtusely trigonous, broadly ovoid to subglobose, smooth, glabrous; mature achenes pale brown, immature achenes shining white; hypogynium small, with 3 very short triangular lobes, pearly-white or white with fine, reddish-brown vertical stripes.

**Distinguishing Characters**

| **Rhizome** | stout, horizontal, with short or long internodes. |
| **Leaves** | crowded towards base of culm, their bases thick and spongy. |
| **Inflorescence** | of a single terminal panicle, usually without a foliaceous bract. |
| **Achene** | glabrous, smooth, subglobose, grey brown. |
Hypogynium: small, with three very short, obtusely triangular lobes, usually brown.

This species is unlikely to be confused with any other. It is very robust, forms dense, pure stands in shallow coastal pans, has leaves which are very much broader and thicker than those of any other local species and is the only Southern African species other than S. lacustris with a very small hypogynium with three obtusely triangular lobes. The two species are allopatric and differ in their habit.

Specimens Examined

MOZAMBIQUE

2632 (Bela Vista) (-BD) Sul do Suvc, Maputo, iii. 1952, M. Myre and M.F. de Carvalho 1147 (NU).

SOUTH AFRICA, NATAL

2732 (Ubombo) (-BA) Bazwana sand flat, i. 1964, Strey 5137 (NH).

(-BB) Maputa, iv. 1968, Strey 8199 (PRE, NH, UD-W).

(-CD) Hlabisa district, N. of St Lucia, iv. 1960, collector un-named (PRE 39070); St. Lucia Park near Brodie's Crossing, iii. 1962, Ward 4024 (PRE, NH, NU).
SOUTH AFRICA, NATAL (contd.)


(-AD) W. of Mount Tabor, iii. 1978 Ward 9166 (UD-W).

INDIA

Assam, Ind. Or., Wallich Cat. 3537 (K ex Herbarium Hookerianum 1867, duplicate of Koenig type x).

PHILIPPINES

Sheet bearing a note by C.B. Clarke, June 1890, which reads "This is a type specimen of Presl's own". Duplicate of Haenke s.n. (K, type of Scleria oryzoide ex Herbarium Forbes Young).

Lectotype: Angola, Welwitsch 6959 (BM).

Syntypes: Madagascar, Baron 1870 (K); Hildebrandt 3751 (K).

Scleria acriulus (Ridl.) C.B. Cl., 1.c. (1902).

Type: Congo, Gentil s.n. (BR).

Scleria friesii Kükenthal in Wiss. Ergebn. Schwed. Rhodesia - Kongo Exped., 1911 - 12, 1: 9 (1921)
Type: Zambia, Fries 743 (K, UPS).

Habit: robust rhizomatous perennial.
Rhizome 6 - 10 mm thick; scales brown or reddish-brown. Culms 100 - 200 cm tall, smooth and glabrous, more-or-less contiguous or arising at intervals from the rhizome, often red. Leaves crowded towards the base of the culm, 5 - 12 mm wide, rigid, glabrescent or hispidulous with smooth, setulose-ciliate or scabrid margins; rarely unequally laterally praemorse in the distal part of the lamina;
sheaths glabrescent or hispidulous, the mouth concave with minutely setulose-ciliate margin. Inflorescence terminal and lateral, lax, very copious; lateral panicles 4 - 7 at 2 - 3 nodes, on slender, pendulous red peduncles exserted up to 20 cm from the sheaths. Male spikelets c. 5 mm long, six to eight times as numerous as the female, dark reddish-black proximally, pale castaneous distally, hispidulous on the midrib and with setulose-ciliate margins distally. Female glumes hispidulous on the midrib and awn, thickly lined with stiffly upward-pointing hairs on the distal half of the inner (abaxial) surface, with setulose-ciliate margins, dark reddish-black proximally, pale castaneous or greenish distally. Achene c. 6 mm long, 3.5 mm broad, broadly ovoid, laterally flattened, sharply apiculate, smooth, glabrous, pale brown or pinkish-brown, sometimes with violet blotches at maturity; hypogynium unlobed, zoniform, pale or dark brown.

Distinguishing Characters

Rhizome : stout, horizontal, with short or long internodes.
Leaves : crowded towards base of culm.
Inflorescence : of terminal and lateral, copiously branched panicles, laterals 4 - 7 at 2 - 3 nodes.
Female glumes : densely villous adaxially in distal half.
Achene : glabrous, smooth, ovoid, strongly beaked, pinkish-brown.
Hypogynium: more-or-less zoniform, brown.

This species may be confused with S. melanomphala from which it is distinguished by having its leaves crowded towards the base of the culm, by its lax, copiously branched panicles, by its adaxially densely-hirsute female glumes and by its strongly-beaked achene which lacks the black apex seen in S. melanomphala. The hypogynia of the two species are alike.

Specimens Examined

ZAIRE

0515 (-AA?) Kinshasa, Madimba Kinkosi, ii. 1960, P. Compère 1534 (K).

0718 (-BC?) Kinshasa, Kahemba district, valley of Lutschima River, iv. 1957, R. Devred 1901 (K).

0726 ( ) Rivière Mwanzangoma (E. Dibaya), i. L. Lieben 2312 (K).

1026 (-AC) Kansenia (Katanga), forest margin near road 1550 - 1600 m, vii. 1957, Michel Lukuesa 100 (K).

+ 1027 Haut-Shaba, Kundelungu plateau, bank of river Kalunda, 1500 m, i. 1971, S. Liskowski 10640 (K); Shaba Province. (Katanga), Kundelungu plateau, marsh between source of Lofoi and Katshapa Rivers, 1700 m, iii. 1975, S.S. Hooper and C.C. Townsend 553 (K).
UGANDA


ZAMBIA

0831 (-CD) Abercorn, Lake Chila plain, v. 1952, W. Siame 209 (NU); Abercorn, undated, probably 1959, M. McCallum-Webster s.n. (NU).

ZIMBABWE

1930 (Umvuma) (AB - BC?) Chilimazi district, Umvuma, ii. 1971, O. Chiparawasha 349 (NU).

SOUTH AFRICA, NATAL

2832 (Mtubatuba) (-AB) Lower Umfolosi district, Lake St Lucia, Eastern Shore, x. 1963, P.G. Stewart 293 (PRE).

3130 (Port Edward) (-AA) Port Edward, xii. 1930, Moss 19166 (J); Izingolweni road, i. 1951, K.D. Huntley 781 (NH, NU) Beacon Hill East, i. 1967, Strey 7251 (PRE, NH); Braemar Farm, Umtamvuna river reserve, x. 1976, H.B. Nicolson 1598 (PRE).

MADAGASCAR

± 2047 Ost Tmerina, Central Madagascar, xi. 1880, Hildebrandt 3571 (K, syntype of Acriulus madagascariensis); Central Madagascar, x. 1882, R. Baron 1870 (K, syntype of Acriulus madagascariensis
Photographs/Photostats Examined

CONGO

( ) no locality given, undated, Gentil
s.n. (BR, type of Acriulus titan\(^x\)).

ZAMBIA

+ 1230 Rhodesia bas orien. Mare ad Bangweulu,
1911 - 12, R.E. Fries 743 (K, isotype
of Scleria fricsii\(^x\)).

Types: Madagascaria, Cap. b. spei; in oram orientali legit Drège (?B).

Lectotype: South Africa, Drège s.n. [4246 of C.B. Cl.]/ (K).

**Habit**: robust, rhizomatous perennial. Rhizome 4 - 7 mm thick, more-or-less straight, with dark brown scales. Culms up to 250 cm tall, bases 3 - 9 mm thick, glabrous near base, hairy above below nodes, arising at intervals of 1.5 - 2.5 cm from the rhizome. Leaves spaced throughout the middle part of the culm, 6 - 16 mm wide, glabrous, scabrid on margins and adaxially on major veins, usually unequally laterally praemorse in distal part of lamina, the lower reduced to almost bladeless sheaths; sheaths glabrous or more often villous below the mouth, mouth produced into a rounded-deltoid tongue 2 - 5 mm long. Inflorescence terminal and lateral, the lateral panicles single at 3 - 7 nodes on erect, more-or-less shortly exserted peduncles; panicles rather compact, 3 - 4 (6) cm long. Male spikelets 3.5 - 4 mm long, the glumes hispidulous on keels and distal margins. Female glumes glabrescent or hispidulous on keels and distal margins, 3 - 3.5 mm long, pale brown with darker reddish streaks. Achene ovoid to ovoid-globose, 2.25 - 3.5 mm long, 1.8 - 2.3 mm broad, smooth,
glabrous, dark purple at maturity, violet or white when immature; hypogynium barely 3-lobed, fimbriate on upper margin, brown.

**Distinguishing Characters**

**Rhizome**
- stout, horizontal with long internodes.

**Leaves**
- evenly spaced along length of culm, the tips praemorse.

**Inflorescence**
- of terminal and lateral panicles, laterals single at 3 - 7 nodes.

**Achene**
- glabrous, smooth, globose, violet or dark purple.

**Hypogynium**
- margin fimbriate, brown.

This species is distinct from all others of the region by its praemorse leaves, its violet or purple achene and its fimbriate hypogynium.

**Specimens Examined**

**MOZAMBIQUE**


**SOUTH AFRICA, NATAL**

2632 (Bela Vista) (-DC) Ingwawuma district
x. 1958, Tinley 254 (PRE, NH, NU); Sihadla stream, South Kosi Lake system, ix. 1961, Ward 3712 (PRE, NU); Northern shore of Lake Nhlange, Kosi Bay, ix. 1961, Edwards 2559 (PRE, NU).

(-DD) Sihadla river crossing, ix. 1967 Moll and Strey 3907 (PRE, NH); Maputa area, Nkankini stream near Star of the Sea Mission, x. 1972, Ward 8083 (PRE).

2730 (Vryheid) (-CB) Utrecht, viii. 1934, Pole-Evans 3562 (K).

2831 (Nkandla) (-DC) Ungoya, Zululand, v. 1887 Wood 3863 (K, NH, BOL); Mtunzini district, Ngoye Forest Reserve, ii. 1964, B.J. Huntley 898 (NU).

2832 (Mtubatuba) (-AD) Hlabisa district, Lake St Lucia, Eastern Shore, xi. 1973, R.H. Taylor 120 (NU).

(-CA) Richards Bay, ix. 1970 Strey 9905 (PRE, NH).

(-CC) near Richards Bay i. 1949 Ward 717 (NU).

2931 (Stanger) (-AD) Lower Tugela district, 2 miles from Stanger, ix. 1965 Moll 2188 (NH, NU).

(-CA) Sheffield Beach, Umhlali, ix. 1950, Ward 1186 (NU).
3030  (Port Shepstone) (-CC) Umtamvuna bridge
   xii. 1966 Strey 7108 (K, PRE, NH, UD-W).
   
   (-CD) Ramsgate, ix. 1967, Strey 7705 (PRE, NH); Wichmann's farm, ii. 1974, Strey 11306 (PRE, NH).

TRANSKEI

3130  (Port Edward) (AA) Natal or Pondoland (sic), between Umtentu and Umzimkulu rivers below 150 m, ii. 1840,
   Drège [4246] (K, Lectotype x).
7. General Discussion

Not since 1874 when Boeckeler's comprehensive treatise on *Scleria* was published, has there been a revision of the genus as a whole, although several accounts of the genus for particular geographical areas have appeared (see Chapter 1). No general agreement has been reached on the circumscription of the genus, its subdivision, on its tribal affiliation or on the systematic position of its tribe within the family Cyperaceae. Such lack of consensus reflects the changing state of knowledge of *Scleria* and related genera and differences in the interpretation of, in particular, the morphology of inflorescences and flowers. Until agreement is reached with regard to interpretation of these structures the present unsatisfactory state of affairs is likely to persist.

