PART 2

THE TRIBE ARISTIDEAE

2.1. HISTORY

2.1.1. Taxonomic Studies

For a detailed discussion of the history of the nomenclature of the genus the reader is referred to Henrard's introduction to his Monograph (1929) as well as Schweickerdt's introductory remarks in his treatment of the South African species (1941).

In the past, *Aristida* has almost invariably been placed in the tribe *Stipeae* which, in turn, is treated either as a distinct tribe or as a subtribe or a group of the *Agrosteae*.

Since 1875, when Duval-Jouve studied the anatomy of the leaf-blade of two *Aristida* species, it has been known that the anatomy of this genus differs from that of *Stipa*, the type genus of the *Stipeae*. These anatomical differences were, however, not regarded to be of sufficient value to exclude *Aristida* from the *Stipeae*, and, should there have been no other differences between *Stipa* and *Aristida*, one would have been inclined to agree. Avdulov (1931), Prat (1936) and others have, however, shown that the type of anatomy of the leaf-blade is usually closely correlated with karyological and organographical characteristics. Probably influenced by these observations, Roshevitz (1937) transferred the genus *Aristida* to the tribe *Sporoboleae*. Roshevitz's concept of the *Sporoboleae* is a wide one and includes very heterogeneous elements. Anatomically *Aristida* and *Sporobolus*, however, agree fairly closely and a distant affinity between *Aristida*, *Sporobolus* and the genera of the *Eragrosteae*, which have a generally similar anatomy, seems probable. A discussion of the relationship of the *Aristideae* with other tribes of the Gramineae is given later in this paper.

In 1940 Hubbard & Vaughan created a new tribe, the Aristideae, to accommodate the single genus Aristida but gave no description. In most recent works on the classification of the Gramineae this tribe has been accepted. A valid description by Hubbard appeared in Bor's Grasses of Burma, Ceylon, India and Pakistan (1960). The latest account of the Aristideae was prepared by Pilger (1956, p. 118) edited by Eva Potztal, and posthumously published in the Pflanzenfamilien. In this treatment Pilger enlarged the concept of the tribe by including the two Australian genera Amphipogon and Diplopogon. The reasons why the latter two genera are excluded from the Aristideae by the present author are given on p. 221.

2.1.2. Anatomical Studies

Duval-Jouve (1875, p. 319 and Pl. 17, fig. 10) was one of the first to investigate and describe the anatomy of a member of the *Aristideae*. His drawing of *Arthratherum pungens* (*Stipagrostis pungens*) gives an excellent representation of the structure of the leaf-blade, and agrees closely with that of *Stipagrostis namaquensis* studied by the present author. In both taxa the presence of a single chlorophyll-bearing bundle sheath can be seen clearly.

The most valuable study of *Aristida* undertaken up to the present is probably that of Holm (1901, p. 101-133), who came to many conclusions similar to those arrived at independently by the author of this study.

Holm studied 32 species of the section *Chaetaria*, two species of section *Streptachne* and three of section *Arthratherum* sensu stricto. All these species have naked awns and were found by Holm to be characterized by having two chlorophyll-bearing bundle sheaths, or as he described them "a double parenchyma sheath", as well as having the chlorenchyma arranged in radial "palisades". All *Aristida* species possessing plumose awns, some of which had been referred to the section *Arthratherum* by various authors until Bentham and Hooker and Hackel transferred them to the section *Stipagrostis*, were found by Holm to possess a single chlorophyll-bearing sheath while the inner sheath was usually composed of thick-walled cells devoid of chloroplasts.

On basis of these observations Holm (p. 129) suggested that the species with plumose awns and a single chlorophyll-bearing sheath should be removed from *Aristida* proper, the latter having naked awns and a double chlorophyll-bearing sheath. Henrard obviously also considered this possibility but for various reasons decided otherwise. Species of this group investigated by Holm are *A. plumosa*, *A. acutiflora*, *A. brachyathera*, *A. ciliata*, *A. pungens* var. *pennata* and *A. pennata*. Holm's observations were fully verified in the present investigation and were shown to be applicable to the South African species. In addition Holm studied many other genera either purported to be related to, or ecologically associated with, the genus *Aristida*. None of these genera, however, exhibited a double chlorophyll-bearing sheath, a characteristic up to the present met with only in *Aristida* sensu stricto. Holm was one of the first authors to point out the difference between the chlorenchyma organization of *Stipa*, where the cells show no regular radial pattern, and that of *Aristida*, *Muehlenbergia* and *Lycurus*, where the chlorenchyma cells are radially arranged in a single row of " palisades".

Theron (1936, p. 4) apparently misinterpreted the structure of the bundle sheaths, so clearly described by Holm, and stated that he had not found constant differences in this respect between the species with plumose awns and those with glabrous awns. Theron investigated the anatomy of the leaf-blades using material taken from herbarium specimens only and probably did not have access to living or preserved wet material. This may explain the incorrect detail in many of his drawings. Failure to recognize the difference in the bundle sheaths of the sections *Stipagrostis* and *Schistachne* on the one hand, and the remaining sections on the other, led him to divide the species into "anatomical groups", which have very little bearing on taxonomic relationship based mainly on organography.

Jelenc (1950) made a general anatomical study of the North African species of *Aristida* but, as in the case of Theron (1936), was apparently not aware of the work of Holm (1901). Jelenc, however, correctly interpreted the differences in the bundle sheaths of the plumose-awned and glabrous-awned species, but could not, as he states himself, interpret the structure of the chlorenchyma on basis of the slides prepared from dry material, nor could he detect any bicellular hairs as observed by Prat (1936). The presence of bicellular hairs was likewise not observed by Theron. In the present paper these structures are clearly illustrated (Fig. 157E). Jelenc pointed out the differences in the structure of the silicified cells in the epidermis of the two groups: being (1) circular in the species with plumose awns and (2) dumb-bell-shaped in the species with glabrous awns. Although the shape of the silicified cells is not of specific diagnostic value throughout, it nevertheless is usually a good indication of the affinities of the species.

Several other authors have studied *Aristida* species in more generalized papers on grass anatomy but none of these has expressed opinions on the taxonomy of *Aristida* or its sections. Practically all the information contained in these papers strongly supports the evidence gathered by Holm and Jelenc and that presented by the present author.

Papers mentioning only one or two species are the following: Volkens, 1887, A. ciliata; Guenzel, 1921, p. 3, A. pungens; Sabnis, 1921, p. 225, A. funiculata and A. hirtigluma; and Zemke, 1938, p. 399, A. ciliata.

Several South West African species were investigated by Guenzel (1913, pp. 16–22). He reported on the presence of bicellular hairs in addition to unicellular long hairs, furthermore on the differences in the bundle sheaths of the plumose and non-plumose species. For the non-plumose group *A. adscensionis* and *A. barbicollis* and for the plumose group *A. uniplumis*, *A. ciliata*, *A. obtusa* and *A. namaquensis* are mentioned.

Lommasson (1947) offered a critical appraisal of the interpretation of the homology of the "double parenchyma sheath" in *Aristida*. He concluded that there was no obvious reason for regarding the two "parenchyma sheaths" of the naked awned species as being different from (i.e. not homologous with) the two sheaths found in most grasses [as indicated by Holm (1901, p. 103)]. He suggested that the enlargement of the inner sheath cells was a result of the acquisition of chloroplasts by the cells of that layer. He pointed out that practically in all grasses the parenchyma cells on the chlorophyll-vascular boundary (the outer-sheath) were enlarged in a similar way. In *Aristida* this boundary has shifted to the inner sheath thus occupying the same position as the "mestome sheath" present in other grasses, the cells being large and containing chloroplasts, whereas the outer sheath cells have become smaller and are functionally part of the chlorenchyma surrounding the bundle. This change (that has taken place in *Aristida*) should be regarded, therefore, as one of function: the inner sheath is homologous with the "mestome sheath" present in other grasses.

Finally, Kinges (1961, pp. 50–93) studied the structure of the embryos of a large number of grasses including some *Aristida* species and Caceres (1961, p. 1) investigated eight Argentinian *Aristida* species.

2.2. DELIMITATION

Until Pilger (1956, p. 118) widened the concept of the tribe to include *Diplopogon* and *Amphipogon*, *Aristida* was the monotypic representative of the *Aristideae*. The former two genera are organographically very different from *Aristida* and an anatomical study of the leaf-blade of *Amphipogon* has revealed additional supporting differences. *Diplopogon*, of which no material was available for investigation, is closely allied to

Amphipogon (and probably also agrees with the latter in anatomical characteristics). In the anatomy of the leaf-blade, Amphipogon somewhat resembles that of some Danthonia species. Even though the leaf-blades of *Plectrachne* and *Triodia* (Burbidge, 1946) differ considerably from *Amphipogon* in anatomical detail, they are nevertheless basically similar. The presence of two-celled hairs observed in *Plectrachne* and the agreement of the characteristics of the embryo with that met with in the Danthonieae, raises the question as to whether these genera could be included in the Danthonieae. Whereas the lemma of Amphipogon resembles that of Triodia, not only in general texture but also in the tri-lobed apex, and occasionally in indumentum, this organ is three-nerved in Amphipogon, but often several nerved in Triodia. Nevertheless there is a tendency towards a reduction in the number of nerves in *Triodia*, some species having only three nerves with vestiges of additional ones at the base of the lemmas (Burbidge, 1946), so that this character seems less important. Finally the structure of the embryos of Amphipogon and Triodia agree with that of Danthonia. Thus, in spite of possessing one-flowered spikelets Amphipogon appears to be related to Triodia, which has many-flowered spikelets. The subtribe Triodiinae created, and probably misplaced, by Pilger (1956) in the tribe Festuceae should therefore be reinvestigated on the lines suggested above in order to determine whether it should be transferred to the tribe Danthonieae.

The differences between Amphipogon and Aristida are summarized below.

- 1. Chlorenchyma continuous between the bundles and several to many layers thick
- 2. Embryo inserted very obliquely at the base of the caryopsis; embryo about $\frac{1}{4}$ of the length of the grain; hilum punctiform and basal; pericarp loose, occasionally slightly crustaceous
- 3. Lemma loosely enveloping the grain, often with vertical rows of hairs between the nerves dorsally
- 4. Palea well-developed and produced into two bristles apically

- 1. Chlorenchyma, a single layer of tabular cells radially arranged around the bundles.
- Embryo inserted on the ventral face of the caryopsis; embryo 1/2 to 1/2 the length of the grain; hilum linear, at least half the length of the grain; pericarp tightly adhering to the grain.
- 3. Lemma tightly enclosing the grain, scabrid or glabrous or with very sparse, scattered, appressed hairs.
- 4. Palea a small chartaceous scale never much more than half the length of the lemma.

The inclusion of *Amphipogon* (and *Diplopogon*) in the *Aristideae* therefore does not seem justifiable and for this reason the tribe should be limited to the genus *Aristida* sens. lat.

2.3. PHYLOGENETIC POSITION

As may be seen from the historical account, *Aristida* and *Stipa* with its allies have almost invariably been closely associated taxonomically. For this reason a careful re-examination of the characteristics of the *Aristideae* and of representatives of several genera of the *Stipeae* was undertaken.

The remarkable superficial similarity of the florets and grains of the Aristideae and Stipeae presents one of the most striking examples of convergent evolution in the Gramineae, a family in which this phenomenon is particularly well-developed. In spite of this resemblance the characteristics separating the two tribes are profound and easily detected, even on a purely organographic basis. After a thorough study of the South African, as well as a number of non-indigenous, representatives the following table, contrasting the organographical, anatomical and cytological characteristics of the two tribes was drawn up. Information drawn from the considerable literature on the anatomy and cytology of these tribes, especially the more recent papers by authors such as Reeder (1957), Brown (1958), Lommasson (1957) *et alia*, was also made use of.

Stipeae

- 1. Ligule membranous.
- 2. Lemmas 3-7 (usually 5)-nerved.
- 3. Awn, including the column, a solid structure with a distinct demarcation from the body of the lemma; seta of the awn with three vascular bundles and groups of diffusely arranged chlorenchyma cells
- 4. Lodicules 3 (rarely 2), large, membranous, fleshy at the base, obtuse
- 5. Embryo $\frac{1}{4}$ the length of the grain (rarely $\frac{1}{4}$)
- 6. Embryo characterized by-
 - (a) a large well-developed epiblast;
 - (b) the absence of a cleft between the coleorrhiza and base of the scutellum;
 - (c) the vascular strand diverging into the scutellum directly below the base of the coleoptile
- 7. Chlorenchyma of leaf-blade diffuse and continuous between the bundles, composed of several layers of irregular or circular cells
- Bundle sheaths 2; the outer of large thin-walled cells containing chloroplasts and often not well differentiated from the chlorenchyma; the inner of smaller cells with at least the tangential walls thickened, without chloroplasts
- 9. Bicellular hairs absent from the epidermis.
- Basic chromosome number 6, 11 or 12 (or their derivatives); chromosomes small or of medium size
- 11. Distribution mainly in the temperate areas of both hemispheres with extensions into the warm temperate areas, rarely into the tropics

Aristideae

- 1. Ligule ciliate.
- 2. Lemmas 3- or rarely 1-nerved.
- 3. Awn consisting of a grooved column formed by the attenuated upper part of the lemma, column divided at the apex into 1-3 awnlike lobes, or, when the column is absent, the apex of the lemma divided into three very narrow awn-like lobes; setae of the awns each with a single vascular bundle with radially arranged chlorenchyma cells.
- 4. Lodicules 2 or 0, fleshy at the base, obtuse,
- 5. Embryo $+\frac{1}{2}$ the length of the grain.
- 6. Embryo characterized by-
 - (a) the absence of an epiblast;
 - (b) the presence of a deep cleft between the coleorrhiza and the base of the scutellum.
 - (c) the vascular strand diverging some distance below the base of the coleoptile and with a distinct thickened internode leading up to the base of the coleoptile.
- Chlorenchyma of leaf-blade radially arranged in a single layer of tabular cells around the bundles, this layer separated from the adjacent by irregular groups of parenchyma cells which contain no or few chloroplasts.
- Bundle sheaths 2; the outer of larger or smaller cells than the inner, well differentiated from the chlorenchyma; both sheaths thinwalled or the inner with thickened walls; both sheaths, or only the outer, containing chloroplasts.
- Bicellular hairs always present on the epidermis.
- Basic chromosome number 11 (no other basic number so far determined with certainty); chromosomes small.
- 11. Distribution pan-tropical with extensions into warm temperate areas.