Analysis by Eiten (1976) of Southern American representatives of the genus indicated that the classical interpretation of the spikelet of *Scleria* as a monopodial structure is correct. Before reading Eiten's paper I had come to the same conclusion after examining the inflorescences of Southern African species. Neither Eiten nor I found any evidence to support the interpretation of the spikelet as a sympodial structure (see Chapter 3).
Eiten's survey of the branching patterns of the ultimate inflorescence units extended to all the genera of Cyperaceae represented in Brazil and also some non-Brazilian genera. Based on her findings she was able to offer a scheme of classification for the Cyperaceae which differs in several respects from other schemes (see Chapter 1). In her scheme, the old tribe Sclerieae was dismembered by the separation of the name genus from the assemblage. By its exclusion, the need arose to provide a new name for the tribe to which the four genera previously included in Sclerieae were assigned. Since the earliest legitimate generic name in the new tribe is Bisboeckelera, the name Bisboeckelereae was applied to it.

The genus Scleria was not assigned to any of the tribes proposed by Eiten, nor was it accorded tribal status.

I have proposed (Chapter 6) that the tribe Sclerieae be maintained, and that its circumscription be modified so that it includes (in the present state of our knowledge) only the name genus.

In the structure of ultimate inflorescence units and in the gender of the flowers in the spikelets, Scleria is similar to Schoenoxiphium and Kobresia, both
members of the tribe Cariceae, but differs from these genera in lacking an utricle or semiutricular prophyll around the female flower. The closest natural affinity of *Scleria* seems therefore to lie with Cariceae, with which it cannot be included because of the absence of an utricle. Other tribes with true racemose spikelets of true unisexual flowers such as are found in *Scleria* and Cariceae are Bisboeckelereae and Lagenocarpeae. Therefore Sclerieae (*Scleria*), Cariceae, Bisboeckelereae and Lagenocarpeae which form, on the basis of their inflorescence patterns and other characteristics, what seem to be a natural group, are assigned to the subfamily Caricoideae.

Subfamily Caricoideae is considered to occupy a position in the family intermediate between Rhynchosporoideae which on the basis of its hermaphrodite flowers is considered to be less advanced, and Mapanioideae, which on the basis of its unisexual flowers aggregated in pseudanthia is considered to have reached the highest level of specialisation.

Although the distinctiveness of *Scleria* has long been recognised, there is still some difference of opinion with regard to the relationship of *Scleria* and Diplacrum, and *Scleria* and Acriulus. Diplacrum is maintained as a separate genus by most cyperologists,
but Kern (1961, 1974), Koyama (1961) and Raymond (1966) included it in *Scleria*. Eiten (1976) has demonstrated that the fundamental branching patterns of the ultimate inflorescence units of *Scleria* and *Diplacrum* differ, so that, far from being congeneric, these taxa must, on this basis, be assigned to different tribes.

The genus *Acriulus*, described by Ridley in 1884, was reduced by Clarke (1902) to congenerity in *Scleria* and subsequently (1908) restored by him to generic rank. *Acriulus* was once more reduced to synonymy by Kern (1963) who based his re-assessment upon a far more comprehensive array of specimens than had been available to Clarke. In the same publication the number of species was reduced from three to one (*Scleria greigiifolia*), and the spelling of the specific epithet was corrected. Although I do not agree with Kern's interpretation of the inflorescence of *Scleria*, I agree that the inflorescence structure in *Scleria* and *Acriulus* is fundamentally the same. I accept the validity of his argument in favour of reducing *Acriulus* to cogenerity in *Scleria*, and offer additional evidence in support of this course.

I consider *Acriulus* and *Scleria* to be congeneric for the following reasons:-

1. The type of habitat occupied by *Acriulus* is the same as that occupied by some species of *Scleria*
for example, *S. poaeformis*.

2. The habit of *Acriulus* is like that of some species of *Scleria*, for example, *S. poaeformis*.

3. The fundamental branching pattern of the inflorescence of *Acriulus* and *Scleria* is the same.

4. Spikelet morphology of *Acriulus* and some species of *Scleria* is the same.

5. Morphology of the flowers of *Acriulus* is fundamentally the same as that of *Scleria*.

6. Achene morphology of *Acriulus* and some species of *Scleria*, such as *S. melanomphala* is very similar, *Acriulus* being distinguished only by its pronounced beak, a feature which may occur in species of *Scleria* not represented in Southern Africa.

7. The hypogynium of *Acriulus* is similar to that of some species of *Scleria*, notably *S. melanomphala*.

8. The achenes of *Acriulus* and *Scleria* are silicified in the same manner, and to an extent not known in any other genus in Cyperaceae.

9. Structure of the pericarp is fundamentally the same in *Acriulus* and *Scleria*.
10. No anatomical feature of the root, rhizome or lamina of *Acriulus* is not shared by one or more species of *Scleria*.

11. Most anatomical features of the culm of *Acriulus* are shared by one or more species of *Scleria*, the exception being the possession, by *Acriulus*, of some, (not all) amphivasal bundles. It is possible that this feature too may be shared by some *Scleria* spp. from regions other than Southern Africa.

In my opinion, no valid reasons can be found to maintain *Acriulus* as a genus distinct from *Scleria*, a judgment first made by Clarke (but which he subsequently altered), and shared by Brain (1934), Kern (1963), Napper (1964), Robinson (1966) and Gordon-Gray (1972).

*Scleria* is a large, pantropical genus of approximately 200 species. It has long been recognised that the genus comprises several natural assemblages which have been variously designated as subgenera, sections and series. Little agreement on the hierarchical levels of infrageneric groups, or their delimitation has been reached. Opinions as to whether evolution has been monophyletic, diphyletic or
polyphyletic vary.

Analysis of habitat preferences, habit, morphology and anatomy of Southern African species has led me to conclude that evolution in *Scleria* has been diphyletic (see Chapter 6). Although the two evolutionary pathways are referred to as "lines", I am aware that this term is something of a misnomer, for each line comprises, not a linear sequence of taxa, but a far more complex dendritic pattern of ascending, interlinked branches of different lengths.

Subgeneric rank has been proposed for each of the two co-lateral lines, a treatment first proposed by Clarke in 1894, but abandoned by him in later publications (1898, 1900, 1902, 1908). Subgenus *Hypoporum* (Nees) C.B.Cl. comprises slender, narrow-leaved, sometimes hairy plants of open, seasonally dry, often temperate habitats. They are either annuals, or have perennial subterranean organs and annual aerial parts. The evolution of drought/cold escape mechanisms (completion of the life-cycle in a season, or withdrawal of food reserves into a protected subterranean organ) has permitted this subgenus to exploit a wider range of habitats than is available to taxa without such escape-mechanisms, such as predominate in subgenus *Scleria*.
Subgenus Scleria (Berg.) C.B.Cl. comprises more-or-less robust, usually broad-leaved, often evergreen perennials, and, less often, annuals. Many of the species in this subgenus are shade-dwellers, and the majority are hygrophilous or hydrophilous and are restricted to tropical and subtropical habitats. The annual species occupy tropical habitats in areas where seasonal drought may be experienced and it is suggested that the annual habit is a drought-escape mechanism in such species. Among the Southern African representatives of this subgenus, one species is known which has annual aerial parts and a perennial rhizome with swollen, persistent, culm-bases. It is significant that this species, *S. transvaalensis*, occurs at higher, more temperate altitudes than other local species in the subgenus.

The more robust habit and greater breadth of the laminas of most members of subgenus Scleria is consistent with the longer lifespan of the aerial parts of these plants, compared with that of members of subgenus Hypoporum. The shady habitat occupied by some members of this line is also conducive to increased stature and breadth of laminas. It is suggested that the lateral, pseudodorsiventral wing of laminar tissue present in some species is a modification which, by increasing surface area and volume, may increase the photosynthetic capacity of some shade-dwelling species.
A feature of the laminas of shade-dwelling species is the absence of stomata from the adaxial epidermis (except a few in the pseudodorsiventral laminar extension when it is present), which is wholly bulliform except where it overlies mechanical tissue in the lateral ribs. The role of the bulliform cells is not known, but I suggest that, since a wholly-bulliform adaxial epidermis is present only in shade-tolerant species, it may serve as a light transmitting layer. Epidermal cells of *Scleria* are a repository for silica. Since the walls of bulliform cells are silicified, and their lumina often filled with silica, the uninterrupted layer is rigid, so that laminas which possess such a layer are maintained in a fully-expanded state, which may be an advantage in a shady habitat.

Thickness of laminas is greatest in lacustrine, heliophilic taxa and is an external manifestation of the development of an extensive air-space system in the mesophyll. Such laminas are amphistomatic, as are the laminas of members of subgenus *Hypoporum*, and, as in *Hypoporum*, may lack intercostal bulliform cells in the adaxial epidermis or may have files of bulliform cells alternating with files of smaller cells in which stomata are present.

Although the fundamental branching pattern of the inflorescence of all species of *Scleria* (including
Acriulus) is the same, modification has taken place in two ways. Progressive contraction of all or most ramuli has given rise to the "glomerate-spicate" inflorescence characteristic of subgenus Hypoporum. Progressive contraction of some ramuli and progressive elongation of others has given rise to the "interrupted-paniculate" inflorescence of subgenus Scleria. In Hypoporum it is postulated that the taxa with many glomerate-spicate branches in the inflorescence, such as some specimens of S. woodii, are more primitive than those such as S. aterrima in which the inflorescence is invariably simply glomerate-spicate. Taxa such as those assigned by Clarke (1894, 1908) and Kern (1961, 1974) to section Corymbosae, none of which is represented in Southern Africa, probably exhibit the greatest degree of contraction of the inflorescence yet attained in the subgenus.

In subgenus Scleria, it is postulated that the greater the degree of elongation of proximal internodes in the inflorescence, and the greater the number of such elongated ramuli, the more highly specialised the inflorescence. Based upon these criteria, the Southern African species with the least specialised inflorescences are S. lacustris and S. poaeformis and those with the most specialised are S. greigiifolia and S. angusta.
Glomerate-spicate inflorescences are characteristic of taxa which occupy seasonally dry, grassland habitats. The achene-bearing spikelets which are androgynaeceous, are often held stiffly erect. Since there is no elaboration of the distal part of the achene stipe to form an hypogynium which, by increasing the width of the achene towards its base may force the female glumes apart, the achenes remain firmly clasped by the glumes even after silicification of the pericarp is complete and the achene is detached from its pedicel. Achenes are usually shed only when the annual aerial parts die back to the ground in winter. The inevitable result is that achenes reach the substratum in the immediate vicinity of the parent plants, thereby ensuring that, when germination takes place, the seedlings are in a suitable habitat. Since germination is likely to occur more-or-less simultaneously with the onset of favourable conditions in spring, shedding of achenes over an extended period would confer no advantage on such plants.

Taxa with interrupted-paniculate inflorescences are, with few exceptions, evergreen perennials which occupy permanently damp or wet, tropical or subtropical habitats. The inflorescences, achene-bearing spikelets and achenes of these plants have become modified so that achenes mature progressively, not simultaneously, and can be shed from the inflorescences instead of being
retained in them for the extended lifespan of the inflorescence. By elongation of their proximal internodes the partial panicles have become pendulous, so that the spikelets often hang upside-down. The achene-bearing spikelets have lost, in whole or in part, the distal male part, so that the solitary female flower appears to be terminal. By loss of the distal male part of the spikelet, and assumption of a pseudoterminal position by the female flower, mechanical obstruction to the spreading of the female glumes is removed. The achene stipe has become elaborated to form an hypogynium which, by increasing the width of the achene towards its base, forces the enveloping glumes apart to a greater extent than would be possible if there were no such structure. When the process of silicification is complete, the hypogynium becomes desiccated and shrinks slightly, and the achene becomes detached from its pedicel and drops out of the inflorescence.

There is, therefore, evidence that in Scleria, evolution of two different types of plants, two different types of inflorescence, different types of achene-bearing spikelets and two different types of achene has occurred in response to differences in habitat.
Insufficient evidence has been accumulated in this study to permit grouping of the species in subgenus Hypoporum into more than one section. Pending worldwide revision of the genus, a single section, Hypoporum (Nees) Endlicher, is recognised, with the characters of the subgenus.

Subdivision of subgenus Scleria into sections is possible, based partly upon the presence or absence of male rudiments in the achene-bearing spikelets. Only in this subgenus do functionally female spikelets occur. To section Scleria (Bergius) Endlicher are assigned those taxa in which most functionally female spikelets retain rudimentary distal male parts. The less specialised condition is one in which there are some fully androgynaecous spikelets as well as functionally female and male spikelets in the same inflorescence, and the more specialised condition is that in which there are some female spikelets without male rudiments as well as subandrogynaecous and male spikelets present. The hypogynia, although morphologically different in different taxa, all have entire margins. Members of this section inhabit damp, partially shaded forest margins, sheltered streambanks, open swamps or shallow lakes.

Those taxa in which the functionally female spikelets are (with rare exceptions) without male rudiments, have
been assigned to three sections, namely Acriulus (Ridley) C.B. Clarke, Schizolepis (Nees) C.B. Clarke and Ophryoscleria (Nees) C.B. Clarke. Section Acriulus is monotypic, *Scleria greigiifolia* being distinguished from members of section *Scleria* by its strictly female spikelets; by its adaxially hirsute female glumes; by its long-beaked achene, and by the presence of amphivasal bundles in the culm. Its hypogynium is like that of some members of section *Scleria*, notably *S. melanomphala*. Acriulus is maintained as a section pending world wide revision of the genus which may show that the characters enumerated are shared by some members of section *Scleria*, in which case *S. greigiifolia* would have to be placed in that section and the sectional diagnosis amended.

The habitat of *S. greigiifolia* is open swamp or stream-bank, a preference shared by some members of section *Scleria*.

Members of sections Schizolepis and Ophryoscleria occupy swamp-forest habitats, are alike in habit and have praemorse leaves. The sections are distinguished by their hypogynia which, in Schizolepis have fimbriate margins, and in Ophryoscleria are corky, cupuliform, exceed the achene in width and have ciliate margins.

Although there are hydrophilous taxa in all sections of subgenus *Scleria*, none but the members of section Ophryoscleria have buoyant achenes. Buoyancy of the
fruit is attributable to the highly specialised type of hypogynium. If the hypogynium is chipped away from the achene, the fruit sinks when dropped into water. Buoyancy undoubtedly increases the distribution range of the fruit thereby facilitating population spread. It is therefore likely that taxa with this type of morphologically distinctive hypogynium which serves a biologically important function not attained in any other group, has reached the highest level of specialisation in *Scleria*.

The least homogeneous section in subgenus *Scleria* is section *Scleria*. Members of this section occupy a greater variety of habitats and show a wider range of morphological diversity than do members of the more highly specialised sections.

Within section *Scleria* it is possible to discern groups of species which share similar morphological and anatomical features, for example, among Southern African members of this section, *S. achatensis*, *S. unguiculata*, and *S. lagoensis* have similar habit, similar lamina anatomy, hirsute achenes and trilobed hypogynia with acute lobes; *S. transvaalensis* and *S. natalensis* have similar habit, similar lamina anatomy, glabrous, strongly-patterned achenes and trilobed hypogynia with rounded lobes. Since Southern African representatives of the section represent only a small proportion of the
whole, circumscription of species groups is impossible. Only when all species are known and their life histories understood, may such circumscription be attempted.

The morphology of the achene of *Scleria* provides useful characters for the separation of taxa at subgeneric sectional and species levels. Achenes without hypogynia characterise subgenus *Hypoporum* and achenes with hypogynia, subgenus *Scleria*. The margin of the hypogynium is entire in sections *Scleria* and *Acriulus*, fimbriate in *Schizolepis* and ciliate in *Ophryoscleria*.

When used in conjunction with other characters, the morphology of the achene is also of value in species recognition. The shape, texture and colour of the hypogynium when present; the size, shape and colour of the achene itself; the patterning, if any, of the achene surface and the presence or absence of hairs may provide diagnostic characters. It has been found that, while most of these characters are reasonably constant, there are some species in subgenus *Hypoporum* in which achene surface patterning is variable, sometimes even on the same plant. Such inconstancy may be indicative of a lower level of specialisation in members of subgenus *Hypoporum* than in members of subgenus *Scleria*.

Very little is known of the sexual reproductive process in *Scleria*, therefore many questions remain
unanswered. What specialised rôle, if any, does the silicified pericarp play in the life history? Why do some species have smooth achenes and others have patterned fruit? Why are some achenes hirsute and others glabrous? What is the function, if any, of achene hairs? What factors, physical and physiological, govern germination? Do achenes of all species germinate or is apomixis the rule in some species? If there are apomictic taxa, are they obligate or facultative?

Only when the answers to these and other questions related to the breeding systems of these plants are known will it be possible to establish precise phylogenetic pathways at the lower levels of the taxonomic hierarchy.

The pantropical distribution of Scleria suggests that the genus was part of the Gondwanaland flora. Present day disjunct distribution of species such as S. poaeformis (Australasia, Asia and the east coast of Africa), S. foliosa (India, Madagascar, Africa), S. lagoensis (Madagascar, Africa, South America), S. greigiifolia (Madagascar, Africa), S. melanomphala (Madagascar, Africa, South America), S. lacustris (Madagascar, Africa, West Indies, South America), S. pergracilis (Asia, Africa), S. nutans (Madagascar, Africa, South America) suggests that these species were already in existence prior to the fragmentation of
Gondwanaland, and have persisted, themselves unchanged, since the Cretaceous, in areas unaffected by climatic changes occasioned by geophysical effects.

Other species, for example, *S. woodii*, *S. bulbifera* in Africa, have wide distribution ranges within a single continental land mass which suggests that their origins are more recent. Yet others are endemics, for example, *S. sobolifer*, *S. natalensis* and *S. transvaalensis* in Southern Africa, their range limited by climatic and edaphic factors. Whether such species are neoendemic or palaeoendemic cannot be determined until interspecific relationships are better understood, but it is suggested that some endemic species which occur at the southern extreme of the distribution range of the genus may be new species which arose during the southwards migration which followed the southerly movement of the equator in post-Cretaceous times.

Subgenus Hypoporum, with its cold/drought escape mechanisms, is adapted to seasonal climates as are some taxa in section Scleria of subgenus Scleria. Such taxa may have a greater potential for diversification than members of sections Acriulus, Schizolepis, Ophryoscleria and members of section Scleria which lack such escape mechanisms and are therefore restricted to moist tropical habitats.
Circumstantial evidence indicates that Scleria is an old genus; that two evolutionary lines had already become established prior to the separation of the land masses that comprised Gondwanaland; that some extant species of each subgenus were already in existence in the late Cretaceous; that speciation has continued subsequently and migration of subgenus Hypoporum and section Scleria of subgenus Scleria has taken place northwards as far as North America and parts of Asia; that the post-Cretaceous northward drift of the southern continents may have resulted in migration of species from their original southern limits southwards towards the present southern limits of the genus.

It has become clear during the course of this regional revision of Scleria that much more remains to be done, both in the field of alpha-taxonomy and in the biosystematic field. The need for a monographic (alpha-taxonomic) treatment of the genus is clearly apparent, but to persuade a young taxonomist to undertake such an unfashionable line of research may not be easy. The biosystematic investigation of many aspects of the life-history of these plants is equally important if interrelationships of taxa at the lower hierarchical levels is to be understood and it is hoped that some of the questions posed in this revision
will stimulate some younger taxonomists to embark on programmes of biosystematic research which will provide the answers to these questions.
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APPENDIX A

ORIGINAL DESCRIPTIONS

1. GENUS


Type: *Scleria flagellum-nigrorum* Bergius

Bergius, P.J. (1765) in Svenska Vetenskaps Academiens Handlingar, Stockholm 26: 142-144.

*SCLERIA*, Character genericus

*Flores masculi* in eadem panicula cum foemineis mixti.

CAL. *Gluma* 5-vel 6-valvis, distiche imbricata, ovata, multiflora: valvulis ovatis, acuminatis, carinatis, concavis, arcite clausis, integerrimis, persistentibus; inferioribus, minoribus, augustioribus.

COROLLA. *Valvulae* plurimae, oblongae, persistentes, calyce paulo longiores, stamina distinguishentes.

STAM. *Filamenta* plerumque 3 setaceae, longitudine Corollae, intra unamquamque valvulam corollae. Antherae incrassatae.

*Flores foeminei*

CALYX ut in masculo sed uniflorus.

COROLLA bivalvis, valvulis lanceolatis acutis, oblique flexis, calyce brevioribus.


PERICARP nullum.

SEMEN unicum globosum, subosseum, magnum, nitidum, apice tuberculatum, basi cinctum calyce.
2. SUBGENERA / SECTIONS

2.1. Section Hypoporum (Nees) Endlicher, Gen. Pl. 112 (1836)


Type: Hypoporum pergracile Nees ab Esenbeck


HYPOPORUM N. ab E.


2.1.2. Endlicher, Stephano (1836) Genera Plantarum 112.

HYPOPORUM Nees.

2.2. Section Scleria (Bergius) Endlicher, Gen. Pl. 112 (1836)


Type: Scleria flagellum-nigrorum Bergius


SCLERIA, Character genericus
Flores masculi in eadem panicula cum foemineis mixti.

CAL. Gluma 5-vel 6-valvis, distiche imbricata, ovata, multiflora - valvulis ovatis, acuminatis, carinatis, concavis, arcte clausis, integerrinis, persistentibus; inferioribus minoribus, angustioribus.

COROLLA. Valvulae plurimae, oblongae, persistentes, calyce paulo longiores, stamina distinguentes.

STAM. Filamenta plerumque 3 setacea, longitudine Corollae, intra unamquamque valvulam corollae. Antherae incrassatae

Flores foeminei

CALYX ut in masculo, sed uniflorus.

COROLLA bivalvis, valvulis lanceolatis acutis, oblique flexis, calyce brevioribus


PERICARP nullum.

SEMEN unicum globosum, subosseum, magnum, nitidum, apice tuberculatum, basi cinctum calyce.
2.2.2. Endlicher, Stephano (1836) Genera Plantarum 112.


2.3. Section Hymenolytrum (Nees) Core in Brittonia 2 : 1 : 8 (1936)

Type: Hymenolytrum comosum Nees
Nees ab Esenbeck in Martius, Flora Brasiliensis 2 : 1 : 158 (1842)

2.3.1. HYMENOLYTRUM N. ab. E.
Spiculae femineae in eodem ramulo inferae, sessiles, uniflorae, masculae pedunculatae. Cupula pateriformis, stipitata. Perigynium membranaceo-trilobum lobis parvis distantibus

2.3.2. Core, E. in Brittonia 2 : 1 : 8 (1936)
Hypogynium present. Pistillate spikelets lowest in each branch, sessile, one-flowered; the staminate on distinct long peduncles.


Type: *Acriulus greigiifolius* Ridley


**ACRIULUS**, N. gen.


**ACRIULUS**

Female spikelets with no male rudiments, so that the female flower appears terminal. Hypogynous disc merely the stalk of the nut. Rather stout plants, with copious panicles.