From the foregoing it follows that the Aristideae and Stipeae cannot be regarded as being closely allied. Hence in any "natural" classification they should be widely separated, as was actually done by Brown (1958) and by Stebbins (1956). In a diagrammatic presentation of the relationship of the main grass groups based primarily on the anatomy of the leaf-blade, Brown placed the Aristideae between the Pappophorea and Maydeae but indicated that the first mentioned was an isolated group; whereas the Stipeae was placed amongst isolated tribes like the Danthonieae, Oryzeae and Arundineae. Brown's diagram agrees in most respects with an earlier diagram published by Stebbins (1956) setting out the evolutionary interrelationships of the grasses.

Of the various tribes of the Gramineae, the *Eragrosteae* probably exhibits the greatest number of characters in common with the *Aristideae*. The *Sporoboleae*, the *Chlorideae* and the *Pappophoreae* are likewise related to the *Eragrosteae* and thus the placing of *Aristida* in the *Sporoboleae* (which differs from *Eragrosteae* only in the one-flowered spikelets) by Roshevitz (1937), is not as anomalous as it may appear to be on first sight. Examination of the following table contrasting the features of the *Eragrosteae* and the *Aristideae* leaves no doubt, however, as to the distinctness of these two tribes. Differences between the tribes are printed in italics.

Aristideae

- 1. Ligule a fringe of hairs.
- 2. Spikelets strictly one-flowered.
- 3. Lemmas 3-nerved, indurate and *tightly clasping the grains*
- 4. Apex of the lemma always produced into 1-3 awns; the awn(s) formed by much narrowed apical lobe(s) of the lemma
- 5. Lodicules 2, rarely absent; usually rather elongate, fleshy only at the base and with a membranous obtuse apex
- 6. Embryo $\frac{1}{2}$ the length of the grain.
- 7. Internal structure of embryo characterized by-
 - (a) the absence of an epiblast;
 - (b) the presence of a deep cleft between the base of the scutellum and the coleorrhiza;
 - (c) the vascular strand diverging some distance below, and with a distinct thickened internode leading up to, the base of the coleoptile
- 8. Hilum of the embryo linear, more than half the length of the grain
- 9. Chlorenchyma of the leaf-blade radially arranged in a single layer of tabular cells around the bundles, each layer separated from the next by irregular groups of parenchyma cells containing a few or no chloroplasts
- 10. Bundle sheaths 2, both containing chloroplasts (*Aristida*) or the inner without chloroplasts (*Stipagrostis*)
- 11. Bicellular hairs present on the epidermis.
- 12. Silicified cells of the epidermis dumb-bell-shaped or subcircular, paired with variously shaped suberised cells
- 13. Basic chromosome number apparently always 11
- 14. Distribution mainly in tropics and subtropics including desert areas

Eragrosteae

- 1. Ligule a fringe of hairs or membranous.
- 2. Spikelets usually many-flowered, rarely 1–2-flowered.
- 3. Lemmas 3-nerved, membranous to chartaceous, loosely enclosing the grains.
- 4. Apex of the lemma not awned or with 1-3 awns or lobes; the awn(s) when present formed by much narrowed apical lobe(s) of the lemma.
- 5. Lodicules 2, rarely absent; usually short, fleshy, and truncate, or truncate with a small loteral horn.
- 6. Embryo _____ the length of the grain.
- 7. Internal structure of embryo characterized by----
 - (a) the presence of an epiblast;
 - (b) the presence of a deep cleft between the base of the scutellum and the coleorrhiza;
 - (c) the vascular strand diverging some distance below, and with a distinct thickened internode leading up to, the base of the coleoptile.
- 8. Hilum of the embryo punctiform and basal.
- Chlorenchyma of leaf-blade radially arranged in a single layer of tabular cells around the bundles, each layer separated from the next by irregular groups of parenchyma cells containing few or no chloroplasts.
- 10. Bundle sheaths 2, the inner without chloroplasts.
- 11. Bicellular hairs present on the epidermis.
- 12. Silicified cells of the epidermis usually kidneyshaped; paired with subcircular suberised cells.
- 13. Basic chromosome number 7, 8, 9, 10, 12.
- 14. Distribution in the tropics and subtropics including desert areas.

The main features in which the *Aristideae* differs from the *Eragrosteae* may be summarised as follows: spikelets always with one floret; lemma indurate, tightly clasping the grain; lodicules with an obtuse membranous apex, fleshy only at the base; epiblast absent; hilum linear.

Pilger (1956), in his revised Gramineae II, recognizes amongst others the tribes *Eragrosteae*, *Aristideae* and *Chlorideae* and places them next to each other in the subfamily *Eragrostoideae* whereas the *Sporoboleae* is regarded as a subtribe of the *Eragrosteae*. This classification is in conformity with modern data and probably gives a good reflection of the natural affinities of these groups. The placing of the *Pappophoreae* in the subfamily *Festucoideae*, however, does not conform with the anatomical, cytological and embryological data available for this tribe, and it should probably be placed near the *Eragrosteae* and *Aristideae* in Pilger's subfamily *Eragrostoideae*, as well as at the fact that it is placed far from the *Stipeae* in Pilger's classification. De Wet is of the opinion that the two tribes are closely alled and were probably both derived from "the primitive *Arundineae* complex".

possible that the *Stipeae* could have been derived from "the primitive *Arundineae* complex" this seems unlikely for the *Aristideae*, because of its strong resemblance to those of the subfamily *Eragrostoideae*.

In his discussion of the anatomical features of *Aristida* Metcalfe (1960, p. 40) favours affinities with the *Stipeae*. This view is, however, no longer tenable.

In 1961 Caceres published an anatomical investigation of eight Argentinian species of *Aristida*, and concurred with the opinion expressed by other authors, that *Aristida* has an "Eragrostoid" anatomy and should be included in the subfamily *Eragrostoideae*.

2.4.

ARISTIDEAE C. E. Hubbard

In Bor, Grasses of Burma, Ceylon, India and Pakistan 685 (1960)

Annual or perennial herbs or occasionally suffrutices. Ligule a fringe of hairs. Leaf-blades terete to expanded, narrow, linear. Spikelets all alike, bisexual, 1-flowered, arranged in contracted or open panicles. Rhachilla disarticulating above the glumes, not produced beyond the floret. Glumes persistent, usually exceeding the lemmas. Lemmas terete, becoming rigid and indurated, scabrid or smooth, or very rarely with a few appressed hairs, 1–3-nerved, the nerves converging towards the apex but not anastomosing, and each, or only the central nerve, produced into an awn, or upper part of lemma produced into a caniculate 3-nerved twisted column, each nerve produced into an awn at the apex; callus usually well developed, obtuse, pungent or bifid, bearded. Palea much shorter than the lemma, indurate. Lodicules 2 or 0. Stamens 3 or 1. Caryopsis tightly embraced by the lemma; hilum linear, more than half the length of the grain, embryo

ANATOMY

Leaf-blade variously shaped in cross section, usually without a distinct keel; keel rarely developed but always without colourless parenchyma. Silicified cells circular to dumb-bell-shaped, usually accompanied by short to long, thin-walled suberized cells with undulate walls. Stomata usually present in the ab- and adaxial epidermis. Hairs: one-celled and acute, as well as two-celled, cylindrical hairs present, the latter with the apical cells usually longer than the basal, thin-walled and deciduous. The bases of these cells persist, but the apical cells which are extremely thin-walled usually wither or are rubbed off when epidermal scrapes are prepared. Even when present they are not easily detected. Usually only the basal cell is depicted in the drawings. Vascular bundles with a double sheath: outer sheath of small or large cells containing chloroplasts and always relatively thin-walled ; inner sheath of larger or smaller cells than the outer, with or without chloroplasts, and the cells thin-walled or with regularly thickened walls. Chlorenchyma consisting of a single layer of tabular cells, radially arranged around the bundles. Irregular parenchyma cells often present between the bundles below the motor cells. Stereome consisting of typical thick-walled fibres or more rarely adaxially of large thick-walled parenchyma cells. Motor cells consisting of more or less triangular groups of colourless parenchyma occupying $\frac{1}{3}$ to the whole width of the leaf.

Awn with column grooved, or rarely subcircular, containing three vascular bundles; setae each with a single bundle. *Embryo* without an epiblast, with a deep cleft between the lower part of the scutellum and the coleorrhiza; the margins of the first leaf of the embryo (sheathed by the coleoptile) not overlapping.

Genera: Aristida, Stipagrostis. (Sartidia, a genus of uncertain affinity, is here tentatively placed near Aristida. Because of its divergent anatomical features the characteristics of this genus have not been included in the general description of the tribe).

Type species: Aristida adscensionis L.

The Aristideae are mainly sub-tropical in distribution occurring in the drier areas with relatively high winter temperatures.

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2.5. The Genera of the Aristideae

Investigation of the South African representatives of *Aristida* sensu lato has shown that the genus can be divided into three well defined groups. It has long been known that the sections *Stipagrostis* and *Schistachne* differ in anatomical structure from the other sections. All previous authors have either regarded the anatomical features as insufficiently important to create two genera, or else, due to the incompleteness of the data available, have refrained from creating two genera.

For the purpose of this paper all the South African species, and in addition a number of the type species, or representatives, of the various sections from other areas, were studied anatomically. The agreement between the grouping of the species based on anatomy and the classification based exclusively on external morphology, is strong and shows that the sections give on the whole, a fair reflection of the true relationship of the species. This is in direct contrast with the conclusions arrived at by Theron (1936) who investigated about 40 of the South African species (see p. 201).

In the course of this investigation a third well-defined group was discovered in which the structure of the chlorenchyma differs strongly from that of the two groups already discussed above. On anatomical features *Aristida* can therefore be divided into three groups as follows:—

(1) Sections Stipagrostis and Schistachne.

chyma cells

(2) Sections Chaetaria, Pseudochaetaria, Arthratherum, Pseudarthratherum and Streptachne.

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(3) The divergent species A. jucunda, A. angolensis and A. vanderijstii.

To facilitate comparison of these three groups, the differences are contrasted as follows:---

	Group A		Group B		Group C
	Stipagrostis and Schistachne	(Chaetaria, Pseudochaetaria, Arthratherum, Pseudarthra- therum, Streptachne		A. jucunda, A. angolensis and A. vanderijstii
1.	Lemmas with one or three awns, at least the central awn plumose, or if solitary and not plumose, with a pencil of hairs at the junction of awn and lemma	1.	Lemmas with one or three awns, awns scabrid, never plumose nor pencilled at the base	1.	Lemmas 3-awned, awns scabrid never plumose, not pencilled at the base.
2.	Column present or absent	2.	Column present or absent	2.	Column present or absent.
3.	Embryo $\frac{1}{3}-\frac{1}{2}$ the length of the grain	3.	Embryo the length of the grain	3.	Embryo not more than $\frac{1}{4}$ the length of the grain.
4.	A cleft present between the coleorrhiza and the base of the scutellum	4.	A cleft present between the coleorrhiza and the base of the scutellum	4.	A cleft absent between the coleorrhiza and the base of the scutellum.
5.	Starch grains compound, com- posed of numerous granules	5.	Starch grains compound, composed of numerous granules	5.	Starch grains compound, composed of 3–4 granules.
6.	Hilum linear, on the surface of the grain, or lying in a shallow groove	6.	Hilum linear, rarely lying in a groove	6.	Hilum linear, lying in a groove.
7.	Coleoptile 2-nerved	7.	Coleoptile 2-nerved	7.	Coleoptile 3-nerved.
8.	Chlorenchyma cells radially arranged around the bundles in a single row, the groups separated by groups of paren-	8.	Chlorenchyma cells radially arranged around the bundles in a single row, the groups separated by groups of	8.	Chlorenchyma cells not radially arranged around the bundles; several cell layers thick and continuous

parenchyma cells

between the bundles.

Group A

Stipgrostis and Schistachne

- 9. Two bundle sheaths present, the outer usually of larger cells than the inner, and only the outer containing chloroplasts; well differentiated from the tabular chlorenchyma cells
- 10. Silicified cells of the epidermis usually circular or more or less square in outline, occasionally dumb-bell-shaped; bicellular, cylindrical hairs present
- 11. Column of the awns furnished with three vascular bundles, the central bundle without a layer of chlorenchyma cells, the lateral bundles partially sheathed by a single layer of chlorenchyma cells
- 12. Confined to the Old World, mainly in desert areas (250 mm or less precipitation per annum)
- 2n = 44 (rarely 2n = 22)

Group B

Chaetaria, Pseudochaetaria, Arthratherum, Pseudarthratherum, Streptachne

- 9. Two bundle sheaths present. the outer usually of smaller cells than the inner and both containing chloroplasts; well differentiated from the tabular chlorenchyma cells
- 10. Silicified cells of the epiderusually dumb-bellmis shaped, rarely more or less circular or substituted by the paired elements of the stozone; matal bicellular, cylindrical hairs present
- 11. Column of the awns furnished with three vascular bundles, all bundles partially sheathed by a single layer of chlorenchyma cells
- 12. Pantropical, often in low 12. Three species only: the rainfall areas but not confined to these
- 13. Chromosomes usually with 13. Chromosomes with 2n = 22 13. Chromosomes with 2n = 22(rarely 2n = 44 or 55)

A. jucunda, A. angolensis and A. vanderijstii

- 9. Two bundle sheaths present. the outer of larger cells than the inner, and only the outer containing chloroplasts; poorly differentiated from the surrounding chlorenchyma cells which are circular or irregular in shape.
- 10. Silicified cells of the epidermis dumb-bell-shaped or cylindrical; bicellular hairs present.
- 11. Column of the awns furnished with three vascular bundles, each bundle flanked by two many-celled groups of diffuse chlorenchyma cells.
- Congo Republic, Angola and South Africa.
- (S. jucunda).