2.5. Section *Schizolepis* (Nees) C.B. Clarke in Hooker f. Fl. Brit. Ind. 6 : 694 (1894)

*Schizolepis* Schrad. ex Nees in Martius, Fl. Bras. 2(1) : 186 (1842)

Type: *Schizolepis latifolia* (Swartz) Nees ab Esenbeck

**SCHIZOLEPIS** Schrad.

Spiculae polygamae, monoicae, plerisque geminae, altera **mascula** pedunculata minore pluriflora, altera **androgyna** apice uniflora feminea accedente spicula mascula squamiformi infra flosculum, bi-trivalvi, uniflora, di-triandra, inclusa; **squamae** spiculae androgynae distichae, 3-5 latae. membranaceae; masculae propriae tristichae. Stamina spiculae masculae integrae tria, antheris mucronatis. **Stigmata** tria, elongata. **Cupula** perigynio minor, coriaceae, obsoleto triloba, lobis intergerrimis, horizontaliter bipartibilis, parte inferiore patelliformi in apice rhachillae residente, quandoque et tota cupula una cum perigynio fructui adhaerente. **Perigynium** cupula majus, membranaceum, coloratum, trilobum repandumve margine inciso-dentato libero. **Caryopsis** chartaceocrustacea, subglobosa aut subtrigona, saepe tuberculata.


Type: Ophryoscleria racemosa Nees ab Esenbeck

2.6.1. Nees ab Esenbeck, C.G.D. (1842) in Martius, Flora Brasiliensis 2 : 1 : 182

Ophryoscleria Nees in Martius, Fl. Bras. 2 : 1 : 182 (1842)

Schizolepis (Genus), Nees in Mart. Fl. Bras. ii (pars. 1) 158, 186 (char. extended).

Character of Elatae, but rim of disc-margin with numerous triangular or lanceolate teeth.

Ophryoscleria Nees in Martius, Fl. Bras. 2 : 1 : 182 (1842)

Spiculae diclines, monoicae, subconformes, feminineae in eodem fasciculo cum masculis sessiles uniflorae; masculae vel sessiles vel pedunvulatae tre - quadriflorae.

INFLORESCENTIA: spica axillares, pro familia graciles, angustae, basi ramosae, decrescentes neque in terminales ampliorem abeuntes. Spiculae saepe fasciculato-ternae, subsecundae, feminea in fructu glandiformi, vel una sessili duabusque masculis angustioribus pedunculatis, vel omnibus sessilibus media mascula. Vaginae alatae, alis lateralibus evidentioribus. Lobolus oppositifolius angustus. Spiculae glabrae, pallidae, florentes ovales aut oblongae; femineae squamae 4 - latires, una et altera inferius accedente minore; masculae squamae 6-8 inferioribus staminifer minoribus et tenerioribus.

2.6.2. Clarke, C.B. (1900) in Urban, Symbolae Antillanae 2 : 138

3. SPECIES


Clarke, C.B. (1898) in Thisdt.-Dyer, Flora Capensis 7: 295

*S. woodii*, panicle compound, lax, with capillary branches; spikelets in clusters, about 1/5 in. long, pale brown or rusty brown; bracts and bractlets (lowest empty glumes) aristate; nut obovoid, rather longer than broad, white, smooth or obscurely reticulate; otherwise as *S. dregeana*.


*Scleria welwitschii* C.B. Cl.

*S. junciformis* Welw. mss. ex Ridl. in Trans. Linn. Soc., Ser. 2, II (1884) p. 168 (non Tw.)

Afr. austro occ.: Angola, Welw. 7138, 7139.

3.2.2. Clarke, C.B. (1902) in Thisdt.-Dyer, Flora of Tropical Africa 8: 501

*S. WELWITSCHII*

Nearly glabrous, except the leaf-sheaths. Rhizome 1/4 in. in diam., shining yellow after the scales have worn off. Stems 1 ft. long, stouter than in the preceding species (*S. Rehmannii*). Leaves 8 - 12 by 1/8 - 1/6 in., many of the lower abbreviated
3.2.3. Ridley, N.H. (1884) in Transactions Linnean Society, Series 2, Botany 2: 168.

*S. JUNCIFORMIS*, Welw. MSS.; rhizomate repente crasso lignose squamis ovatis striatis tecto, radicibus rubris; culmis seriatis bipedalibus validis triquetris striatis glabris; foliis linearibus acute carinatis longis, inferioribus raro hispidulis vaginis integris striatis ore albo-ciliatis, inferioribus purpurascentibus, angulis longe ciliatis, superioribus glabris; paniculae ramis paucis triquetris suberectis, faciculis compositis; spiculis linearibus glabris pallide sanguineo-maculatis vel sanguineis; bracteolis spiculis brevioribus ovatis mucrone longo; squamis inferioribus lanceolatis breviter mucronatis, superemis lanceolatis acuminatis; caryopsi globulosi trigona minuta alba brevissime mucronata.

Huilla, in pratis sylvaticis alte graminosis prope Catumba, no. 7138; in pratis paludosis ex Monino ad Eme, frequens, no. 7139, Jan.-Mart. 1860.
This species is closely allied to *Scl. erythracrrhiza*, but is distinguished by the tuft of white hairs at the mouths, and the long white cilia on the angles of the vaginae, the paniculate arrangement of the inflorescence, and the glabrous spikelets with entire lanceolate acuminate glumes. The rhizome is, as in that species covered with ovate scales, the parenchyma of which decaying away leaves the fibro-vascular bundles. The rhizome is yellow, and resembles that of *Juncus balticus*, Willd.; the culms are somewhat distant, and 2 - 2½ feet in height; the leaves on the culm are 6 inches in length, excluding the vagina, and nearly always glabrous.


*S. Rehmannii;* spike more branched; spikelets 1/6 - 1/5 in. long, chestnut-brown; nut minute, depressed-ovoid (broader than long), white, shining, otherwise as *S. drègeana*.


*S. Rehmannii. Slightly hairy or glabrate. Rhizome 1/4 in. in diam., stout, rugged, Stems 12 - 10 in. long, not tufted, nor bulbous at the base. Leaves 4 - 12 by 1/8 - 1/6 in. Panicle 2 - 3 in. long,
bracts setaceous, inconspicuous, clusters of few (usually 3) spikelets, chestnut-coloured. Spikelets 1/6 in. long. Nut less than 1/20 in. in diam., depressed ovoid, smooth, white. - C.B. Clarke in Dyer, Fl. Cap. 7 : 295 (1898).

3.4. **Scleria longispiculata** Nelmes in Kew Bull. 13 : 1 : 150 (1958)


*Scleria longispiculata* Nelmes, sp. nov.; affinis *S. welwitschii* C.B. Clarke sed inflorescentia haud ramosa, apicis longioribus, glumis femineis majoribus, achaeniis multo majoribus praecipue differt. - Type: Milne-Redhead and Taylor 9739 (K., holotype).

A tall and rather stout scaberulous plant 45 - 105 cm high, with a thick and short rhizome. **Rhizome** horizontally creeping, 4 - 6 mm. thick, pale fulvous clothed with sheathing scales. **Stems** 45 - 105 cm. tall, 1.5 - 2 mm. thick, scaberulous on the angles, glabrous or villous on the sides. Leaves usually much shorter than the stems, 2.5 - 5 mm. wide, plicate to flattish, glabrous or villous, lower reduced to leafless sheaths, which are glabrous or villous, slightly rough, lower often dull reddish, mouth of sheath produced into a triangular or apically rounded, glabrous or villous tongue, 0.5 - 5 mm. long. **Inflorescence** 5 - 13 cm long, composed of 4 - 8 sessile glomerules, each of 1 - 5 spikelets, upper glomerules about their own length apart, lower more longly spaced, erect or suberect, 2 - 10 mm. broad; **spikelets** 8 - 9 mm long. Bracteoles glumiform with a long, smooth to minutely hispidulous awn, much shorter than to about as long as the glomerule. **Female glumes** 4 - 6 mm. long, minutely hispidulous, light greenish-brown, midrib excurrent in a minutely hispidulous plane.
long. Achene ovoid with a truncate base, obtusely trigonous, 3.5 - 5 mm long, 2.2 - 2.75 mm broad, shining whitish, smooth, very shortly beaked.


*Scleria bulbifera* Hochst. in pl. Schimp. Abyss., sect III, no. 4557

*Scleria atrosanguinea* Hochst. in pl. Schimp. Abyss., sect I; no. 327.

S. culmo erecto sesquipedali aut bipedali triquetro, laevi glabro, basi inflato, tuberculato, tuberculo ovoideo tunicato extremitate digiti minimi aequante; foliis linearibus angustis, acutis, scaberulis culmo brevioribus; spicis glomeratis sessilibus spicam interruptam efformantibus; flore inferiore femineo, caeteris masculis; bracteis appresse imbricatis oblongis apice obtuso mucronatis, colore intense castaneis, bractea ad basin spicarum longe subulata ciliata; akenio globoso obtuse et obsolete trigono, laevi aut lacunose; disco vix distincto.

Crescit in graminosis montis Selleuda mense Augusto, et in provincia Chirè mense Octobre (Quartin Dillon) et in montibus propri Tecli, mense Augusto (Schimper).


Herba perennis habitu caespitoso. Culmi erecti, ad 1 m. alti, glabri, triquetri, robusti, 1 - 3 mm. lati, basi aliquantulo incrassati et vaginis marcidis dense obtecti. Folia 2 - 7 mm. lata, paene glabra vel + dense hirta. Inflorescentia plerumque simpliciter spicata, 5 - 12 (15) cm. longa, e glomerulis 4 - 8 sessilibus composita; raro e glomerulis inferioribus producti sunt ramuli glomeruliferi ad 2 cm. longi; glomeruli densi, multispiculata, ad 14 mm. lati. Spiculae androgyna et masculae. Glumae castaneae brunnea vel nigrobrunnea, viridicarinatae, aristatae, + pilosae; pili nigri vel pallidi. Glumae femineae 5 - 6 mm. longae, arista inclusa. Achaenium 2 mm. longum, 1.3 - 1.6 mm. latum, acute trigonum, late obovoideum, distincte reticulato-trabeculatum, cinereum; rostrum nullum (Fig. 3/1 - 9 p. 504).


Kunth, C.S. (1837) Enumeratio Plantarum 2 : 354

*Scleria Dregeana*. Culmo elongato, gracili vaginisqu triangularibus foliisque glabris, margine scabriusculis, linearibus, planis, membranaceis; spica composita interrupte fasciculato - glomerata; spicis propriis fasciculatis, androgyinis; flore inferiore feminco; reliquis masculis, diandris, squamis exterioribus mucronatis, atro - sanguineis, carina virescente, glabris; achenio breviter stipitato, cum stipite articulato, osseo, subovo-globoso, mucronato, trigono, laevi, lacteo - albo, nitido, basi cuneato-attenuato. - Cap. b. spei. Drège legit - Ligula nulla.
Herba perennis, gracilis, habitu sobolifero. Sobole 1 – 1.5 mm crassa, ad nodos radicantes, internodiis albidis vinaceo maculatis, 8 – 47 mm longis squamis porphyreis in parte obtectis. Culmi erecti vel debiles, 18 – 101 cm longi, basi 0.8 – 1.2 mm crassi, trigoni, glabri vel parce hirti. Folia 1.1 – 2.6 mm lata, inflorescentiam raro excedentia; laminae pagina inferiore glabra superiore ad nervos parce hirta; vaginae parce pilosae, ore truncato dense piloso. Inflorescentia plerumque simpliciter spicata, 2 – 6.5 cm longa, e glomerulis 2 – 6 sessil composta; glomeruli densi, 2 – 5 spiculati, 2.5 – 5 mm lati, parte superiore inflorescentiae contiguai, in inferiore usque 20 mm distantis bracteolae e basi breviter glumiformes, late ovatae, in apicem aristatum usque 8 mm. excurrentes, 6.5 – 10 mm longe aristis inclusis, margine proximale parce hirta distali scaberula, stramineae aliquantus rubro-striatae praeter aristan rubro-brunneam. Spiculae androgynae at masculae, c. 4 mm longae. Glumae spicularum androgynarum 2 – 2.5 mm longae aristis exclusis, late ovatae, in apicem aristatum usque 1.6 mm excurrentes, in nervo medio apicem versus glabrae vel parte hispidulae stramineae aliquantus rubro-striatae praeter carinam viridem vel rubro-brunnescentem. Glumae masculae 1.7 – 2.6 mm longae aristis exclusis, ovato lanceolatae, in apicem aristatem usque 1.5 mm excurrentes, in nervo medio apicem versus, glabrae vel parte hispidulae stramineae aliquantus rubro-striatae, carina viridi straminescenti. Achaenium 1.5 – 1.8, 1 – 1.2 mm, subglobosum, obscure trigonum, obtuse rostratrum, glabrum, undulato-tuberculatum, candidum vel cinereo lineis 3 fuscioribus interangularibus notat.


*Hypoporum pergracile* (N. ab E.;) culmo erecto filiformi simplici triquetro, glomerulis spicatis alternis paucifloris bracteam membranaceam aequantibus, nuce depresso-globosa mucronata tuberculato-echinata alba, subtus sulcis tribus eporosis impressa - **Scleria**, Wall. Cat. n. 3406.


*S. pergracilis*. Culmis vaginisque triquetris, glabris; foliis anguste linearibus, rigidulis, margine scabris; spica composita interrupte glomerata, gracili; spicis propriis per ternas vel geminas congestis, subquincefloris; flore inferiore femineo; reliquis masculis, monandris?; squamis glabris, mucronatis; acheno lapideo, subdepresso-globoso, umbonato-submucronato, trigono, subechinato-tuberculato, lacteo-albo, nitido; basi cuncato-attenuata, trigona, disculo fusco trilobo adnato cincta; faciebus eporosis; disco patelliformi, planiusculo, integro. *Hypoporum pergracile* Nees ab Esenb. in Edinb. n. phil. Journ. 1834. n. 34. 267 (Wall. Cat. no. 3406), in Wight. Bot. 118 et in Linnaea 9. 303 - India orientalis. 4 - ligula nulla.


var. *brachystachys* Nelmes, var. nov.; a typo inflorescentiis brevioribus crassioribus, bracteis longioribus differt. - Southern Rhodesia, Brain 3710.


*Scleria dieterlenii* Turrill (*Cyperaceae - Caricoideae*).

*S. dregeanae* Kunth, affinis, sed inflorescentiis hispidis nucibus valde transverso-verrucoso-muricatis recedit. *Rhizoma verticale, unituberiferum,* gracile. *Culmi erecti, usque ad 2.4 dm. alti,* laeves, basi squamis brunneis obtecti. *Folia linearia,* spica acuta, usque ad 10 cm. longa at 2 mm. lata, fere glabra vel pilis hic illic instructa. *Inflorescentia terminalis,* spicata, circiter 3 - 4 cm. longa; rhachis hispida. *Spiculae 1.75 mm. latae.* *Glumae ovatae vel elliptico-ovatae,* acutae vel leviter acuminatæ, usque ad 4 mm. longæ et 1.75 mm. latae, extra hispidæ. *Stamina 3,* filamentis 4.5 mm. longis. *Discus inconspicuus,* tridentatus, 0.5 mm. altus. *Nux obovoideae,* distincte trigona, breviter stipitata, 1.5 mm. longa, 1 mm. diametro, valde transverso verrucoso - muricata.

3.11. **Scleria nutans** Willdenow ex Kunth, Enum. Pl. 
2 : 357 (1837)

Kunth, C.S. (1837) Enumeratio Plantarum 2 : 351


*S. hirtella* Swartz

Rhizomate elongato repente nodulosō pennam gallinaceum crasso vaginis
squamiformibus suborbiculatis pururascentibus vestito; culmis approximatis subscriatis strictis filiformibus 16 - 6 poll. alt. pluri- (7) - 4- foliatis triquetris uno latere canaliculatis, cum vaginis angustis truncatis folliisque hirsutis v. interdum pubescenti-hirsutis; his patentibus, inferioribus magis approximatis; herbaceis linearibus 2/3 - 1 1/4 lin. lat. planiusculis acute carinatis supra sulcato-nervatis breviter acutatis 6 - 2 poll. longis; spica 1 1/2 - 2 poll (rariss. ad 5 poll) longa; spiculis paucis v. pluribus dense fasciulatis foemineis masculis intermixtis; lineari-oblongis 2 - 2 1/2 lin. long; fasciculis erectis v. reflexis; bracteis bracteolisque setaceis spiculas superantibus hirsutociliatis; squamis pallide ferrugineis v. pururascentibus aut atropurpurcis ovato-lancolatis, exterioribus setaceo-cuspidatis, carina margineque v. interdum ubique hirsutis; caryopsi minute globosa obsolete trigona mucronulata basi leviter cuneato-attenuata, supra basin interdum porosa v. sulcata, saepius laevissima, lactea pernitida perigynio minuto obsolete trilobo patente, tardius a fructu secedente.


Scleria hirtella, Sw. var. aterrima; foliis hispidioribus; culmis validulis; capitulis magnis atterrimis.
Huilla, in decliviis spongiosi editioribus sylvarum mixtarum ad Morro de Lopollo, frequens, at solummodo hoc loco mihi obvia, no. 7143.

The African specimens of this species are usually stouter, and with larger capitula than the American ones. The variety above described is remarkable for the large size of the nodding capitula, \( \frac{1}{2} \) inch in length and \( \frac{1}{4} \) in breadth, and for the black glumes and hairs, which make it a very striking plant. Besides occurring in other parts of Africa and in Madagascar, it is abundant in America from the Southern States to Brazil.


*Scleria aterrima* (Ridley) Napper, comb. & stat. nov.

In the account of the Cyperaceae in Durand and Schinz, *Consp. Fl. Afr.*, Clarke cites *Scleria hirtella* Boeck. *non* Sw. as a synonym of *S. catophylla*. Clarke, however, failed to exclude from the synonymy two other names which fall within the circumscription of *S. hirtella* Boeck., namely the American species of *S.* *interrupta* L.C. Rich. (1792) and *S.* *distans* Poir. (1806). Thus in the absence of any expressed intention to the contrary *S. catophylla* must be regarded as a superfluous name for *S. interrupta* L.C. Rich. and another name has to be provided.
for the African plant which is known as S. catophylla and which is distinct.


2700 SCLERIA LACUSTRIS sp. nov. culmis solitariis erectis infernee laxe vaginatis superne arcte triquetris ad angulos retrorsim scabris; vaginis trialatis inferioribus submersis (semper?) retrorsim strigosis purpurascetibus; foliis praelongis latiuscule linearibus margine antrorsum spinuloso-scabris; ligula rotundata membranaceo-marginata; paniculis 2 laterali minore remota ramis angustis; glomerulis 2-3 floris bractea setaceo subulata superatis; spiculis masculis oblongis vix compressis multifloris; squamis interioribus membranaceis anguste lanceolatis castaneotinctis; staminibus 3 antheris linearibus purpureo-mucronatis; spicis foemineis unifloris compressis; squamis paucis carinatis mucronatis spice sanguineo-tinctis; stylo trifido; achenio ovato obscure trigono albo fuscescente; disco interiore trigono planiuscula vel leviter convexo achenio arcte connato, exteriore conformi soluto concavo (Sine numero).

En lagunas cerca de Pinar del Rio.


Herba perennis, erecta. *Rhizoma* fere nullum praeter connectivum inter culmorum bases usque 8-10 mm incrassatas sublignaeas confertas. *Culmi* usque 125 cm longi, 3-4 mm crassi, glabri, triquetri. *Folia* 4-10 mm lata, glabra, in marginibus distalibus et nervis principalibus scaberulis, infima ad vaginas vix vel breviter laminatas reducta; *vaginæ* praeter os pilosum glabrae vel sparse pilosæ, ore in linguam obtuse cuncatam 2-5 mm longam margine membranaceæ productae, inferiores rubescentes. *Inflorescentiæ* terminalis et lateralis; *panicula terminalis* densa, 4.5 - 9 x 2-4.5 cm; *paniculae laterales* 1.5-5.5 cm longae, singulae vel binæ ad nodos 1-2(-3) distantæ, pedunculis anguste alatis pro maiore parte glabræ (vel apice brevissime pilosis) e vaginis 2-12 cm exsertis; *bracteæ* foliaceæ, inflorescentiæ excedentes, subulatae. *Spiculae masculæ* 5-6 mm longæ, sessiles vel breviter pedicellatae; *glumæ* glabrae vel minute hispidulae, apicem versus in nervo medio rubro-brunnææ, praeter carinam viridem vel paene omnino rubro-brunnææ. *Glumæ foeminae* 4-5 mm longæ, late ovatae, in apicem aristatum and 1 mm excurrentes, glabrae, rubro-brunnææ praeter carinam viridem. *Achaenium* glabrum, oblongo-subglobosum, 2.5-3 mm longum, c. 2 mm latum, tessellato-lacunosum vel tuberculato-lacunosum, pallide brunneum; *hypogynium* obtuse 3-lobatum, stramineum.


*S. natalensis*; medium sized; nut 1/12 in. long, fenestrate; disc (at the apex of the gynophore) of 3 broad, short, rounded, subreflexed white, earshaped lobes; otherwise as *S. melanomphala*.

Closely allied to *S. melanomphala*, of similar habit and ragged panicle; but not likely to be mistaken for it as it is considerably smaller in all its parts.

**Name** published in Durand and Schinz, *Conspexitus Florae Africae* 5: 673 (1895) without description.


Richard, A. (1851) *Tentamen Florae Abyssinicae* 2: 509-510

**Scleria foliosa** Hochst. in pl. Schimp. Abyss., sect. ii. 1232. *S. culmis foliisque caespitosis; culmo erecto vix pedali, argute triquetro, retrorsum scaberrimo; foliis linearibus acutio, hirtellis margine ciliato-scabris; racemoterinali ramoso, ramis trquetris, hirtis; e spicis conglomeratis alternis composito; spicis femineis unilloris pluribus lateralibus; squamis saepius 4 basi latis oblongis acuminatis; spicis masculis terminalibus; femincarum disco trilobo,
lobis obtusis integris; akenio ovoideo lapideo albo, nitente areolata (an siccatione?) spicis masculis pedicellatis solitariis angustis, plurifloris.

Crescit in locis humidid planitiei montanae Chiré, mense Octobre (Quartin Dillon) et in locis humidiusculis prope Guendepta, mensae September (Schimper).

OBSERVATION - Espèce voisine de la Scleria verrucosa Willd., en différant par ses gaines lisses et non à trois ailes, per ses fruits légèrement coniques au sommet.


Herba perennis, erecta. Rhizoma nihil fere nisi connectivum inter culmor bases ad 3-4(5) mm. incrassatatas et in congeriem subligneam confertas. Culmi ad 135 cm. longi (saepius) tamen non 100 cm. exedunt), 1-2 mm. lati, glabri, triquetri, striati. Folia 1.5-4 mm. lata, glabra vel sparse pilosa; vaginae pilosae, ad os vel truncatae vel in linguam brevem rotundatam productae. Inflorescentia interrupta, ita elongata ut a nodo infimo paniculifero distet inflorescentiae apex ad 70 cm.; paniculi 1.5-3 cm. longi, laterales raro singuli, saepius 2-4(5) ad nodos 2-3, in pedunculis pendulis ad 26 cm. e vaginis exsertis. Spiculae 4-5 mm. longae, in pedicillis sacpius ipsis spiculis brevior sed nonnumquam ad 10 mm longis. Glumae 3.5-5 mm. longae, ovatae, acuminatae, glabrae, stramineae vel brunneae, viridi-carinatae. Achaenium ovoideum
ad globosum, 2.7-2.8 mm longum, 1.7-1.9 mm. latum, leviter striato-lacunosum, hirtum (pilis saepius albis, raro fulvis), brevissime rostratum, cinereum vel pallide brunneum, lineis longitudinalibus fuscioribus distinctum, hypogynium zoniforme, brunneum vel pallide brunneum, cum lobis 3 anguste apiculatis achaenium quasi unguiculis amplectens usque ad medium partem; item hypogynii ipsius margo inter lobos in angulos 3 deflexus est (Fig. 14).