Constant differences between groups A and B are the plumose awns and single large-celled outer chlorophyll-bearing sheaths surrounding the vascular bundles in group A, and the glabrous awns and double chlorophyll-bearing sheaths, of which the outer sheath usually consists of much smaller cells than the inner, in group B. Furthermore the two groups differ in distribution: group A being confined to the Old World and, with very few exceptions, occurring only in areas with a rainfall of less than 250 mm, whereas group B has a pantropical distribution and the species are adapted to a wide range of habitats (see chapter on distribution).

Other significant differences which do not hold for all species are the usually circular silicified cells of group A (3 of the annual species have dumb-bell-shaped cells) and the dumb-bell-shaped silicified cells of the great majority of the species of Group B.

Most of the species of the section *Stipagrostis* and *Schistachne* (Group A) investigated cytologically have 2n = 44 while *Chaetaria* and related sections (Group B) frequently have 2n = 22. In addition the general facies of the species belonging to the sections Stipagrostis and Schistachne is different from that of the species belonging to the other sections of Aristida.

All these characteristics, taken together, are, in the author's opinion, sufficient reason for the establishment of two distinct genera, namely (1) Stipagrostis, composed of the sections Schistachne and Stipagrostis, and (2) Aristida composed of the sections Aristida (Chaetaria), Pseudochaetaria, Arthratherum, Pseudarthratherum and Streptachne. That Henrard had contemplated a similar decision is indicated by a remark in his Monograph (1929, p. 25): "From the geographical distribution of both sections treated here, one might conclude that we have here a distinct genus before us, a hypothesis we cannot wholly reject if we consider the morphological and anatomical characters of these sections". Jelenc (1951) in a study of the stem and leaf of the Aristida species of North Africa, also noticed some of the distinguishing characteristics mentioned

above, and in his summary expressed surprise that Henrard did not divide the genus into two subgenera on basis of the presence or absence of a double parencnyma sheath (bundle sheaths). Jelenc investigated about 20 species, but regarded the information as insufficient to bring about such a fundamental change in the classification of the genus. Henrard mentions 46 species for the section *Stipagrostis* and *Schistachne* and of these 34 (29 by the present author) have now been studied anatomically. So far all species investigated conform to the general pattern described above. Since the external morphological characters are quite striking, even though not easily expressed in words, no difficulty should be experienced in identifying a single lemma as that belonging to a member of this group even after the plumose awns have dropped.

The importance attached by some authors, such as Holm (1901), to the unique feature of double chlorophyll-bearing bundle sheaths found in *Aristida* sensu stricto is, as pointed out by Lommasson (cf. p. 27), over-emphasized. As a generic difference it is certainly of importance but it cannot be regarded as of sufficient phylogenetic significance to exlude a genus such as *Stipagrostis* lacking this characteristic, from the *Aristideae*.

A full account of the genus Aristida and its sections can be found on pages 234–238.

The third group, comprising the species *A. angolensis*, *A. jucunda*, and *A. vanderijstii*, agrees closely with the section *Aristida* (*Chaetaria*) of *Aristida* in the external morphology of the spikelets, with the exception of certain characteristics of the caryopsis. However, the very different leaf-anatomy taken in conjunction with the differences in the caryopsis, indicates that these species should not be retained in *Aristida*. These species constitute the genus *Sartidia* (described on p. 381).

2.6.1. KEY TO THE GENERA BASED ON ORGANOGRAPHIC CHARACTERS

Awns three or one, glabrous scabrid or smooth:

- Embryo $\frac{1}{3}$ $\frac{1}{2}$ the length of the caryopsis; caryopsis terete or compressed (rarely grooved); glumes usually 1-nerved (rarely 3-nerved)..... Aristida
- Embryo up to $\frac{1}{4}$ the length of the caryopsis; caryopsis always deeply grooved ventrally; glumes 3-5-nerved; awns spirally contorted at the base Sartidia

2.6.2. KEY TO THE GENERA BASED ON ANATOMICAL CHARACTERS

- Chlorenchyma radially arranged around the vascular bundles in a layer only one cell thick:
 - Bundle sheaths two, both containing chloroplasts; the outer sheath consisting of smaller (or at least not larger) cells than the inner sheath, cells of both sheaths relatively thin-walled; silicified cells of the epidermis usually distinctly dumb-bell-shaped or rarely irregular or sub-circular in shape.. Aristida
- Chlorenchyma continuous between the bundles, diffusely arranged and several to many cells thick; bundle sheaths two, only the cells of the outer sheath containing chloroplasts, the inner sheath consisting of strongly lignified cells, the outer sheath of thin-walled cells; sheaths not very well differentiated from the surrounding chlorenchyma; cells rather variable in size and shape.. Sartidia

THE GENUS ARISTIDA

2.7.1. HISTORY (see history of the Tribe on p. 219)

2.7.2. DISTRIBUTION AND ECOLOGY (Fig. 5 and 6)

2.7.

The genus Aristida occurs in the tropics and subtropics of both hemispheres. The areas of highest concentration of species lie mainly along the Tropic of Cancer in the northern, and along the Tropic of Capricorn in the southern hemisphere. The genus is well developed in both hemispheres with a slight bias in the number of species in the southern hemisphere.



FIG. 5.-World distribution of the section Aristida of the genus Aristida.



FIG. 6.—World distribution of the sections of the genus Aristida excluding the section Aristida. 5752152-2

The distribution of the different sections of the genus varies considerably. Of these the section Aristida (Chaetaria) has both the widest distribution and the least advanced floral structure and should be regarded as the most primitive of the sections. It shows four areas of high concentration of species: (1) the southern part of the United States including Mexico, (2) Eastern and Central South America particularly Brazil, (3) the Rhodesias, Transvaal, Angola and South West Africa on the continent of Africa and (4) Queensland and New South Wales in Australia. All these areas fall within the regions which have a 50° F mean temperature for the midwinter month (after Hartley, 1958). The influence of winter temperatures on the distribution of Aristida is therefore well-marked. In many respects the distribution of Aristida sensu stricto, and especially the section Aristida (Chaetaria), agrees in general features with that of the tribe *Eragrosteae* as set out by Hartley (1958). The area of maximum development of the *Eragrosteae* in North America is, however, not paralleled by the section Aristida. For the section Aristida, the northern boundary of the "peak area" in North America lies further south inside the 50° F. mean temperature of winter month isotherm. A similar discrepancy is found in the distribution of the tribe Paniceae when compared with that of the section Aristida, but here the "peak area" in North America lies further east than for the *Eragrosteae*. The inclusion of all the sections in a general distribution map of Aristida does not bring about an extension of the distributional area, nor has it an effect on the positioning of the areas of "peak abundance". Should, however, the genus Stipagrostis be included the centres of " peak abundance" would be strongly affected in the Old World, to which the latter genus is confined. A secondary "peak area" adjacent to the one occupying the centre of Southern Africa and a new one in North Africa would then be created. For this reason the distribution of *Stipagrostis* is discussed separately (Fig. 81). From the maps it is evident that the majority of Aristida species grow in areas with relatively high winter temperatures and, that no species are found in regions which have very cold winters. Rainfall seems to have less effect on the distribution, but few species occur in areas with more than 1,500 mm per year while the number of species tolerating less than 250-500 mm annually is also relatively small. Even though there seems to be a certain correlation between the occurrence of grasslands and deciduous forests and the occurrence of areas with high numbers of Aristida species, discrepancies occur, the most striking of which is the high incidence of species found in Florida, in areas covered mainly by evergreen coniferous forests and with an annual rainfall of between 1,000–1,500 mm. Records, however, show that in Florida most of the species occur in open pine barrens on poor stony or sandy soil or on the sandy coastal plains. This is in agreement with the occurrence of Aristida species in Africa in ecologically similar habitats. It can be assumed therefore, that low humidity (or low available soil moisture) is a secondary factor determining the distribution, while relatively high midwinter temperatures are of primary importance.

The section Arthratherum is fairly small, containing about 40 species, and occurs in both the New and Old Worlds. About five species occur in the United States and Mexico but none is found in the West Indies or South America. Three species occur in India and Pakistan, one in the Phillipines and about seven in Australia, mainly on the eastern side of that Continent. Over 20 species occur in Africa. There are two areas with high concentrations of species in Africa: Somaliland has six species and South Africa 8 species. In both these areas the species are found mostly in areas of low rainfall, on sandy, poor soils, or on rocky outcrops, usually in areas free from frost.

The section *Pseudarthratherum* has 21 species some of which are doubtfully distinct so that the number of species may have to be reduced. No members of this section occur in North America, two are found in South America, while five occur in the Galapagos Islands. The remainder of the species are found in Africa and Arabia one of which extends into India. Due to the small number of species and their scattered distribution, no distinct areas of high concentration are discernable. Eritrea on the one hand, and central South Africa and Southern Rhodesia on the other, have four species each. Most of the species occur in arid areas.

The section Streptachne, as clearly stated by Henrard, is not a uniform group, but consists of species related to members of the section Aristida and are only classified together on basis of the reduction or absence of the lateral awns. The distribution of the species confirms Henrard's observation that it would probably be better to unite them with the section Aristida. Eight species occur from the Southern United States and Mexico to Panama; one occurs in Colombia in South America; one species occurs in North East Africa; another in India and three in Australia. It seems likely that they represent advanced types, derived from species belonging to the section Aristida, and that they developed independently in or near the areas where they occur today. The same applies to A. parvula the type of a monotypic new section occurring only in South West Africa and the Northwestern Cape.

The last section, namely *Pseudochaetaria* contains three species and is confined to Africa. All three species occur in the western half of the African continent: one is limited to the Cape Verde Islands another to Senegambia; the third occurs from Senegambia to South West Africa and eastwards to Southern Rhodesia and Abyssinia.

The majority of the species of Aristida occur in areas with an annual rainfall of 250 to 750 mm. Even those occurring in areas where the rainfall is high usually grow in localities where the available moisture is limited. A few species, however, prefer habitats where the soil is water-logged for at least part of the year: A. recta is found mainly on boggy slopes where seepage water is available during the rainy seasons. In the areas of the Transvaal, South West Africa and Angola, with an annual rainfall of less than 750 mm A. junciformis is found exclusively in depressions and gullies where water collects and remains for long periods during the rainy season. It is increasing, however, in the mountain sourveld [Ngongoni Veld, Acocks (1953, p. 35)] of Natal where over-grazing and burning have caused a deterioration of the veld. In these areas it forms large stands in situations which, apparently, are not very wet. The Natal mountain sourveld has an annual rainfall of between 750 and 1,500 mm, which is probably high enough to support growth even in apparently dry habitats. This predisposition for high rainfall, or habitats where moisture collects during the rainy seasons in areas of lower rainfall, may explain why there is no tendency for A. junciformis to extend its distribution and form pure stands in over-grazed areas in drier regions. A. junciformis subsp. galpinii grows at high altitudes in the mountains of Natal, Basutoland and the Cape where the annual precipitation is high. A. monticola, a species of very limited range in the Natal Drakensberg, shows a preference for wet habitats occurring in great abundance along mountain streams and in seepage areas along this escarpment.

In general, Aristida species are regarded as poor pasture and animals graze them mainly in the very young stages. In the semi-desert areas of South West Africa and the North Western Cape species such as A. engleri, A. dasydesmis and others, are grazed fairly extensively but this is probably due to the scarcity of better fodder. The Aristida species are of the most important pioneers in over-grazed or denuded veld and, as such, are of economic value in the reclamation of these areas (Bews, 1929, p. 209). On the other hand they are regarded as a pest in sheep-farming areas since the "seeds" get entangled in the wool. Cases have been reported of the sharp calli of the florets penetrating the skin of animals, causing irritation and pain, resulting in a general fall-off in the condition of the animals.

As could be expected the anatomy of *Aristida* shows less typical adaptations to extreme arid conditions than that of *Stipagrostis*, which occurs mainly in desert areas. It is striking that of the few species of *Aristida* growing in areas with less than 150 mm of rain, at least one shows adaptations of the leaf structure similar to that found in

n 10 11 12 13 15 16 18 17 19 20 21

FIG. 7.—Chromosomes of: 1, Aristida curvata, 2n = 22; 2, A. effusa, 2n = 22; 3, A. meridionalis, 2n = 22; 4, A. transvaalensis, 2n = 22; 5, A. junciformis, 2n = 44; 6, A. aequiglumis, 2n = 22; 7, A. stipitata var. stipitata, 2n = 22; 8, A. spectabilis, 2n = 22; 9, A. congesta, 2n = 22; 10, A. stipitata var. graciliflora, 2n = 22; 11, A. hordeacea, 2n = 22; 12, A. scabrivalvis, 2n = 22; 13, A. diffusa var. burkei, 2n = 22; 14, A. canescens, 2n = 55; 15, Stipagrostis namaquensis, 2n = 44; 16, do; 17, S. hochstetteriana var. hochstetteriana, 2n = 44; 18, S. obtusa, 2n = 44; 19, S. uniplumis var. uniplumis, 2n = 44; 20, Sartidia jucunda, 2n = 22; 21, Stipa dregeana, 2n = 48.

Stipagrostis. This species, A. dasydesmis, is endemic in the north-western coastal areas of the Cape, and has terete, folded leaves with the bundle units strongly projecting adaxially and very well developed stereome tissue (Fig. 51).

2.7.3. KARYOLOGY (Fig. 7: 1-14)

Fifteen species of *Aristida* sensu stricto were investigated by the author and in all of them the basic number was found to be 11. Most of the species proved to be diploids, one a tetraploid and one a pentaploid. In the table below the species investigated are given with a reference to the locality, and the collector and number of the specimen preserved. In the different sections the species are arranged alphabetically.