**Scleria achtenii** De Wild.

(1) **Scleria achtenii**; Circ. 70 cm. longa, glabrata v. parce pilosula; radice fibrosa, fibrillis purpurascentibus; culmis pluribus fasciculatis, triangularibus; foliis linearibus ciliatis; spica usque 17 cm longa, spiculis solitaribus vel geminatis; bracteis setaceis, inferioribus spiculas superantibus; squamis ovatis, acuminatis v. ovato-lanceolatis, dorso apicem versus glabris; caryopsi albida, obovidea, obtuse trigona, breviter apiculata, reticulata et plus minus dense alveolata, irregulariter pilosa; perigonio brevissimo, trigono, cupuliformi, persistente, trilobato, lobis bidentatis, dentibus acutis.

Boeckeler, O. (1869) Videnskabelige Meddelelser fra den naturhistoriske Forening i Kjøbenhavn 1869 : 151-152.

S. lagoensis Bcklr. n. sp., rhizomatae repente nodoso duro; culmis subseriatis approximatis 1 1/4 ped. alt subinfirmis tenuibus acute triquetris leviter compressis, lateribus duobus profunde canaliculatis, superne ad angulos scabridis, basin versus subbifoliatis, vaginis angustulis approximatis subbrevisibus, ligula herbacea subdimidiato-ovata obtusissima margine hirta; foliis herbaceo-rigidulis acuminatis planis 2 - 1 1/2 lin. latis 10 - 3 poll. long., superficie apicem versus punctulato-asperulis as pubescentibus ibique et nervis et marginibus subtiliter serratulis; spica terminalis ramosa laxa 1 1/2 - 1 3/4 poll. longa e spicularum fasciculis 4 composita, altera perremota (quandoque tertia minore consociata) subramosa unciam circ. longa pedunculata bracteaque elongata suffulta; pedunculo setaceo erecto firmulo 2 - 3 poll. longo compresso, margine scabrido; fasciculis oligostachyi quam bracteis suis angustis scabriusculis brevioribus; spiculis subbinatis, masculis lineari-oblongis compressiusculis 2 1/2 lin. long.; squamis lanceolatis acutato-submucronatis stramineo-ferruginescentibus concoloratis v. lateribus purpurascensibus, carina viridi superne scabra v. laevi; Caryopsi majuscula sessilia abbreviato-ovata tereti apice cicatricula notata, haud umbonata, basi truncata, obsolete reticulata sparsimque pubescente lacte v. albida nitidula; perigynio superiore rigidulo annulliformi obsolete trigono margine trilobata pallide luteo, lobis lanceolatis cuspidatis adpressis; inferiore incluso altero
adpresso plano-patelliformi profunde trilobo, lobis rotundato-obtusis, cum illo superiore concolorato. - S. scabriusculae Schldl. et S. Moritzianae Bcklr. proxime affinis.

In paludibus et pratis humidis, nunc etiam in marginibus silvarum juxta campos circa Lagoa Santa frequens: floret Dec. - Mart. (Warmg).

3.20. **Scleria melanomphala** Kunth, Enum. Pl. 2 : 345 (1837)

Kunth, C.S. (1837) Enumeratio Plantarum 2 : 345

* S. melanomphala. Culmis vaginisque triquetris, angulis retrorsum scabris; foliis elongatis, linearibus, trinerviis, planis, rigidis, apicem versus scabriusculis; ligula abbreviata, rotundata, rigida; paniculis in apice culmi geminis, altera axillari, pedunculata, altera terminali, simplicibus, spicato-contractis, oblongis; floribus masculis triandris; achenio lapideo, ovali, laevi, lacteo-alba, apice rotundato et nigro, nitido; disco obsolete trilobo, ciliato, extreme sinuoso, adnato. - Cap. b. spei; in ora orientali legit Drège 4.

3.21. **Scleria poaeformis** Retzius, Obs. 4 : 13 : (1786)


29. Scleria poaeformis, culmo aphyilo, paniculae contractae ramis flexuosis, spiculis sessilibus: foemineis axillaribus, masculis bifloris.


\textit{Acriulus greigifolius} (sic) Ridley
A. greigifolius; radicibus crassiusculis, foliis viridibus, coriaceis ensiformibus pedalibus 1/2 uncia latis quam culmus brevioribus striatis et costis duabus distinctis munitis, marginibus spinis armatis, culmis 2 foliatis triquetris marginibus scabris, panicula pedali, ramis elongatis gracilibus triquet scabris, bracteis lineari-lanceolatis scariosus, spiculis masculis dissitis fere sessilibus 5 - 8 floris, squamis lanceolatis acutis, apice longe hyalinis, basi purpureis vel purpureo-maculatis, inferioribus 2 vel 3 vacuis superioribus 4 masculis inferioribus tribus flavis apiculatis, apiculo rubro noduloso. Spiculae femineae desunt.


Scleria greigifolia (Ridl.) C.B. Cl.

S. greigifolia, Glabrous or nearly so. Stolons slender. Stem 12 - 16 in. long, with only 1 leaf-bearing node in the middle. Leaves (close to the base) several, 8 - 12 by 1/3 - 1/2 in., flat, 3-nerved (prominently on the upper surface), bristle scabrous on the edges and on the keel beneath; stem-leaf only 3 in. long. Panicle 9 in. long, of numerous partial peduncles and slender branches; bracts remarkably few. Spikelets all 1-sexual, 1/6 in. long, ellipsoid. Stamens 3; anthers linear - cristate as usual in Scleria. Female spikelet of 3 glumes,

3.23. **Scleria angusta** Nees ex Kunth, Enum. Pl. 2 : 346 (1837)

Kunth, C.S. (1837) Enumeratio Plantarum 2 : 346

**Scleria angusta** Nees ab Esenb. in Kth. herb et in Linnaea 9. 303

Culmis vaginisque triangularibus, glabriusculis; foliis planis, rigidus, margine scabris; ligula abbreviato-ovata, obtusa, rigida; paniculis terminalibus et axillaribus, ramosis, pedunculatis; ramis, patentibus; floribus masculis triandris; achenio lapideo, ovato-elliptico, obtuso, laevi, pallide violaceo, nitido; disco trilobo; lobis multifidis.

Madagascaria, Cap. b. spei; in oram orientali legit Drège. 4 - Fructus in specimine capensi saturatius violacei. Affinis S. laevi.
APPENDIX B

Photographs of Type Specimens

1. S. achttenii
   A, Achten 97 A ................................ (BR) 562
   B, Achten 97 B ................................ (BR) 562
   C, as S. substriato-alveolata
       Vanderyst 1060 .......................... (BR) 563
   D, as S. subintegriloba
       Vanderyst 2839 .......................... (BR) 563

2. S. angusta
   A,B Drège (4246) (2 sheets) .......... (K) 564

3. S. aterrima
   A, as S. hirtella var. aterrima
       Welwitsch 7143 .......................... (K) 566
   B, as S. catophylla
       Barter 1561 .......................... (K) 567

4. S. bulbifera
   A, Schimper 1557 .......................... (K) 568
   B, Quartin-Dillon & Petit s.n. .......... (K) 568
   C,D, as S. atrosanguineca
       Schimper 327 (2 sheets) .............. (K) 569
   E, as S. schweinfurthiana
       Schweinfurth 2193 .......................... (K) 570
   F,G, as S. buchanani
       Buchanan 32; 1272 .......................... (K) 571
   H, as S. verdickii
       Verdick 398 .......................... (BR) 572
   I, as S. thomasii
       Thomas 1202 .......................... (BR) 573
5. **S. dieterlenii**

   Dieterlen 749 .............................. (NH) 574

6. **S. drègeana**

   A, A¹, Drège [3934] (1 ½ sheets) .......... (K) 575
   B, Flanagan 1260 (½ sheet) .............. (K) 575
   C, D as **S. holcoides**
     Drège [4381] (2 sheets) .............. (K) 576
   E, as **S. setulosa**
     Buchanan 36 .............................. (K) 577

7. **S. foliosa**

   A, Schimper 1232 .......................... (K) 578
   B, as **S. dumi cola**
     Welwitsch 7122 ............................ (BM) 579
   C, as **S. perrieri**
     Perrier de la Bâthie 12704 .......... (P) 579

8. **S. greigiifolia**

   A, as **Acriulus greigifolius**
     Welwitsch 6959 ...........................(BM) 580
   B, as **A. madagascariensis**
     Baron 1870 ............................... (K) 581
   C, Hildebrandt 3751 ........................ (K) 581
   D, as **A. titan**
     Gentil s.n. .............................. (BR) 582
   E, as **S. friesii**
     Fries 743 ............................... (K) 582
9. *S. lacustris*
   A, Wright s.n. ..............................(K) 584
   B, as *S. aquatica*
     Le Testu 5845 ............................(P) 585

10. *S. lagoensis*
    A, B, Warming s.n. (2 sheets) ..........(C) 586
    C, as *S. canaliculato-triquetra*
       Schweinfurth 2474 ......................(K) 587
    D, as *S. diurensis*
       Schweinfurth 2389 ........................(K) 588
    E, as *S. cervina*
       Welwitsch 7127 ............................(BM) 589
    F, as *S. mayottensis*
       Boivin ....................................(P) 589

11. *S. longispiculata*
    A, B, C, Milne-Redhead & Taylor 9739
       (3 sheets) ...............................(K) 590-1

12. *S. melanomphala*
    A, A¹, Drège 4369/ (1½ sheets) ....(K) 592
    B, as *S. centralis*
       Le Testu 2436 ............................(P) 593
    C, Tisserant 1233 ...........................(P) 593

13. *S. natalensis*
    Buchanan 352 ...............................(NH) 594
14. *S. nutans*
   A, as *S. mollis*
     Sellow s.n. .......................(K) 595
   B, as *S. hirtella var. chondrocarpa*
     Thomas 95 .......................(K) 596
   C, as *S. hirtella var. tuberculata*
     Burke 62 .......................(K) 596

15. *S. pergracilis var. brachystachys*
    Brain 3710 .......................(K) 597

16. *S. poaeformis*
    as *S. oryzoides*
     Haenke s.n. ...................(K) 598

17. *S. rehmannii*
    Rehmann 5626 ...................(K) 599

18. *S. sobolifer*
    Ward 5128 .........................(UD-W) 600

19. *S. transvaalensis*
    Arnold 336 .........................(PRE) 601

20. *S. unguiculata*
    Robinson 5056 ...................(K) 602
21. S. veseyfitzgeraldii
   A, B, Robinson 4220 (2 sheets) ...........(NU) 603

22. S. welwitschii
   Welwitsch 7138 .........................(BM) 604

23. S. woodii
   Wood 3994 ..............................(NH) 605

Schlimmer 1557 and Lehm. Nutt. et
Nutt. Specimens are mounted the second
on top of the first, apparently.

1. Two spikes at 3/4 of stem base narrower and
more slightly deflexed.

Scleromer 127

1. With thick capsule. Nuts in this capsule crenulate
similarly to these at Pat. of plant. Schlimmer 1557
2. With small capsule. Nuts of these slightly deflexed
+ slightly crenulate. (No nut = these plants.)

Sermepis uter Alphonstom

Ex. Sermon.
Schimpfia mit Aegimia

1232. Schimpfia hypnoides Hochst.

Aegimia hypnoides

578.
Rheed in Eumenognatha-alpina woodland or brown moony lizes: KO.  m.

Perenniai with thickened contorted stems; at nodes, but bases not bulbose; lower sheaths dark brown; sheaths pale green; leaves green.