	2 <i>n</i>	Locality	Collector and Number
§Aristida—		·	
A. aequiglumisA. canescensA. curvataA. curvataA. effusaA. junciformisA. scabrivalvisA. transvaalensis	22 55 22 22 44 22 22	Pretoria: South Africa Pretoria: South Africa Windhoek: South West Africa Windhoek: South West Africa Pretoria: South Africa Pretoria: South Africa Pretoria: South Africa	de Winter 7515 de Winter 7561 de Winter 7112 de Winter 7132 de Winter 7766 de Winter 7512 de Winter 5982
§Pseudochaetaria—			
A. hordeacea	22	Otavi: South West Africa	de Winter 6799
§Arthratherum—			
A. diffusa var. burkei A. meridionalis A. spectabilis A. stipitata var. graciliflora	22 22 22 22 22 22 22	Pretoria: South Africa Windhoek: South West Africa Pretoria: South Africa Pretoria: South Africa Pretoria: South Africa	de Winter 795 de Winter 6711 de Winter 7516 de Winter 7562 de Winter 5981
§Pseudarthratherum			

A. congesta...... 22 Pretoria: South Africa..... de Winter 7514 Of the twenty-nine species of which the chromosome number is known, only six have been reported to have the chromosomes not in multiples of 11. These are as follows:—

§Aristida-

A. junciform's	2n = 24	de Wet, 1954
	2n = 36	de Wet, 1958
A. canescens	2n = 48	de Wet, 1954
A. transvaalensis	2n = 24	de Wet & Anderson, 1956
A. rhiniochloa	2n = 38	Thomas, ex Darl. & Wylie, 1955

§Pseudarthratherum-

A. barbicollis..... 2n = 24 de Wet, 1954

§Arthratherum-

A. diffusa var. burkei...... 2n = 36 de Wet & Anderson, 1956

It will be noticed that three sections are represented in these species so that n = 12 cannot be regarded as characteristic of any particular section. Of the above mentioned species four were re-investigated (*A. junciformis, A. canescens, A. transvaalensis* and *A. diffusa* var. *burkei*). In the material examined the basic number proved to be n = 11 for all four species. *A. rhiniochloa* and *A. congesta* subsp. *barbicollis* (*A. barbicollis*) could not be re-examined because of lack of material. It therefore seems likely that the basic number of 11 is typical for *Aristida*.

The basic chromosome number is of value in distinguishing the tribe Aristideae from related tribes such as *Eragrosteae* and *Sporoboleae*, but offers no additional characteristics in the delimitation of genera, and sections of genera. Polyploidy is uncommon and as far as is known is limited to the section Aristida which is regarded by the author as the most ancient of the sections on basis of the primitive floral features exhibited by many of the species.

The chromosomes of *Aristida* are of the same small type as those met with in the *Eragrosteae* and *Chlorideae*. Due to their small size no morphological studies of the individual chromosomes were undertaken.

In the course of the study of a large number of karyological preparations many cases were observed where the nucleolus persists to the early metaphase. This, in agreement with the findings of Brown & Emery (1957, p. 587), is an additional character which the *Aristideae* has in common with the *Eragrosteae*, *Pappophoreae* and the *Sporoboleae*.

2.7.4.

ARISTIDA L.

Aristida L., Sp. Pl. 1: 82 (1753); Kunth, Enum. Plant. 187 (1833) pro parte; Trin. & Rupr., Gram. Stip. 99 (1842) exclud. §*Stipagrostis*; Bentham in J. Linn. Soc. Bot. 19: 30 (1855) exclud. §*Stipagrostis* Nees and *Schistachne* Fig. & De Not.; Steud., Syn. Pl. Glum. 1: 132 (1855) exclud. §*Stipagrostis*; Hack., True Grasses 101 (1896) exclud. §*Stipagrostis* and §*Schistachne*; Henrard, Mon. Gen. Aristida 1: 13 (1929) exclud. §*Stipagrostis*, §*Schistachne*, and A. sericans; Hubbard in Hutch. Fam. Fl. Pl. 2, 2: 214 (1934) exclud. §*Stipagrostis* and §*Schistachne*; Pilger in Bot. Jahrb. 76, 3: 330 (1954) exclud. §*Stipagrostis* and §*Schistachne*.

Spikelets solitary, pedicelled, borne in terminal contracted or open panicles. *Rhachilla* disarticulating above the glumes, not produced beyond the base of the floret. Floret 1, hermaphrodite, equalling, or shorter than, or exceeding the glumes, narrowly oblong to linear in outline, terete or laterally compressed. Glumes persistent, narrow, acuminate to obtuse, or emarginate and mucronate, or shortly to distinctly awned, 1-3 (5)-nerved, nerves anastomosing or evanescent. Lemma cylindrical or laterally compressed, convolute, or with margins involute forming a shallow ventral groove, indurated at maturity, glabrous or finely to coarsely scabrid, rarely sparsely hairy, 3-nerved, nerves converging towards the apex but not joining, and each produced into an awn, or the upper part of the lemma narrowed into a canaliculate, 3-nerved, usually twisted, long or short column, each of the nerves, more rarely only the central nerve, excurrent into an awn at the apex of the column or lemma, lemma not articulated, or articulated between the apex of the lemma and the base of the column, or between the apex of the column and the base of the awns; awns glabrous or scabrid, never plumose, usually 3, or more rarely the lateral awns much reduced, or quite absent and then only the central awn remaining; callus well-developed, obtuse, truncate, emarginate, bifid or acuminate, bearded with usually short stiff bristly hairs, or rarely callus hairs up to half as long as the lemma and very fine, rarely callus almost glabrous. *Palea* usually less than half as long as the body of the lemma, inducated or membranous, nerveless or 2-nerved, not keeled, the margins incurved, glabrous. Lodicules usually two, rarely 3 or absent, fleshy at the base, membranous upwards, with several nerves, obtuse. Stamens 1 or 3, anthers elongated. Ovary glabrous; styles free, stigmas plumose, laterally exserted. Caryopsis tightly enclosed by the lemma, usually free, rarely more or less adhering to the lemma; hilum linear, slightly shorter than the grain; embryo usually about 1/2 the length of the grain; starch grains compound, composed of numerous granules.

Densely tufted perennials or annuals, usually without a rootstock or, rarely, a well-developed rootstock present. Culms erect, simple or branched, usually solid Leaf-blades linear, expanded or folded, mostly well-developed in a basal tuft, in annual species borne mainly on the culms. Ligule a dense fringe of hairs. Panicles very dense and spike-like, to effuse and divaricate.



ANATOMY

Shoots long attenuated or rarely short and thick when very young; circular in cross section or rarely compressed; leaf-blades conduplicate in the bud; sheaths tightly enrolling the young blades, tapering towards the free margins (Fig. 10, D, E, F).

Leaf-blades flat, V-shaped or horseshoe-shaped in cross section. Silicified cells dumb-bell-shaped or rarely circular in shape (A. dasydesmis), occasionally rather irregular (circular, kidney- or dumb-bellshaped in A. diffusa), short or much elongated, very narrow in the constricted middle section, the distended ends usually containing a number of crystal-like bodies; usually large in the wider zones and smaller in the narrower zones. Suberized cells variable in shape, thin-walled and usually accompanying a silicified cell; from broader than long, to as long as the silicified cells, and with walls undulate. Hairs of two kinds: (1) unicellular sharp hairs which vary from short broad-based retrorse barbs to long thin hairs from a relatively narrow base, and (2) bi-cellular hairs arising from a narrow basal cell usually situated in or flanking the stomatal zone; basal cell of bi-cellular hair thin-walled or with slightly thickened walls, usually widening towards the truncate apex of the cell which is topped by a very thin-walled, linear, obtuse cell, the latter deciduous and thus only the basal cell persisting. These hairs usually lie longitudinally, closely appressed to the surface. Bundle sheaths: outer sheath usually of much larger cells with somewhat thickened walls and likewise containing chloroplasts; sheaths complete or variously interrupted by the stereome strands. Chlorenchyma consisting of a single row of tabular cells radially arranged around the bundles, occasionally with a few irregular cells below the adaxial stereome flanking chlorenchyma, and with a few cells surrounding the air spaces below the stomata.

Awn (Fig. 8, C & D): Column of the awn triangular or rarely subcircular in cross section, deeply grooved ventrally, furnished with three vascular bundles of approximately equal size, all partly surrounded by a single layer of radially arranged chlorenchyma cells; stomata present in the groove opposite the chlorenchyma. Setae with a single vascular bundle surrounded by a usually complete, single-layered sheath of radially arranged chlorenchyma cells. Lignified cells surrounding the bundles and chlorenchyma usually strongly asymmetrically thickened, likewise the epidermal layer. In transitional areas such as the junction between column and lemma, and at the branching point of the awns at the apex of the column, the bundles are all devoid of a chlorenchyma sheath.

Embryo large, from slightly over $\frac{1}{3}$ to $\frac{1}{2}$ the length of the grain, usually with a slight constriction between the coleoptile and the coleorrhiza (Fig. 9, R, S, T, U) in sagittal section showing the absence of an epiblast, the free lower part of the scutellum which is separated from the coleorrhiza by a deep cleft and the distinct elongation of the vascular tissue between the point of divergence of the scutellum bundle and the base of the coleoptile (Fig. 9, M, N, O). The cross section of the coleoptile shows the first embryonic leaf with the margins meeting, not overlapping and with five vascular bundles; the coleoptile sheath with two lateral bundles, and the scutellum with one median bundle (Fig. 9; P, Q).

Type species: Aristida adscensionis L.

A genus consisting of about 260 species, widely distributed in the tropics and subtropics of both hemispheres. Characteristic of poor dry soils in areas of relatively low rainfall but a few moisture-loving species are known. Although most species prefer a drier climate they are not true desert grasses such as most species of *Stipagrostis*.

2.7.5. Enumeration of the South African Sections

Aristida is divided into six sections, one of which viz. Schizachne was described originally by Trinius and Ruprecht as a monotypic section of the genus Stipa.

1. §Schizachne

§Schizachne (Trin. & Rupr.) de Winter in Kirkia 3: 132 (1963).

Stipa §Schizachne Trin. & Rupr., Gram. Stip. 53 (1842). Type species: A. parvula (Nees) de Winter (=Stipa parvula Nees).

Annual; lemma with a distinct column and an articulation between the apex of the lemma and the base of the column; callus obtuse and furnished with very long, fine hairs more than half the length of the body of the lemma; lemma convolute; awn single, *twice geniculate*.

2. §Pseudochaetaria

§Pseudochaetaria Henrard, Rev. Gen. Aristida 34 (1929). Type species: A. hordeacea Kunth.

Annuals; lemma with an articulation situated at the base of the awns; column absent; callus obtuse; margins of the lemma somewhat involute and spikelets shallowly ventrally grooved; awns three.



FIG. 9.—A, seedling of S. uniplumis, I B, seedling of S. hochstetteriana; C, S. anomala, longitudinal section of the embryo; D, S. obtusa, do; F, S. obtusa, cross section of the embryo; G, S. ciliata, do; H, S. anomala, ventral view of caryopsis; I, S. ciliata, do; J, S. obtusa, do; K, L, young seedlings of A. stipitata var. graciliflora and A. curvata; M, N, O, longitudinal sections of the embryos of A. hubbardiana, A. hordeacea and A. scabrivalvis; P, Q, cross sections of the embryos of A. hubbardiana and A. hordeacea; R, S, T, U, ventral views of grains of A. stipitata var. graciliflora, A. coneesta subsp. barbicollis, A. hordeacea, A. scabrivalvis.



FIG. 10.—Cross sections of shoots: A, S. amabilis (de Winter 3398); B, S. anomala (de Winter 3407); C, S. obtusa (de Winter 3204); D, A. congesta (de Winter 7565); E, A. canescens (de Winter 795); F, A. hordeacea (de Winter 2729).

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3. §Aristida

Chaetaria P. Beauv., Essai Agrost. 30 (1812). Aristida §Chaetaria (P. Beauv.) Trin., Gram. Unifl. et Sesquifl. 175 (1824). Type species: A. adscensionis L.

Annuals or perennials with or without a column; articulation always absent; callus obtuse or acuminate; lemmas convolute, or the margins involute, and spikelets shallowly ventrally grooved, awns three, always glabrous.

4. §Arthratherum

Arthratherum P. Beauv., Essai Agrost. 32 (1812). Aristida §Arthratherum (P. Beauv.) Reichenb., Consp. 50 (1828). Type species: A. hygrometrica R. Br.

Annuals or perennials with a distinct column and an articulation between the apex of the lemma and the base of the column, if articulation absent then callus bifid; callus truncate, emarginate, bifid or acute; lemmas convolute; awns three.

5. §Pseudarthratherum

§Pseudarthratherum Chiov. ex Henrard, Mon. Gen. Aristida 34 (1929). Type species: A. astroclada Chiov.

Annuals or perennials with a distinct, sometimes short, column, and an articulation between the apex of the column and the base of the awns; callus sub-obtuse, acute or acuminate; lemmas convolute; awns three.

2.7.6. Key to the South African Sections

1. Awn single; articulation situated between the summit of the lemma and the foot of the column; callus furnished with very long fine hairs more than half the length of the body of the lemma

1. Schizachne

- 1a. Awns three, the lateral occasionally weakly developed; articulation absent or present; hairs of the callus bristly never half as long as the body of the lemma:

 - 2a. Articulation present, or if absent then callus bifid:
 - Articulation situated between the apex of the lemma and the foot of the column; column of the awns usually well developed; if column or articulation absent then callus bifid
 4. Arthratherum

3a. Articulation situated between the summit of the column and the foot of the awns or, when column absent, between the summit of the lemma and the foot of the awns; callus acute or rounded:

2.7.6.1. Key to the South African Species Based on Organographic Characters

1. §Schizachne

Awn single; hairs of the callus more than half the length of the body of the lemma. 1. A. parvula

2. §Pseudochaetaria

Articulation situated between the apex of the lemma and the branching point of the awns; body of the lemma somewhat furrowed ventrally; only South African species known. 2. A. hordeacea

3. §Aristida

1. Internedes glabrous or scabrous, rarely with some short hairs below the nodes:

2. Annuals or sub-perennials with soft, easily compressible internodes, if sub-perennial then inflorescence effuse and very large; lemmas often coarsely scabrid, never with a twisted column, at most narrowed into a beak:

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- 3. Spikelets small, usually 2.5 cm or less in length including the awns, if up to 3 cm then lemma narrowed into a beak and inflorescence short, dense and spike-like:
 - 4. Panicle contracted and spike-like, or contracted and interrupted:
 - Panicle spike-like, very dense and short, up to 6 cm long; body of the lemma very scabrous, furrowed ventrally and narrowed into a short beak: glumes shortly awned
 A. hubbardiana
 - 5a. Panicle contracted, usually elongate and interrupted; lemma not narrowed into a beak:

 - 6a. Panicle contracted but not very dense, the branches usually with a fairly long, naked basal part; lemmas usually strongly exserted from the glumes when mature

5. A. adscensionis subsp. guineensis

4a. Panicle effuse and open with the branches remote and divaricate:

7. Body of the lemma included in the glumes, not exserted beyond them:

- in length; short-lived perennials usually with a basal tuft of leaves 9. A. bipartita
- 7a. Body of the lemma exserted beyond the glumes at least in the mature spikelets; glumes variable in length, awnless:

 - 9a. Spikelets diffusely scattered on the branchlets, not densely clustered on them; lemmas usually scabrid on the keel only..... 5. A. adscensionis subsp. guineensis
- 3a. Spikelets large and coarse, scabrid all over, or rarely the lemma scabrid only on the keel, 3-5 cm long including the awns; glumes reddish-brown or purplish in colour 4. A. rhiniochloa
- 2a. Perennials usually with firm hard culms, or with a dense fibrous base; body of the lemmas usually produced into a beak, or with a twisted column; glabrous or finely scaberulous, rarely without a beak or column:
 - 10. Lower glume longer than the upper; culms much branched; base rhizomatous 13. A. monticola
 - 10a. Lower glume shorter than the upper, or glumes subequal but the lower at least slightly shorter than the upper:
 - 11. Lemma without a beak or column, only slightly narrowed upwards:

12. Culms terete; leaves expanded with the marginal nerves raised and prominent 10. A. canescens

11a. Lemma with a long or short column which is usually somewhat twisted:

- 13. Glumes more or less subequal the upper only 1-1.5 mm longer than the lower, awnless, occasionally mucronate; internodes of culm not, or only slightly compressed:
- 13a. Glumes very unequal: the lower about $\frac{1}{2}$ to $\frac{2}{3}$ as long as the upper; awned or awnless:

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4. §Arthratherum

1. Callus truncate, obliquely truncate, rounded or even slightly emarginate; culms fascicled from

1a. Callus bifid, or conical and acute; culms branched or unbranched:

- 2. Callus bifid:
 - 3. Auricles and ligule pubescent or ciliate, not woolly; culms glabrous; glumes very unequal, apices never membranous:
 - 4. Lemmas smooth, glabrous or slightly scaberulous on the keel upwards; culms unbranched (very rarely somewhat branched)..... 18. A. diffusa
 - 4a. Lemmas scabrid on the back in the upper half; culms branched or unbranched

20. A. engleri

- 3a. Auricles with a dense flake of wool, or lower internodes woolly to pubescent; glumes subequal or unequal, apices membranous or firm:
 - 5. Lower internodes pubescent to woolly, the upper often glabrous; column of the awns rather short, about 6.5 mm long..... 19. A. vestita
 - 5a. Lower and upper internodes glabrous; column of the awns $1 \cdot 0 3 \cdot 5$ cm long;
 - 6. Glumes subequal or somewhat unequal, usually straw-coloured, with the apices membranous, hyaline and delicate, often torn or broken...... 21. A. spectabilis
 - 6a. Glumes very unequal, lower not more than 1, usually about half the length of the upper, often purplish, the apices firm, not distinctly hyaline:
 - 7. Column of the awns usually exceeding 2 cm long; annual plants.. 23. A. stipoides
 - 7a. Column of the awns usually not exceeding 2 cm; perennial plants 22. A. meridionalis
- 2a. Callus conical and acute, never bifid:
 - 8. Internodes woolly or densely tomentose especially towards the base of the culms:
 - 9. Panicle spike-like, long, contracted and narrow...... 24. A. mollissima 9a. Panicle often narrow but effuse and divaricately branched...... 25. A. argentea
 - 8a. Internodes quite glabrous or minutely scaberulous only, never woolly or pubescent

26. A. stipitata

3. A. hubbardiana

5. §Pseudarthratherum

- 1. Panicles contracted but much branched, the branches erect or slightly spreading, never spikelike; robust, erect perennials, with inflorescence up to 20 cm long...... 27. A. pilgeri
- 1a. Panicles spike-like and dense, or somewhat interrupted, the branches short, usually bearing spikelets to the base, or panicles lax and open, the branchlets ending in a dense cluster of

2.7.6.2. Key Based on Anatomical and Vegetative Characters

Due to the great difficulty in distinguishing many of the species on anatomical or vegetative grounds it was not possible to draw up a full key. The guide given below may, however, be useful in limiting the number of species to be considered in the identification of sterile material of any particular species.

1. Annuals with soft, compressible culms; midrib usually protruding abaxially; stereome strands of the third order bundles rather weakly developed, often consisting of a few fibres only:

- 2. Culms densely scabrous or scabridulous:
- 3a. Culms densely covered with spreading or reflexed, short, stiff hairs..... 2. A. hordeacea

2a. Culms quite smooth, or only very sparsely puberulous:

- 4. Many short innovation shoots present at the base of the plant; auricles and margin of the
- - A. curvata
 A. effusa

 - 8. A. scabrivalvis
 - 1. A. parvula

1a. Perennials with firm, hard culms; midrib of the blade not protruding abaxially:

- 5. First order bundles, except for midrib, concentrated on the margins of the blade, usually only one, or occasionally two, on each margin but then closely associated, much exceeding the 3rd order bundles, as well as the midrib; the midrib flanked by 2-4 third order bundles and only very slightly exceeding these in size; stereome strongly developed opposite the motor cell groups, but absent or weakly developed opposite the third order bundles:
 - 6. Culms unbranched or occasionally branched:
 - 7. Leaves erect, not curled when dry; 3rd order bundles without abaxial stereome strands 11. A. aequiglumis
 - 7a. Leaves curled when dry; 3rd order bundles with abaxial stereome strands 10. A. canescens
 - 6a. Culms much branched especially from the upper nodes:

 - 8a. Plants without well developed rhizomes, densely caespitose; base tough, fibrous 12. A. transvaalensis
- 5a. First order bundles more or less uniformly spaced over the whole width of the leaf, or at least a well developed first order bundle present between the marginal bundles and the midrib; if first order bundles marginal, then all bundles subequal in size:

 - 9a. Adaxial stereome strands of all bundles consisting of typical small, very thick-walled fibres; internodes of culms glabrous, woolly or pubescent:
 - 10. Leaf-blades narrowly to widely V-shaped in cross-section; first and third order bundles subequal, and gradually decreasing in size towards the midrib; stereome strands usually absent abaxially opposite the 3rd order bundles, but strongly developed opposite the motor cell groups:
 - 11. Epidermal cells much smaller than the cells of the inner bundle sheaths 14. A. junciformis
 - 11a. Epidermal cells exceeding the cells of the inner bundle sheath in size..... 15. A. recta
 - 10a. Leaf-blades expanded, or if horseshoe- or crescent-shaped then with the bundle units very unequal in size; stereome strands occasionally weakly developed, but present opposite the motor cell groups as well as the bundles:
 - 12. Auricles of the leaf-blade with a flake of wool:

13. Annual plants 23. A. stipoides
13a. Perrenial plants22. A. meridionalis21. A. spectabilis
2a. Auricles of leaf-blade without a flake of wool:
14. Basal internodes of the culms woolly or pubescent 25. A. argentea 19. A. vestita
24. A. mollissima
14a. Basal internodes of the culms glabrous:
15. First order bundles much exceeding the 2nd and 3rd order bundles in height:
 16. Adaxial stereome elements of first order bundles much larger and thinner- walled than the abaxial fibres; culms fascicled from the lower nodes; leaves subterete in cross section
16a. Adaxial and abaxial stereome strands both consisting of typical, thick- walled fibres
15a. First order bundles subequal to or only slightly exceeding the third order bundles in height:
17. Marginal first order bundles usually with a third order bundle between them:
18. Very robust unbranched culms, up to 2 m high 21. A. spectabilis 26. A. stipitata 27. A. pilgeri
18a. Smaller plants with branched or unbranched culms, usually not exceeding

27. A. pilgeri 17a. Marginal first order bundles usually adjacent...... 28. A. congesta & subspp.

26. A. stipitata 20. A. engleri

1 m in height.....

2.7.7. Description of the South African Species

1. A. parvula (Nees) de Winter in Kirkia 3: 132 (1963)

Stipa parvula Nees, Fl. Afr. Austr. 169 (1841). Type: Great Namaqualand; stony Karoo hills, Drege 2551 (B⁺; PRE, fragment of holo.!).

Annual, very small and compact (6 cm high) to loose, spreading and up to 40 cm high. Culms erect, or sprawling and semi-prostrate, geniculate, simple or much branched from the upper nodes (in older plants, wiry and brittle) pallid to deep purple; nodes glabrous; internodes smooth and usually glossy. Leaf-sheaths usually much shorter than the internodes, the bare culms being a feature of robust plants, glabrous except for the sparsely villous, membranous margins. Leaf-blades narrowly linear,



FIG. 11.—A. parvula: cross section of the leaf-blade (Schweickerdt 2220).



FIG. 12.-A. parvula: abaxial epidermis of the leaf-blade.

convolute or expanded, up to 2 mm wide, up to 12 cm long. *Panicle* effuse, 4–12 cm long, longer than wide, the branches and spikelets spreading when mature; branches binate, clustered or solitary, angular, scabrid on the angles. *Spikelets* usually purple or rarely pallid, spreading. *Glumes* unequal, boat-shaped, lanceolate, 1-nerved strongly awned, glabrous except on the prominent scabrid midrib; lower shorter than the upper, $4 \cdot 5 - 5 \cdot 5$ mm long, bifid, awn about 2 mm long; upper $6 \cdot 5 - 7 \cdot 5$ mm long, bifid, awn about 2 mm long; upper $6 \cdot 5 - 7 \cdot 5$ mm long, bifid, awn about 2 mm long including the callus, coarsely scabrid upward especially on the keel, pallid, purple or mottled with purple, articulated at the apex of the lemma; column grooved, about 5 mm long, 3-nerved, twisted, scabrous, kneed at the articulation and at the junction of column and awn; awn solitary 6–9 mm long, finely scaberulous; callus truncate, bristly with bristles half as long as the body of the lemma. *Palea* a firm, broadly oblong, sub-truncate, 2-nerved scale, about 1 mm long. *Lodicules* fleshy in young flowers later membranous, lanceolate, 5-8-nerved, about 1 \cdot 5 mm long. *Anthers* linear about 1 \cdot 5 mm long. *Ovary* glabrous, styles distinct, stigmas elongate, narrow plumose. *Caryopsis* linear; hilum linear; embryo about $\frac{1}{2}$ the length of the grain.

ANATOMY (Fig. 11, 12 & 159: 1)

Leaf-blade V-shaped or more or less expanded in transverse section, upper and lower surface slightly undulate the bundle units hardly projecting; lower surface almost glabrous, upper hispidulous; midrib slightly projecting; margins obtuse. Abaxial epidermis: stomatal zones with 1–3 rows of stomata and 4–8 rows of elongate, rectangular, ripple-walled cells with strongly undulate walls; silicified cell zones with 3–5 rows of slicified cells alternating with long narrow ripple-walled cells opposite the first order bundles and 1–3 rows opposite the third order bundles, silicified cells dumbbell-shaped, often with a thin, elongate central part, suberized cells square to narrowly oblong and with undulate walls, bicellular hairs present flanking the zones, unicellular retrorse barbs very few. Vascular bundle units: first order units usually 5, groups of 3–4 third order units flanking the midrib, 1–3 third order units soft and single or paired on the margin; units all more or less of same size and square in outline; midrib only slightly larger than the other first order bundles. Stereome strands: abaxially fairly well developed opposite the first order bundles, wery weakly developed opposite the third order bundles and not interrupting the chlorenchyma or bundle sheaths. Motor cells well developed, present alternating with all the bundles in Y-shaped or triangular groups occupying $\frac{1}{3}$ to the full width of the leaf.

CAPE.—Kenhardt: Acocks 17601; Namaqualand: Schweickerdt 2536.

SOUTH WEST AFRICA.—Warmbad: Dinter 5128; Pillans 6372. Keetmanshoop: de Winter 3474; Acocks 18109; Luderitz: Kinges 2691; Oertendahl 193. Omaruru: de Winter 3158; Boss s.n. (Tvl. Mus. No. 36372). Swakopmund: Marloth 1202; Schweickerdt 2220, 2223 and 2239; Boss s.n. (Tvl. Mus. No. 36411). Karibib: Boss s.n. (Tvl. Mus. No. 36372); Boss 4. Outjo: Galpin & Pearson 7420. Kaokoveld: de Winter & Leistner 5874 and 5699.

DISTRIBUTION.—(see Fig. 43).

This species prefers rocky situations in desert and semi-desert areas.