- setting: spikes rather blunt; sterile zone at base of leaf. Male calyx top of sheath; glumes light brown with a green seed; anthers elliptic projecting to show white filaments; sterile fruit greenish.

HERBARIUM

K. 2. 7. 1929

RHABALAS KEWING

Dahomey Coast East Allée Extension 1929

Scleria

TANZANIA: Lake Burundi

P. 167. 166. 165. 164. 163. 162. 161. 160. 159. 158. 157. 156. 155. 154. 153. 152. 151. 150. 149. 148. 147. 146. 145. 144. 143. 142. 141. 140. 139. 138. 137. 136. 135. 134. 133. 132. 131. 130. 129. 128. 127. 126. 125. 124. 123. 122. 121. 120. 119. 118. 117. 116. 115. 114. 113. 112. 111. 110. 109. 108. 107. 106. 105. 104. 103. 102. 101. 100. 99. 98. 97. 96. 95. 94. 93. 92. 91. 90. 89. 88. 87. 86. 85. 84. 83. 82. 81. 80. 79. 78. 77. 76. 75. 74. 73. 72. 71. 70. 69. 68. 67. 66. 65. 64. 63. 62. 61. 60. 59. 58. 57. 56. 55. 54. 53. 52. 51. 50. 49. 48. 47. 46. 45. 44. 43. 42. 41. 40. 39. 38. 37. 36. 35. 34. 33. 32. 31. 30. 29. 28. 27. 26. 25. 24. 23. 22. 21. 20. 19. 18. 17. 16. 15. 14. 13. 12. 11. 10. 9. 8. 7. 6. 5. 4. 3. 2. 1. 0. 11
Planta Africa australis.

Exsiccata Africanae auct. ex annis 1870-1880

1870-1880 Herbarium Linnæanicum, Potsdam

Planta Africae australis.

Collocavit: J. A. Rothmann, 1877

Collected by A. Rothmann

Specimen No. 1717

A. Rothmann
Northern Rhodesia

Collections:
- P. A. Robinson, May 6, 1912
- D.R. Norlend, Dec. 21, 1912
- J.C. Leach

Habitat:
- Perennially wetlands
- Perennial, forming dense clumps

Herb. Kew

Saxifraga inconspicua

Holotype:
- P. A. Robinson (in wax)

Kew
Abbreviations used for Herbaria (Holmgren & Keuken, 1974)

B BERLIN : Botanisher Garten and Botanisches Museum Berlin-Dahlem, Federal Republic of West Germany.

B-W BERLIN : Herbarium Willdenow.

BM LONDON : British Museum (Natural History), Great Britain.

BOL CAPE TOWN : Bolus Herbarium, University of Cape Town, South Africa.

BR BRUXELLES : Jardin botanique national de Belgique, Belgium.

C COPENHAGEN : Botanical Museum and Herbarium, Copenhagen, Denmark.

J JOHANNESBURG : The Moss Herbarium, University of the Witwatersrand, Johannesburg, South Africa.

K KEW : The Herbarium and Library, Royal Botanic Gardens, Kew, Richmond, Great Britain.


LISU LISBOA : Museu, Laboratório e Jardim Botânico, Lison, Portugal.

LZ LEIPZIG : destroyed

NH DURBAN : Botanical Research Unit, Natal Herbarium, Durban, South Africa.
NU PIETERMARITZBURG: Botany Department, University of Natal, Pietermaritzburg, South Africa.

OXF OXFORD: Fielding - Druce Herbarium, Department of Botany, Oxford, Great Britain.


PR PRAHA: Botanické oddelení Prirodověd muzea Národního muzea v Praze, Prague, Czechoslovakia.

PRE PRETORIA: Botanical Research Institute, National Herbarium, Pretoria, South Africa.

RUH GRAHAMSTOWN: Rhodes University, Grahamstown, South Africa.

SRGH SALISBURY (HARARE): National Herbarium, Department of Research and Specialist Service, Causeway, Harare, Zimbabwe.

UD-W DURBAN: Botany Department, University of Durban-Westville, Durban, South Africa.

UPS UPPSALA: The Herbarium, Institute of Systematic Botany, University of Uppsala, Sweden.
Materials used for Anatomical Studies

1. Scleria acchtenii
   - Ward 4937; 7710; 7743 (UD-W).

2. Scleria angusta
   - Ward 8083; 8603; s.n. (UD-W).

3. Scleria aterrima
   - Schweickerdt 2344 (NU);
   - E.A. Robinson 1748; 5055 (NU);
   - M. McCallum-Webber s.n. (NU);
   - Strey 7035 (UD-W);
   - Strey 10102 (PRE);
   - Moll 4759 (NU);
   - Ward 2924 (UD-W).

4. Scleria bulbifera
   - K.D. Huntley 567 (NU);
   - Compton 27364 (PRE);
   - Killick 1579 (PRE);

5. Scleria dieterlenii
   - Bews 471 (NU);
   - Hoener 2040 (UD-W).

6. Scleria drègeana
   - Killick 1084 (NU);
   - K.D. Huntley 425 (NU);
   - Moll 1424 (NU);
   - Breen 67 (NU);
   - Vesey-Fitzgerald 1007 (NU);
   - Acocks 10850 (PRE);
   - L. Smook 1055 (PRE).

7. Scleria foliosa
   - Schweickerdt 2189 (NU);
   - Merxmüller & Giess 2081 (PRE).

8. Scleria greigiifolia
   - K.D. Huntley 781 (NU);
   - M. McCallum-Webber s.n. (NU);
   - P.G. Stewart 293 (PRE).
10. Scleria lagoensis Compton 29644 (PRE).
11. Scleria longispiculata Story 6467 (PRE); de Winter 3915 (PRE).
12. Scleria melanomphala Ward 5077; 7708; s.n. (UD-W); Breen 54 (NU).
13. Scleria natalensis Galpin 10988 (PRE); Arnold 435 (PRE); Ward 4716 (UD-W); E.F. Hennessy 372; 410 (UD-W).
14. Scleria nutans Veczy-Fitzgerald 2301 (NU); T.H. Arnold 796 (PRE); Ward 5075; 5628 (UD-W); K.D. Gordon-Gray 6128 (NU).
15. Scleria pergracilis var. brachystachys Pentz & Acocks 10277 (PRE).
17. Scleria racemosa E.A. Robinson 1716 (NU).
18. Scleria rehmannii de Winter & Marais 5049 (PRE).
19. Scleria sobolifer T.H. Arnold 467 (PRE); H. Bajnath 126 (UD-W); Ward 4737; 4925 (UD-W).
20. Scleria transvaalensis Seagrief 18 (NU); K.D. Gordon-Gray 6020 (NU); T.H. Arnold 336 (PRE); P.J. Müller 2031 (PRE); Compton 24985 (PRE); Smuts & Gillett 3260 (PRE).
21. **Scleria unguiculata**
   P.A. Smith 1980; 2790 (PRE).

22. **Scleria veseyfitzgeraldii**
   E.A. Robinson 422 (NU).

23. **Scleria welwitschii**
   Killick 1233 (NU); Edwards 1127 (NU); Acocks 22171 (PRE); E.F. Hennessy 408 (UD-W); C. Breen 87 (NU).

24. **Scleria woodii**
   K.D. Huntley 910 (NU);
   K.D. Gordon-Gray 2050 (NU);
   M.S. Frankish 318 (NU);
   Gilliland 25046 (PRE); Acocks 11340 (K); Hooper & Townsen 832 (K); E.F. Hennessy 406; 409 (UD-W).
A note on the hairy achenes of four African species of Scleria Bergius (Cyperaceae)

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Accepted for publication December 1978

Surface features of hirsute achenes of four African species of Scleria have been examined by SEM. All bear unicellular, terete hairs with swollen bases. As the achenes mature and dry, the hairs collapse, except for their partly silicified bases, which appear as pit-like depressions from which the now-flattened hairs emerge. If the achene surface is not smooth the hairs are localized on the interfacicular ridges. In addition to the hairs, three of the four species examined show minute papillate pro-
tuberances from the silicified outer tangential walls of the epidermal cells. These papillae form a further ornamentation to the achenes visible only at high magnification. The fourth species entirely
lacks these papillae.

KEY WORDS: Cyperaceae - Scleria achenes - SEM.

INTRODUCTION

Hirsute achenes are not uncommon in Scleria. They have been reported to occur in many non-African species of the genus by Core (1936), Koyama (1961), Kern (1961) and others. Of the African species, sixteen are known to possess, or occasionally to possess, hairy achenes. These are listed in Table 1. Only one South African species, Scleria achtenii De Wild. has a hairy achene. According to Nelmes (1956) the achene of Scleria is usually "ovoid, ellipsoid or subglobose, often white and shining, smooth, reticulate, muricate, verrucose, tuberculare or tessellate, glabrous or hairy". This general description adequately accounts for its

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Table 1. Scleria: African species with hirsute achenes

<table>
<thead>
<tr>
<th>Species</th>
<th>Hairs always present</th>
<th>Hairs sometimes present</th>
</tr>
</thead>
<tbody>
<tr>
<td>S. achenii De Wild.</td>
<td></td>
<td></td>
</tr>
<tr>
<td>S. adpresso-hirta (Kük.) E. A. Robinson</td>
<td></td>
<td></td>
</tr>
<tr>
<td>S. arneta E. A. Robinson</td>
<td></td>
<td></td>
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<tr>
<td>S. bambariensis Cherm.</td>
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<tr>
<td>S. boicinii Steudel (= barteri Boeck.)</td>
<td></td>
<td></td>
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<tr>
<td>S. falcipilosa Peter</td>
<td></td>
<td></td>
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<tr>
<td>S. globonux C. B. Clarke</td>
<td></td>
<td></td>
</tr>
<tr>
<td>S. ingensis Boeck (= conicus-toqueta Boeck.)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>S. makahwame Makino</td>
<td></td>
<td></td>
</tr>
<tr>
<td>S. nyaeensis C. B. Clarke</td>
<td></td>
<td></td>
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<tr>
<td>S. patula E. A. Robinson</td>
<td></td>
<td></td>
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<tr>
<td>S. perlata Preisl</td>
<td></td>
<td></td>
</tr>
<tr>
<td>S. pharacarpos (E. A. Robinson) Napper (= lessinata Willd. var. pharacarpos)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>S. unguiculata E. A. Robinson</td>
<td></td>
<td></td>
</tr>
<tr>
<td>S. xerophila E. A. Robinson</td>
<td></td>
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</tbody>
</table>

* denotes presence of hairs

appearance when viewed through a dissecting microscope at a magnification of 30–60 times. With the aid of SEM it has now become possible to observe surface features of such fruits in considerably more detail and thus to expand the older descriptions.

The ornamentation of the achene surfaces, including gross structure of the hairs, of the local species, S. achenii, as well as of three tropical African species, S. nyaeensis C. B. Clarke, S. globonux C. B. Clarke and S. adpresso-hirta (Kük.) E. A. Robinson, all of which have features in common, is described.

Maceration has yielded information on the silica deposits which constitute an important part of the pericarp of the mature achene, while sectioning of young and fully-formed achenes of the local species which was most readily available, provided information on structural features of the hairs.

MATERIALS AND METHODS

Dry, whole achenes detached from herbarium specimens and achene shells which had been stored in absolute methanol after treatment with strong oxidants were mounted on brass stubs using double-sided adhesive tape. The specimens were then coated in vacuum with gold to a thickness of less than 150 Å in a Polaron Sputter Coating Unit E 5000, then examined in a Philips SEM 500 scanning electron microscope at a voltage of 25 kV. The images were photographed with a 35 mm camera.