Stapf in the Flora Capensis (1896, p. 572) lists *Stipa parvula* as a doubtful *Stipa* and suspected it to be a single-awned *Aristida*. Elias (1942, p. 64) concurred with Stapf's view after a careful morphological examination. Stapf's suspicion has been confirmed by an investigation of the anatomy and external morphology (see Fig. 1 and discussion on p. 212).

The radial arrangement of the chlorenchyma, the presence of two bundle sheaths, the cells of which contain chloroplasts, as well as the grooved column leaves no doubt that this species is a true *Aristida*. The solitary awn would seem to indicate that *A. parvula* should be placed in the section *Streptachne*, which contains those species of *Aristida* where the lateral awns are much reduced or absent. In *Streptachne*, however, the awn is not deciduous, even though an articulation is present, the awns have a single bend and the callus bristles are relatively short. In *A. parvula* the callus bristles are half as long as the body of the lemma, the awn twice geniculate and deciduous. For this reason the monotypic section *Schizachne*, created by Trinius & Ruprecht to accommodate this species in *Stipa*, was transferred to *Aristida*.

Even though A. parvula has an articulated awn, a characteristic not found in any of the annual species of Sect. Aristida (Chaetaria) it resembles species such as A. effusa and A. scabrivalvis so closely both organographically and in the anatomy of the leaf-blade, that it could have originated from an ancestor with features similar to these species.

2. A. hordeacea Kunth, Rev. Gram. 2, t. 173 (1830) A. hordeacea Kunth var. longiaristata Henr., Crit. Rev. Aristida 2: 244 (1927). A. steudeliana, Trin. & Rupr., Gram. Stip. 155 (1842).



FIG. 13.-A. hordeacea: cross section of the leaf-blade (de Winter 3097).



FIG. 14.-A. hordeacea: abaxial epidermis of the leaf-blade.

Annual, usually erect, branched from the base and lower nodes, 10-90 cm high. Culms erect to geniculate, several-noded; nodes pubescent; internodes compressed, densely pubescent, glabrescent. Leaf-sheaths keeled, pubescent; auricles bearded. Leaf-blades expanded or folded, keeled, scabrous below, hirtellous above, up to 30 cm long and 1 cm wide. Panicle exserted, spike-like and very dense, or somewhat interrupted at the base, up to 26 cm long, linear-oblong to sub-ovate. Spikelets greenish or pallid. Glumes lanceolate, awned, 1-nerved, keeled, dorsally scaberulous, lower 6-11 mm long excluding the $2 \cdot 5-5$ mm long awn; upper 7-12 mm long excluding the 1-4 mm long awn. Lemma linear, fusiform, very scabrid all over, ventrally furrowed, up to $7 \cdot 5$ mm long including the callus, distinctly articulated; callus rounded, bearded, about 5 mm long; awns subequal, scabrid, 35-50 mm long. Caryopsis linear-lanceolate, distinctly furrowed ventrally.

ANATOMY (Fig. 13, 14 & 159:2)

Leaf-blade expanded and more or less moniliform in transverse section: both surfaces undulate due to the slightly protruding bundle units; adaxial surface covered with short bristly unicellular hairs mainly flanking the stereome strands; silicified cells strongly protruding; midrib projecting strongly abaxially, forming a distinct keel; margins sub-obtuse. Abaxial epidermis: stomatal zones with one or two rows of stomata, short elements present, often paired, the one cell undulate the other smooth-walled and produced into a small retrorse barb, ripple-walled cells strongly undulate, elongaterectangular, walls thin; bi-cellular linear hairs present; silicified cell zones with silicified cells dumbbell-shaped, often very large opposite the first order bundles, suberized cells rectangular, walls undulate and thin, many retrorse broad-based barbs present flanking the silicified cell zones, or within them in narrow zones. Vascular bundle units: first order units 7, more or less square to sub-circular; second order units sub-circular in outline. Stereome strands ad- and abaxially well developed only opposite the first order bundles, abaxially present in small groups opposite the third order bundles and most of the motor cell groups; adaxially often present in minute groups opposite the third order bundles, usually subtending retrorse barbs. Motor cell groups one to two rows of cells wide and occupying the whole thickness of the leaves.

SOUTH WEST AFRICA.—Otjiwarongo: Volk 2818; de Winter 2729; Bradfield 440. Outjo: Volk 2859. Grootfontein: Schweickerdt 2298; Schoenfelder 511; Kinges 2820; 6799. Okavango: de Winter & Marais 5026; Maguire 2328.

DISTRIBUTION.—(see Fig. 55)

This species is found mainly in shallow depressions and on the edge of small pans where water collects after rain. Almost invariably it is limited to those depressions where the soil is heavy clay.

Its closest relative amongst the South African species seems to be *A. hubbardiana*, with which it agrees in spikelet characteristics as well as general habit. It is distinguished from the latter by the presence of an articulation between the apex of the lemma and the base of the awns, as well as the generally larger spikelets. The leaf anatomy is also rather similar (see Fig. 13 and 15).

3. A. hubbardiana Schweickerdt in Notizbl. Bot. Gart. Mus. Berol. 14, 122: 196 (1938)

Annual, slender and rather lax, up to 50 cm high. Culms erect, geniculate severalnoded; nodes glabrous; internodes exserted, glabrous. Leaf-sheaths glabrous, slightly keeled; auricles usually glabrous. Leaf-blades expanded or folded, almost glabrous on lower surface, scaberulous on the upper up to 10 cm long, 2 mm wide. Panicle well exserted when mature up to 6 cm long, obovate in outline. Spikelets subsessile. Glumes about 7 mm long, linear lanceolate lower awned, scaberulous on the keel and awn, upper shortly awned, keel glabrous. Lemma up to 7 mm long, very scabrid in its upper two-thirds, shallowly furrowed ventrally; callus short, rounded, densely bearded; awns scabrous up to 30 mm long. Caryopsis linear-lanceolate, furrowed ventrally. ANATOMY (Fig. 15, 16 & 159: 3)

Leaf-blade widely V-shaped in transverse section; abaxial bundle units slightly protruding; adaxial surface with the bundles protruding a little less than one-third of their height; bristle-like unicellular sharp hairs present, adjacent to the stereome strands; midrib protruding abaxially to form a slightly projecting keel; margins obtuse. Abaxial epidermis: stomatal zones with very few short elements and usually one row of stomata, ripple-walled cells shallowly undulate; silicified cell zones with silicified cells dumb-bell-shaped often large and elongate, suberized cells of usual type, unicellular sharp hairs as well as bicellular linear hairs present. Vascular bundle units: first order bundle units 5; second order bundle units 3 on either side of the midrib and alternating with the other first order bundles. Stereome strands abaxially present opposite the second order bundles as minute groups of fibres, but well developed opposite the first order bundles. Motor cells in Y-shaped groups 1-3 rows wide at the base, and occupying the whole thickness of the leaf.



FIG. 15.—A. hubbardiana: cross section of the leaf-blade (Schweickerdt 2111).



FIG. 16.-A. hubbardiana: abaxial epidermis of the leaf-blade.



FIG. 17.-Distribution of X A. hubbardiana; O A. transvaalensis.



FIG. 18.-A. rhiniochloa: cross section of the leaf-blade (Codd 5977).

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FIG. 19.-A. rhiniochloa: abaxial epidermis of the leaf-blade.



Fro. 20.-Distribution of O A. rhiniochloa; X A. sciurus.

SOUTH WEST AFRICA.—Tsumeb: de Winter 2936; Dinter 7600 (isotype). Grootfontein: Schweickerdt 2054; 2059; 2094; 2111; 2143; Kinges 2857. Outjo: Volk 2850.

DISTRIBUTION.—(see Fig. 17).

A relatively rare species with a limited distribution in the Outjo, Tsumeb and Grootfontein districts of South West Africa. Like its relative, *A. hordeacea* it occurs mainly in seasonally flooded depressions in calcareous clayey soils (see previous species).

4. A. rhiniochloa Hochst. in Flora 38: 200 (1855) A. andoniensis Henrard, Crit. Rev. Aristida 3: 691 (1928). A. rigidiseta Pilger in Engl. Bot. Jahrb. 51: 413 (1914).

Annual, erect, very scabrid and coarse, up to 60 cm high. Culms erect, rarely geniculate, 3-many noded; nodes minutely pubescent; internodes retrorsely scabrid. Leaf-sheaths rather lax, keeled, scabrous; auricles long-bearded. Leaf-blades expanded, up to 20 cm long and 4 mm wide, keeled, very scabrous on both surfaces. Panicle effuse, or contracted and much interrupted, up to 30 cm long, rhachis and branches very scabrid, axils shortly hairy. Spikelets coarse, pallid or purplish-brown. Glumes broad, very acute, scaberulous to almost smooth, 1-nerved, awned; lower up to 17 mm (usually about 14 mm) long, gradually tapering into the awn; upper up to 15 mm long, with two lateral teeth flanking the awn. Lemma up to 13.5 mm (usually about 11 mm) long with lines of coarse antrorse barbs from base to apex, very rarely almost smooth; keeled on the back, deeply grooved ventrally with in-rolled margins; callus sub-obtuse, bearded; awns rigid, coarsely scabrid 18-30 mm (rarely 40 mm) long. Caryopsis narrowly lanceolate deeply grooved ventrally.

ANATOMY (Fig. 18, 19 & 159: 4)

Leaf-blade expanded in transverse section; abaxial surface flat or slightly undulate, covered with short, sharp, bristly hairs flanking, or opposite, the stereome strands; adaxial surface strongly undulate, due to the projecting bundle units, covered with short bristly hairs; midrib strongly projecting abaxially forming a distinct keel; margins obtuse. Abaxial epidermis: stomatal zones with one or two rows of stomata short elements present but few, these occasionally produced into short sharp hairs; ripple-walled cells elongate-rectangular with strongly undulate, rather thin walls, numerous linear bicellular hairs present; silicified cell zones with silicified cells dumb-bell-shaped, larger in the wider zones, suberized cells rectangular with undulate thin walls; many broad-based retrorse barbs present flanking the wider, and present within the narrower, zones. Vascular bundle units subcircular. Stereome strands ad- and abaxially well developed only opposite the first order bundles, abaxially present in small groups opposite the third order bundles as well as the motor cell groups; adaxially in minute groups the whole thickness of the leaf.

TRANSVAAL.—Kruger National Park: Brynard & Pienaar 4270; de Winter and Codd 647; van der Schijff 1879. Waterberg: Codd 8503. Rustenburg: Acocks 18754; Codd 8678.

SOUTH WEST AFRICA.—Okahandja: Gaerdes 16. Otjiwarongo: Liebenberg 4906; Dinter 5754; de Winter 2723. Tsumeb: de Winter 2927. Outjo: de Winter and Leistner 5138. Kaokoveld: de Winter and Leistner 5378.

DISTRIBUTION.—(see Fig. 20).

A very coarse, hard species occurring on rocky slopes, gravelly flats, sand or loam, in dry to very dry, often disturbed, situations.

A. rhiniochloa is a distinct species with no obvious close relatives. Sturgeon (1954; p. 13) states that A. serrulata described by Chiovenda (and which he later regarded as a variety of A. rhiniochloa) is, in her opinion, a closely related, but distinct, species. No material of this plant was available for study. After examining type material of A. andoniensis it became clear that this species represents a form of A. rhiniochloa with rather glabrous lemmas. The wide range of material of A. rhiniochloa now available for study has shown that the scabridity of the lemma varies considerably.

It is probable that *A. hordeacea*, *A. hubbardiana* and *A. rhiniochloa* are related even though the latter is a much coarser plant than the others, with a different panicle. All three species have deeply ventrally grooved caryopses. In addition they are all annuals, the lemmas are ventrally grooved, scabrid and lack a column. It seems likely that *A. hordeacea* should be regarded as allied to the other two species in spite of the presence of an articulation. Anatomically they also agree by having expanded leaves with abaxially protruding midribs and a very similar type of bundle unit.

5. A. adscensionis L. subsp. guineensis (Trin. & Rupr.) Henrard, Crit. Rev. Aristida 1: 216 (1926)

A. guineensis Trin. & Rupr., Gram. Stip. 137 (1842).

Annual, forming erect to lax sprawling tufts, up to 75 cm high. Culms erect, sometimes strongly geniculate; nodes glabrous; internodes glabrous, smooth, often purplish, the basal ones bare. Panicle narrow but rather laxly branched and interrupted, never spikelike. Spikelets pallid or purplish. Glumes unequal, 1-nerved, keeled, at least upwards, usually tinged with purple, minutely scaberulous on the keels, otherwise glabrous or lower minutely hispidulous; lower 5–7 mm long erose-bifid or acute; upper 6-8.5 mm long erose-bifid and occasionally mucronulate. Lemma 8–14 mm long, well exserted from the glumes when mature, pallid, purplish, or mottled with purple, glabrous and smooth, keels coarsely scabrid in the upper half; callus rounded, shortly bearded; awns scabrid, central 12–17 mm long, lateral 8–12 mm long. Caryopsis linear, terete.



FIG. 21.—Distribution of A. adscensionis subsp. guineensis; A. stipoides.

ANATOMY of the leaf-blade as in A. curvata (Fig. 159: 5, p. 253)

TRANSVAAL.—Pretoria: Repton 1738; 2120. Pietersburg: Briggs 10. Waterberg: Carver 8. Barberton: Thorncroft 43. Kruger National Park: Obermeyer 36088; van der Schijff 396; 1643. Soutpansberg: Codd & Dyer 3904; de Winter & Codd 648; Codd 5801; Acocks 17850.

DISTRIBUTION.—(See Fig. 21.)

Closely allied to A. curvata (cf. notes, p. 254) and A. effusa. Differs from A. effusa in the smaller, more graceful, spikelets and, particularly, in the lemmas which are scabrid on the keels only. A. effusa occurs only in South West Africa and A. adscensionis subsp. guineensis in the Transvaal, from Pretoria northwards into tropical Africa. Anatomically these species are indistinguishable.

6. A. effusa Henrard, Crit. Rev. Aristida 1: 155 (1926) A. caerulescens Desf. var. breviseta Hack. in Engl. Bot. Jahrb. 11: 400 (1889). A. waibeliana Henrard, Crit. Rev. Aristida 3: 679 (1928).



FIG. 22.-A. effusa: cross section of the leaf-blade (de Winter 3526).

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FIG. 23.-A. effusa: abaxial epidermis of the leaf-blade.



FIG. 24,-Distribution of A. effusa; OA. bipartita.

Annual, slender, erect, up to 90 cm high. Culms branched from most nodes; nodes glabrous; internodes glabrous, usually exserted. Leaf-sheaths lax, slipping from the culms; auricles glabrous to ciliate. Leaf-blades up to 30 cm long and 3 mm wide, expanded. Panicles effuse and open, 20–30 cm long and 15 cm wide, or much smaller; branches spreading, flexuous, bearing the spikelets at the apex in short spike-like clusters. Spikelets usually purplish. Glumes equal to slightly unequal; lower lanceolate up to 8.5 mm long, acute or mucronulate, scaberulous towards the apex, scabrid on the keel, 1-nerved; upper to 8 mm long, truncate or very obtuse, 1-nerved, keel smooth. Lemma linear up to 11.5 mm long or much shorter, very scabrous upwards, shortly to much exserted beyond the glumes; callus rounded, bearded; awns etect, scabrid, central awn about 16 mm, lateral awns about 13 mm long. Caryopsis linear, terete.

ANATOMY as for *A. curvata* except that the leaves of *A. curvata* are somewhat more robust (Fig. 22, 159: 6).

SOUTH WEST AFRICA.—Gobabis: de Winter 2467; 2437. Windhoek: Liebenberg 4455; 4432; de Winter and Giess 7126; 7114; 7132; 7134; de Winter 3526. Okahandja: Bradfield 738. Otjiwarongo: de Winter 2725; Volk 2925. Karibib: Kinges 3055; de Winter 2661. Tsumeb: Volk 1672. Grootfontein: Kinges 2882; 2780; de Winter and Giess 6784; Schoenfelder 99; de Winter 2930. Outjo: Volk 2868. Kaokoveld: de Winter and Leistner 5174.

DISTRIBUTION.—(See Fig. 24.)

A species distinguished by its effuse panicle, with the spikelets contracted at the ends of the branches, and by the scabrid lemmas which are exserted from the glumes when mature. Related to *A. adscensionis* subsp. *guineensis*, which has the lemma scabrid only on the keel and the spikelets not congested at the ends of the branches. Distinguished from *A. scabrivalvis* by the awnless glumes and exserted lemma.

7. A. curvata (Nees) Trin. & Rupr., Gram. Stip. 133 (1842).

Chaetaria curvata Nees, Fl. Afr. Austr. 186 (1841). Chaetaria curvata Nees β minor Nees, l.c. p. 187. Chaetaria mauritiana (Kunth) Nees var. nana Nees, l.c. p. 188. Aristida confusa Trin. & Rupr., Gram. Stip. 134 (1842). A. pusilla Trin. & Rupr., l.c. p. 140. A. pygmaea Trin. & Rupr., l.c. p. 133. A. strictiflora Trin. & Rupr., l.c. p. 134. A. adscensionis L. var. pygmaea (Trin. & Rupr.) Dur. and Schinz, Consp. 5: 800 (1894). A. adscensionis L. var. strictiflora (Trin. & Rupr.) Dur. and Schinz, Consp. l.c. A. curvata (Nees) Trin. & Rupr. var. nana (Nees) Henrard, Crit. Rev. Aristida 3: 487 (1928).

Annual, erect or sprawling, 10–100 cm high. Culms erect, geniculate, often branched from the base and lower nodes; nodes glabrous, internodes glabrous. Leaf-sheaths tight or lax, keeled, smooth or scaberulous; auricles pubescent. Leaf-blades linear, expanded or folded, up to 15 cm long and 1-2.5 mm wide, glabrous on the lower surface, scabrid on the upper. Panicle narrow and dense, or interrupted, up to 24 cm long and 1-2.5 cm broad. Spikelets pallid, green, or tinged with purple. Glumes more or less keeled, unequal, linear-lanceolate to lanceolate; lower 4–7 mm long, emarginate and mucronate from the sinus, scabrous on the keel and strigose on the margins; upper up to 6–8 mm long, scaberulous upwards, bifid with a mucro from the sinus. Lemma usually mottled with purple, finely punctulate and scabrous on the keel up to 10 mm long, usually as long as, or slightly shorter than, the glumes, rarely slightly exceeding them; callus rounded, bearded; column absent; awns unequal scabrid, central awn about 20 mm long, lateral awns about 15 mm long. Caryopsis linear, subterete.

ANATOMY (Fig. 25 and 159: 7)

Leaf-blade flat in transverse section; adaxial surface more or less undulate; midrib usually somewhat protruding forming a keel; adaxial surface shallowly grooved due to the slightly protruding bundle units, and with few to many hairs opposite the bundles. Abaxial epidermis: stomatal zones with one to two rows of stomata, and a few to many rows of elongate-rectangular ripple-walled cells with strongly undulate walls; many two-celled linear hairs present; silicified cell zones: silicified cells dumb-bell-shaped, short or elongate with a long, thin, middle portion; suberized cells more or less square to elongate-rectangular, thin-walled with undulate walls; long ripple-walled cells narrower and with finer more compactly undulate walls than those of stomatal zones; short broad-based retrorse barbs present. Vascular bundle units: first order units usually 5 (occasionally 3), mostly larger than the bundles of lower rank, midrib flanked by 4–7 second or third order bundles, bundle units subcircular to ovate (second or third order) or more or less square to subcircular (first order) in outline. Stereome strands usually weakly developed in all bundles or relatively well developed ab- and adaxially opposite the first order bundles; present ab- and adaxially, often as a few fibres only, opposite most of the second and third order bundles. Motor cells in ob-triangular or oblong groups of thin-walled cells, 1–2 cells wide and usually occupying the whole thickness of the leaf.

CAPE.—Campbell: Brueckner 1028; Kenhardt: Codd 1194. Hay: Esterhuysen 2372. Swellendam: Esterhuysen 1819. Namaqualand: Schlechter 11226. BASUTOLAND.—Quthing: Dieterlen 1190.

ORANGE FREE STATE.—Boshof: Pole Evans H11603. Fauresmith: Smith 5571. TRANSVAAL.—Potchefstroom: Louw 1435; 1273. Pretoria: Schweickerdt 1326; Barberton: Thorncroft 43. Potgietersrust: Galpin 8892. Ermelo: Henrici 1473. SOUTH WEST AFRICA.—Warmbad: Oertendahl 118. Keetmanshoop: de Winter 3475. Gibeon: van Vuuren and Giess 1094. Luderitz: van Vuuren and Giess 802; 2340. Rehoboth: Strey 2102. Windhoek: de Winter and Giess 7143; 7125; 7131; 7112. Grootfontein: Kinges 2881. Kaokoveld: de Winter and Leistner 5324.

DISTRIBUTION.—(See Fig. 26.)

Examination of a large number of specimens has shown that the sheets designated by Schweickerdt as A. submucronata can be distinguished from A. curvata only by their generally more robust habit. Due to a lack of specimens from tropical Africa it was not possible to decide whether A. curvata should be regarded as synonomous with A. submucronata and, for this reason, A. curvata is retained as a distinct species. The key character used by Henrard and Schweickerdt, i.e. the acute, minutely awned lower glume of A. submucronata and the erose-bifid mucronate lower glume of A. curvata does not seem to hold for the range of specimens now available. A. curvata is also closely allied to A. adscensionis subsp. guineensis from which it can be distinguished by the smaller spikelets and more open inflorescence of the latter. This whole group (A. curvata, A. adscensionis and A. submucronata) should be re-examined, taking into consideration the entire distribution, as well as the more localized distribution of the various forms. In this connection the reader is referred to the discussion on the interrelationship of the South African species (pages 301-303). Anatomically the species of this group are indistinguishable except for slight variations in the width of the leaf-blade and, to some extent, the development of the stereome strands, characteristics of too little importance to make the anatomy of value in the delimitation of the various species.



FIG. 25.—A. curvata: abaxial epidermis of the leaf-blade (Theron 103).

Guenzel (1913, p. 18) described the leaf anatomy of Aristida adscensionis L. The specimens examined by him, however, came from South West Africa where this species sensu stricto does not occur. He probably described A. curvata since this species has in the past often been mis-identified as A. adscensionis. Guenzel's description and diagramatic drawing of the cross section of the leaf-blade agree closely with the present author's observations on A. curvata.

8. A. scabrivalvis Hack. in Bull. Herb. Boiss, 2, 6: 708 (1906)

Annual, erect or ascending, up to 85 cm high. Culms much branched, 3-4-noded, nodes glabrous; internodes glabrous. Leaf-sheaths lax, keeled, minutely scaberulous or smooth; auricles ciliolate or glabrous. Leaf-blades linear up to 30 cm long and 3.5 mm wide, glabrous on the lower surface, hirtellous on the upper. Panicle open
and divaricate up to 30 cm long or much smaller, ovate in outline. *Spikelets* purple or purplish brown. *Glumes* linear-lanceolate, strongly awned, subequal or unequal, hirtellous, or at least with a scabrid keel; lower up to 9 mm long including the awn, awns up to 2.5 mm long; upper strongly bifid, up to 9 mm long, awn up to 1.5 mm long. *Lemma* linear, as long as or shorter than the glumes, keeled, 5–8 mm long, coarsely scabrid in the upper part or at least on the keel; callus about 1.5 mm, rounded, bearded; awns scabrid about 14 mm long. *Caryopsis* linear, terete.



FIG. 26 .- Distribution of A. curvata.



FIG. 27.-A. scabrivalvis: cross section of the leaf-blade (de Winter 775).



FIG. 28.—A. scabrivalvis: abaxial epidermis of the leaf-blade.



FIG. 29.-Distribution of A. scabrivalvis; Ovar. scabrivalvis; Ovar. contracta; IA. dasydesmis.

ANATOMY as for A. curvata (Fig. 27, 28 and 159: 8)

Fig. 27 is not entirely typical: the two well developed marginal bundles usually alternate with a third order bundle and are not adjacent as in the figure.

A distinct species recognized by the very large inflorescence, awned usually hirtellous glumes, and scabrid lemma, which is subequal to or shorter than the glumes. Allied to *A. effusa* and *A. bipartita*. Differing from *A. effusa* in the awned glumes, and in the lemma which equals, or is shorter than the glumes; and from *A. bipartita* in the upper glume exceeding the lower in length. Two varieties can be recognized.

Panicle branches which arise from the main axis effuse, and bearing several secondary branchlets at least towards the base of the panicle, branchlets effuse or somewhat contracted var. scabrivalvis Panicle branches arising from the main axis contracted, somewhat spike-like and stiffly spreading

var. contracta

(a) var. scabrivalvis.

A. scabrivalvis Hack. in Bull. Herb. Boiss. 2, 6: 708 (1906).

CAPE.—Barkly West: Acocks 1809; Brueckner 1272; Kimberley: Leistner 2274. TRANSVAAL.—Bloemhof: Leistner 28. Vereeniging: Burtt-Davy 4850. Pretoria: Smith 6101. Waterberg: Codd 904. Potgietersrust: Galpin 427; 8891. Kruger National Park: van der Schijff 1683; 1720; de Winter 528.

NATAL.-Estcourt: Acocks 10130; Perry 148. Lower Umfolosi: Letley 22.

SOUTH WEST AFRICA.—Otavi: Dinter 5752. Grootfontein: de Winter and Giess 6794; de Winter 2929. Okavango: de Winter 4068.

DISTRIBUTION.—(See Fig. 29.)

(b) var. contracta de Winter in Kirkia 3: 132 (1963). Type: Transvaal, Soutpansberg, de Winter and Codd 321 (PRE, holo.!). TRANSVAAL.—Letaba: de Winter and Codd 690; 321. NATAL.—Weenen: Acocks 10530; Edwards 1237.

DISTRIBUTION.—(See Fig. 29.)

9. A. bipartita (Nees) Trin. & Rupr., Gram. Stip. 144 (1842) Chaetaria bipartita Nees, Fl. Afr. Austr. 187 (1841).

Perennial or weak perennial up to 65 cm high, with a short erect or oblique rhizome. Culms erect or ascending; nodes glabrous, internodes glabrous. Leaf-sheaths firm, glabrous or minutely puberulous between the nerves; auricles long bearded. Leaf-blades up to 20 cm long and up to 2 mm wide, rigid, smooth or scaberulous on the lower surface, scabrid on the upper. Panicle effuse, up to 30 cm long and nearly as wide but usually much smaller; brarches spreading, solitary, flexuous, naked for most of the length, and bearing clusters of 1-4 spikelets at the apex. Spikelets pallid or purplish. Glumes unequal, the lower exceeding the upper in length, 1-nerved, mucronate or shortly awned; lower smooth or scabrous on the keel upwards, up to 11 mm long, upper smooth up to 9 mm long. Lemma linear, included in the glumes, about 8 mm long, smooth, often mottled with purple; callus obtusely rounded, bearded; awns subequal, central slightly longer scabrous, 7-13 mm long. Caryopsis linear, terete.

ANATOMY (Fig. 30 and 159: 9)

Leaf-blade flat or very widely V-shaped in transverse section; abaxial surface flat with very few hairs; adaxial surface grooved between the protruding bundle units which are furnished with few to many short bristly unicellular hairs. Abaxial epidermis: stomatal zones with usually one row of stomata; long ripple-walled cells elongate-rectangular with strongly undulate walls; two-celled linear hairs present; silicified cell zones: silicified cells dumb-bell-shaped; suberized cells usually shorter than the silicified cells, thin-walled, when very short often irregularly dumb-bell-shaped, when longer with undulate walls; long ripple-walled cells with finer undulations than those of the stomatal zones; short retrorse barbs flanking the silicified zones usually accompanied by a short element (suberized cell). Vascular bundle units: first order units 5, only slightly larger than the third order units; midrib smaller than the other first order units; broadly ovate in outline in contrast with the others which are more or less square in outline; third order bundle units ovate to subcircular. Stereome strands present ab- and adaxially to all bundles or absent adaxially to some of the third order bundles, usually present, even though small, opposite the motor cell units; strands often fused together abaxially opposite the first order bundles and adjacent motor cell groups. Motor cells in groups, one to two cells wide and occupying the whole thickness of the leaf. See also Theron (1936, p. 25).

mmmmmm ST 2000 LC mannannannan nnnnn Lanna with. SC an mannanna mmmm 1.0 CC DO. home min 0.1 mm

FIG. 30.—A. bipartita: abaxial epidermis of the leaf-blade (Acocks 9563).

DISTRIBUTION.—(See Fig. 24.)

CAPE — Komga: Flanagan 1175. Queenstown: Galpin 2578. Stutterheim: Acocks 9563. King William's Town: Story 917.

BASUTOLAND.—Mohales Hoek: Dieterlen 1208.

ORANGE FREE STATE.—Heilbron: Brandmuller 108. Senekal: Goossens 930. Bethlehem: Goossens 1123.

TRANSVAAL.—Lichtenburg: Kinges 1631. Standerton: Marais 10. Pretoria: Mogg 13,727. Waterberg: de Winter 736. Rustenburg: Acocks 8840. Potgietersrust: de Winter 2275.

NATAL.-Hlabisa: Ward 2319. Estcourt: Acocks 9869. Dundee: Codd 200.



FIG. 31.—A. canescens subsp. canescens: cross section of the leaf-blade (de Winter 795A).



FIG. 32.-A. canescens subsp. canescens : abaxial epidermis of the leaf-blade.



FIG. 33.—Distribution of A. canescens: Osubsp. canescens; Osubsp. ramosa; A. engleri: var. engleri; var. ramossissima.

A species recognized by its very lax spreading inflorescence with long flexuous, bare branches bearing a few spikelets at the ends, and by the inverse position of the glumes, i.e. the lower exceeding the upper in length.

Though related to annual species such as A. effusa and A. scabrivalvis, A. bipartita is a perennial with a stronger development of the stereome strands of the leaf-blade. Anatomically it can, therefore, be distinguished from its close relatives.

10. A. canescens Henrard, Crit. Rev. Aristida, Suppl. 708 (1933)

Perennial up to 1 m high, densely caespitose, erect. Culms erect, simple or branched; internodes terete or slightly compressed, glabrous; nodes glabrous. Leaf-sheaths tight, glabrous or scaberulous; auricles bearded or shortly pubescent. Leaf-blades linear, hard and coarse, expanded near the base and curling when old, margins thickened, glabrous or scaberulous on the lower, and scabrid on the upper surface. Panicle erect, lax or contracted, but much interrupted, up to 20 cm long. Spikelets pallid, yellowish green or tinged with purple. Glumes unequal, 1-nerved, lanceolate, emarginate or subtruncate and shortly muconate, only the lower scaberulous on the keel and occasionally on the flanks, $5 \cdot 5-8$ mm long; upper 8-11 mm long. Lemma 7-11 mm long, smooth or scaberulous on the keel, without a column; callus obtuse, bearded; awns scabrid, subequal, central 9-15 cm long, lateral 7-13 mm long. Caryopsis linear, terete; embryo $\frac{1}{2}$ the length of the grain.

ANATOMY (Fig. 31, 32 and 159: 10)

Leaf-blade flat in transverse section with the midrib small (equal to third order bundles) and the lateral first order bundle units enlarged, together forming a strong marginal rib; abaxial surface undulate with very few hairs visible in cross section; adaxial surface shallowly grooved between the slightly protruding third order bundles and with a deep narrow groove between the marginal first order bundles; covered with short bristly hairs opposite the bundles; margins obtuse. Abaxial epidermis: stomatal zones with one to two rows of stomata; short elements few; ripple-walled cells elongate-rectangular or with the end walls oblique, walls very strongly undulate and rather thick; linear bicellular hairs numerous; silicified cell zones: silicified cells dumb-bell-shaped, in the wider zones larger and with elongate, much constricted, central portion; suberized cells rectangular, undulate, thin-walled; few broad-based, unicellular retrorse hairs present, fairly long and thin, or short and barb-like. Vascular bundle units: first order units 5, midrib equal in size to the third order bundles but marginal first order units subcircular or ovate. Stereome strands: most strongly developed abaxially opposite the first order units of the marginal ribs, less strongly so adaxially; the remaining bundle units, including the midrib, with smaller strands present both ab- and adaxially; motor cells supported by abaxial groups of fibres. Motor cells in groups 1–2 rows wide, occupying almost the whole thickness of the leaf, stereome strands present abaxially.

Culms mostly unbranched and erect, often robust.....subsp. canescens Culms geniculate and often branched from the nodes.....subsp. ramosa

(a) subsp. canescens.

A. canescens Henrard, Crit. Rev. Aristida Suppl. 708 (1933).

Erect perennial forming usually dense tufts; culms unbranched.

CAPE.—Taungs: Henrici 39. Vryburg: Theiler 226. Barkly West: Brueckner 837. NATAL.—Weenen: Edwards 1238. Estcourt: Acocks 11424. ORANGE FREE STATE.—Kroonstad: Pont 149. Heilbron: Goossens 425. TRANSVAAL.—Bloemhof: Burtt-Davy 13057. Potchefstroom: Story 755. Bethal: Kinges 1379. Pretoria: de Winter 795A; 7561. Waterberg: Straker 11. Potgietersrust: Galpin 426.

(b) subsp. ramosa de Winter in Kirkia 3: 132 (1963). Type: Cape, Cathcart, Kei Valley at Kei View, Acocks 9691 (PRE, holo!).

Perennial, usually geniculate and branched from the nodes, rarely some culms unbranched.

CAPE.—King William's Town: Sim 2835. Cradock: Brynard 181. Bedford: Story 4554; Acocks 12804.

DISTRIBUTION.—(See Fig. 33.)

The subsp. *ramosa* has a distribution quite distinct from that of subsp. *canescens*. It has so far been recorded only from the central areas of the eastern Cape Province.



FIG. 34.-A. aequiglumis: cross section of the leaf-blade (de Winter 7515).



FIG. 35.— 1. aequiglumis: abaxial epidermis of the leaf-blade.

A distinct species occasionally confused with *A. junciformis* but distinguished from the latter by the terete culms and the coarser spikelets, the lack of a column and the less tough basal parts with thinner fibrous roots. Anatomically readily distinguished from *A. junciformis* by the much enlarged marginal bundle units which in size well exceed the units adjacent to the midrib. In *A. junciformis*, however, all the bundles when viewed in cross section approximately reach the same height, even though the third order bundle units are narrower. Though superficially similar, these two species are not closely related.



FIG. 36.—Distribution of A. aequiglumis; A. vestita.

11. A. aequiglumis Hack. in Bull. Herb. Boiss. 3: 381 (1895)

Perennial, densely caespitose usually about 40 cm high. Culms slender simple or rarely branched from the upper nodes; nodes glabrous; internodes glabrous. Leaf-sheaths glabrous, persistent. Leaf-blades erect, setaceous, convolute, up to 15 cm long. Panicle linear-oblong, contracted or lax and open, about 10 cm long. Glumes 1-nerved with a prominent glabrous or scabrid midrib, scabrid to shortly hairy on the sides, apices usually somewhat recurved; lower 7–11 mm long; upper 7–11.5 mm long. Lemma including the column and callus 8–16 mm long, minutely scaberulous upwards; column twisted 2–8 mm long; awns somewhat unequal, central 15–30 mm and lateral 14–26 mm long; callus bearded obtuse to sub-obtuse. Caryopsis linear, terete.

ANATOMY (Fig. 34, 35 and 159: 11)

Leaf-blade more or less flat to somewhat curved in transverse section; bundle units except for the marginal ones only slightly protruding adaxially, abaxial surface very slightly undulate; marginal units very strongly projecting adaxially and forming distinct marginal ribs; long unicellular hairs present opposite the adaxial stereome strands; midrib smaller than the marginal bundles and not forming a keel; margins obtuse or subacute. Abaxial epidermis: stomatal zones with one to three rows of stomata, and six to twelve rows of more or less rectangular long ripple-walled cells with a few short elements scattered amongst them; bicellular hairs with rather short and broad basal cells present in, or flanking, this zone; silicified cell zones consisting of one to seven files of silicified cells, alternating with one or two rows of long ripple-walled elements; silicified cells dumb-bell-shaped, those opposite the first order bundles very large; suberized cells thin-walled with undulate walls, slightly shorter to much shorter than the silicified cells, and usually alternating with the latter; unicellular hairs often slender and sharp-pointed and usually found flanking or present in the silicified cell zones, occasionally absent. Vascular bundle units: first order units 3, mid-vein small, the marginal units on each side formed by a very large first order unit combined with a third order unit; mid-vein flanked by 3 to 5 small second order bundles. Stereome strands consisting of small thick-walled fibres; well developed both ad- and abaxially opposite the first order bundles, but less so in the midrib than in the marginal bundles; absent abaxially opposite the second order bundles, but present opposite the motor cell groups; small groups present adaxially opposite the second order bundles. Motor cells in Y-shaped groups, occupying the whole width of the leaf and alternating with all bundles.

TRANSVAAL.—Potchefstroom: J. F. v. P. 616. Krugersdorp: Acocks 18718. Johannesburg: Leendertz 6175. Pretoria: de Winter 7515; Schweickerdt 1343; 1328 and 1753. Rustenburg: Codd 1047. Waterbeig: Galpin M 713. Middelburg: Schlechter 4129.

DISTRIBUTION.—(See Fig. 36.)

A reasonably well defined species usually found growing in rocky situations such as on hill slopes. *A. aequiglumis* greatly resembles *A. transvaalensis* and often occurs in association with it. As pointed out by Schweickerdt it can, however, be distinguished by the less contracted inflorescence and larger spikelets. Even though *A. aequiglumis* is occasionally somewhat branched the habit is a useful characteristic to distinguish it from the copiously branched *A. transvaalensis* which, moreover, has the leaves spreading at more or less right angles to the culms, while those of *A. aequiglumis* are erect resulting in a more "bunched" appearance.

Anatomically the two species are very similar; the marginal bundle units being very strongly developed and exceeding the others in size. The marginal units project towards the midrib and in *A. aequiglumis* are more gibbous (in cross-section) than in *A. transvaalensis*.



FIG. 37.—A. transvaalensis: cross section of the leaf-blade (de Winter 7513).

12. A. transvaalensis Henrard, Crit. Rev. Aristida Suppl. 742 (1933)

Densely caespitose *perennial*, up to 70 cm high. *Culms* erect, branched from most of the upper nodes; nodes and internodes glabrous. *Leaf-sheaths* usually lax and slipping from the culms, or culm-sheaths tights. *Leaf-blades* convolute, setaceous, those on the culms spreading, up to 15 cm long, branches solitary, congested. *Glumes*

lanceolate, unequal, 1-nerved, acute, glabrous or scabrid on the keels, lower 5–9 mm long, shortly awned; upper $6 \cdot 5$ –10 mm long, minutely awned from a subtruncate apex. *Lemma* smooth, minutely granular upwards, with the column up to $11 \cdot 5$ mm long; column well developed or almost absent, 1–6 mm long, scabrid, twisted; awns unequal, the central divergent and 6–13 mm long; lateral very short (almost absent) to 8 mm long. *Caryopsis* linear, terete.



FIG. 38.-A. transvaalensis: abaxial epidermis of the leaf-blade.

ANATOMY: as for *A. aequiglumis* except for the marginal units which do not project inwards as strongly as in *A. aequiglumis* [i.e. they are less gibbous in cross section (Fig. 37, 38 and 159: 12, pp. 263 and 395].

TRANSVAAL.—Johannesburg: *Hitchcock* 24116. Pretoria: *Moss* 14259 (isotype); *de Winter* 7513; *Schweickerdt* 1327; 1331 and 1332. Letaba: *Scheepers* 933. Nelspruit: *v.d. Schijff* 3073. Barberton: *Thorncroft* 21. SWAZILAND.—*Meeuse* 10135.

NATAL.-New Hanover: Acocks 13774. Kranskop: Fisher & Schweickerdt 85.

DISTRIBUTION.—(See Fig. 17.)



FIG. 39.—A. monticola: cross section of the leaf-blade (Mogg H. 20634).

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Related to A. aequiglumis and A. canescens.

A species found on rocky outcrops and hillsides, usually mainly on dry northern slopes.

As pointed out by Schweickerdt the lateral awns of this species are often weakly developed so that some spikelets may appear to have a single awn. The column also is very variable, even in spikelets of the same individual.





13. A. monticola Henrard, Crit. Rev. Aristida 2: 355 (1927)

Perennial usually rather sprawling and forming large masses, often rooting at the lower nodes up to 70 cm high. Culms erect, geniculate and usually branched at the nodes; nodes glabrous; internodes glabrous, thin, wiry. Leaf-sheaths tight, shorter than the internodes; auricles long-bearded. Leaf-blades linear, expanded or convolute upwards, up to 12 cm long and 2 mm wide, glabrous on the lower, and scaberulous on the upper, surface with occasionally a few long hairs, margins thickened. Panicle erect, rather open, lanceolate, up to 14 cm long. Spikelets often purplish brown. Glumes linear-lanceolate, 1-nerved, lower 6-8.5 mm long, shortly awned, glabrous with a scabrid keel; upper glabrous, 5-6 mm long, bidentate with a short mucro. Lemma linear, smooth, 6-6.5 mm long and produced into a short twisted column; callus obtuse, bearded; awns unequal, central up to 18 mm, lateral up to 13 mm long. Caryopsis not seen.

ANATOMY: as for *A. aequiglumis* but usually 4-5 third order bundle units flanking the midrib and with the