Silica deposits. Achenes were macerated in concentrated nitric acid and concentrated perchloric acid (Hayward and Parry, 1975) to remove organic constituents, washed in tap water and stored in absolute methanol.
Confirmation of the siliceous nature of the achene shells was obtained by analysis using a JEOL JSM U3 scanning electron microscope fitted with an energy dispersive X-ray analyser (EDX) Model 711. This was carried out at the National Physical Research Laboratory of the Council for Scientific and Industrial Research, Pretoria.

EDX analyses were carried out on both outer and inner surfaces of achene shells. Hair structure. Achenes for sectioning were desilicified by soaking in 10% hydrofluoric acid for several weeks, washed in water for 24 hours, then passed through a tertiary butanol dehydration series, embedded in wax and sectioned at a thickness of 15 μm. These were stained in a safranin and fast green series and mounted in Canada balsam or 'Euparal'.
base, the radial and inner tangential walls of which are silicified (Figs 7, 10). Immature, and mature dry hairs are illustrated in Figure 11. The mature achene surface between the trichome bands is papillate, with numerous compactly situated rounded papillae. The papillae are either solitary or have aggregated in compound clusters comprising 2–3(4) papillae (Fig. 4). The papillae are subhemispherical protrusions from the outer surface of the silicified outer tangential wall of the epidermal cell (Figs 7, 10).

**Scleria nyasensis** C. B. Clarke

The achene of this species was described by Robinson (1966) as “distinctly tessellate-lacunose, hairy” (Fig. 12).

It closely resembles the achene of *S. achenii* in having its hairs distributed in interrupted linear bands, or groups, along the horizontal and some of the vertical interlacunar ridges, and in the distribution pattern of siliceous papillae on its surface (Figs 13, 14).

It differs from the previous species in that the pattern of ridges and lacunae on the achene surface is much more clearly defined, and in that the siliceous papillae are larger and less compactly situated.

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Fig. 2. Achene with hypogynium. Fig. 3. Distal end of achene. Fig. 4. Portion of surface showing collapsed hairs and protuberant papillae. Fig. 5. Siliceous shell of achene after maceration. Fig. 6. Distal end of shell. Fig. 7. Portion of surface of shell showing hair bases and papillae. Fig. 8. Base showing flange to which hypogynium was attached. Fig. 9. Flange region showing outer surface of shell (left), inner surface (right) with radial walls of cells standing proud. Fig. 10. Portion of surface of shell showing hair base and papillae in greater detail.
ACHENES OF SCLERIA

Scleria globonux C. B. Clarke

The achene was described by Robinson (1966) as “hairy, deeply lacunose-tesselate” (Fig. 15).

The horizontal interlacunar ridges bear almost uninterrupted bands of triple or quadruple rows of trichomes and some of the vertical interlacunar ridges are similarly invested (Fig. 16). Siliceous papillae are well-spaced and most are conspicuously compound (Fig. 17).

This achene differs from those of S. achenii and S. nyasensis in shape and in degree of hairiness and pattern of distribution and appearance of the siliceous papillae. Of the three species, S. globonux has the most clearly defined pattern of lacunae and interlacunar ridges and S. achenii the least well-defined. Scleria globonux has a heavier investment of shorter hairs than S. achenii and S. nyasensis which are almost equally hirsute. Siliceous papillae which are present in all three species may be simple or compound, but are most obviously compound in S. globonux and are more regularly spaced in this species than in either of the others.

Scleria adpresso-hirta (Kük.) E. A. Robinson

The achene was described by Robinson (1966) as “smooth, shortly hairy on the lower part, glabrous towards and on the top” (Fig. 18).

Although there are no ridges on the achene surface, the trichomes which occur only in the proximal half are arranged in horizontal groups, not all of which are linear (Fig 18, 20). This achene lacks the protuberant siliceous papillae of the other species described (Figs 19, 20).

It resembles the achene of S. globonux in shape and the achenes of S. achenii, S. nyasensis and S. globonux in the type of hairs with which it is invested and in having the outer tangential walls of its epidermal cells silicified.

It differs from the other three species in lacking ridges and protuberant siliceous papillae.

DISCUSSION

The morphology of the achene of Scleria provides useful characters for the separation of taxa. Among the characters used are the presence or absence of hypogynia; the shape, texture and colour of the hypogynium when present; the size shape and colour of the achene itself; the patterning if any of the achene surface and the presence or absence of hairs. While most of these characters are reasonably constant there are some species in which the surface patterning of the achene is variable even on the same plant. Core (1936), in his discussion of the type collection of the American Scleria leptostachya Kunth which includes plants with smooth and verrucose achenes, remarks that “Such variation in the achenes is somewhat unusual for Scleria and it might be thought that the collection was mixed were it not for the fact that both kinds of achenes may in some cases be found on

Figures 12 to 20. Sclerosis species: scanning electron micrographs of mature achenes. Fig. 12. S. nyasensis (L. D. E. F. Vesey-Fitzgerald 1252) achene with hypogynium. Fig. 13. Distal end of achene. Fig. 14. Portion of surface showing collapsed hairs and papillae. Fig. 15. S. globonux (E. A. Robinson 3450) achene with hypogynium. Fig. 16. Distal end of achene. Fig. 17. Portion of surface showing collapsed hairs and papillae. Fig. 18. S. adpresso-hirta (E. A. Robinson 673) achene with hypogynium. Fig. 19. Distal end of achene. Fig. 20. Portion of surface showing collapsed hairs and lacking papillae.
the same individual”. Nelmes (1955) commenting on Piéart’s classification of *Scleria bulbifera* Hochst. ex A. Rich. into four varieties, three primarily on achene surface characters, noted that he was unable to use Piéart’s classification because: “there are several gatherings of *S. bulbifera* in the Kew herbarium whose fruits have all three kinds of surface sculpture, and sometimes all are found on one and the same plant. Frequently one finds smooth and tubercled, or tubercled and lacunose fruits on the same plant”.

Similarly, there are some species whose achenes are reputedly only sometimes hairy (Robinson, 1966). Although the hairs are large enough to be discernible through a hand lens or a dissecting microscope they are brittle and easily rubbed off. Before accepting or refuting the possibility that there is variation in the degree of hairiness of the achene in some species, it is necessary to be able to recognize, in a herbarium where achenes of different ages are not always available, the difference between a truly glabrous achene and an achene from which hairs have been secondarily removed. To do so one must be able to recognized with certainty the points of origin of the hairs from the achene surface. That this is possible has been conclusively proven and at the same time information on hair structure and some information on pericarp structure has been obtained.

The achenes of the four species described in this paper appear to have constant morphological characters. These and the other twelve African species which are reported to have, or sometimes to have, hairy achenes, all belong by virtue of their paniculate inflorescences, unisexual spikelets and well-developed, entire-margined hypogynia to the section *Scleria* (Berg.) Endl. The achenes of other African species in this section and in the other sections are reputedly glabrous.

Preliminary work has indicated that all the cells of the many layered pericarp of *Scleria* are silicified to a greater or lesser degree. All have silicified radial walls and some also have silicified tangential walls. Because radial and outer tangential walls of epidermal cells are silicified the cells do not separate when the achenes are macerated. Instead, the achenes retain their intact form and appear as perfect hollow translucent shells of siliceous material. An achene shell of *S. achtenii* is illustrated in Figs 5–10. Trichome bases have their radial and inner tangential walls silicified, but the shaft of the trichome which is derived from the outer tangential wall of an epidermal cell, is not silicified. All epidermal cells other than the trichome bases have their radial and outer tangential walls silicified and depending upon the species, there may or may not be papillate protuberances from these silicified outer tangential walls.

The occurrence of siliceous papillae has not previously been reported for the achene of *Scleria*. It is suggested that this may be a useful taxonomic character.

It would be of interest to know whether the type of hair described in this paper is exclusive to *Scleria* or whether it occurs in other genera. It has been noticed that the achenes of *Rhynchospora* may be hairy, but the hairs are of a different type. A similar type of hair to that found in *Rhynchospora* has been seen in one specimen only of the variable species, *Scleria bulbifera* (section *Hypoporum* (Nees) Endl.) but in no other species of *Scleria* thus far examined.

**SPECIMENS EXAMINED**

*Scleria achtenii* De Wild.

SOUTH AFRICA, NATAL: Zululand, Kosi area, lakeside Amanzimnyama forest area. 8. xii. 1958, Tinley 361 (NU); Zululand, Lower Umfolosi district, Richards
ACHENES OF SCLERIA


Scleria nyasensis C. B. Clarke

Scleria globonux C. B. Clarke

Scleria adpresso-hirta (Kük.) E. A. Robinson
ZAMBIA: Kawambwa, 21. vi. 1957, Robinson 2235 (NU); 8 km E of Mufulira, 24. iv. 1960, Robinson 3673 (NU).

ACKNOWLEDGEMENTS

I wish to thank Professor K. D. Gordon-Gray of the Department of Botany, University of Natal, Pietermaritzburg, for supervision of this project; Dr N. R. Comins of the National Physical Research Laboratory of the Council for Scientific and Industrial Research, Pretoria, for EDX analyses and for Fig. 1; Mr T. H. Arnold of the Botanical Research Institute, Pretoria, Dr F. M. Getliffe, now at Friday Harbor, Washington, U.S.A., and Dr J. R. Lawton and Dr H. Baijnath of this Department for helpful criticism of the manuscript; Mrs J. Evers and Mrs E. L. Mulder for help in the preparation of illustrations, and Curators of the herbaria cited for the use of herbarium material.

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KOYAMA, T., 1961. Classification of the Family Cyperaceae. Journal of the Faculty of Science (Botany), University of Tokyo, 1: 5–53: 135–139.
SEM EXAMINATION OF SILICA (SiO₂) DEPOSITS ISOLATED FROM ACHENES OF ScLerio (CYPERACEAE)

E.F. FRANKLIN

(Department of Botany, University of Durban-Westville, P. Bag X54001, Durban)

The occurrence of silica deposits in roots, stems and leaves of hygrophilous monocotyledonous plants, especially Poaceae (grasses) and Cyperaceae (sedges) is common. The form assumed by these silica bodies has been found to be fairly constant in some taxa¹,². Silica bodies may therefore provide the systematist with evidence of taxonomic relationships.

Until recently silica bodies were studied in situ in thick sections, and in epidermal strips viewed by light microscopy. Hayward and Parry³ described a method of isolating silica bodies from leaf tissue of barley, a grass. Such isolated bodies can be examined by SEM.

A modification of Hayward and Parry’s technique has been applied in a taxonomic study of the genus ScLerio⁴. In this as in other genera of Cyperaceae the outer surface of the fruit wall (pericarp) may be variously sculpted, patterned or invested with hairs (trichomes). The type of ornamentation of the pericarp is used as a diagnostic character in sedges. Accordingly, achene surface patterning of all South African species of ScLerio was examined by SEM. Several inexplicable features were revealed (Figs. 1, 2), therefore attempts were made to section the fruit in order to explain the surface peculiarities. No acceptable sections of the hard, brittle fruit were obtained until some specimens were desilicified by prolonged soaking in hydrofluoric acid. Sections could then be made but many of the interesting surface characters had disappeared, which indicated that they were silica deposits.

Achenes were then macerated by warming in concentrated nitric acid to which, with great care, concentrated perchloric acid was added dropwise. This drastic treatment was expected to yield a sediment of isolated silica bodies or isolated siliceous shells of individual cells such as were obtained by Hayward and Parry from barley leaves. Instead, complete achene-shells resulted (Figs. 3, 4), the pure siliceous nature of which was later confirmed by X-ray analysis. After hydrolysis was complete the siliceous shells were simply washed in tap water, then transferred to absolute methanol in which they can be stored indefinitely. The siliceous shells, and isolated silica bodies obtained from other plant organs by the same method, were simply transferred from absolute methanol to brass stubs, coated and examined by SEM.
SEM of Achene of Sclerio ochtenii De Wildeman

Figs. 1, 2, before maceration
Figs. 3, 4, after maceration

References:


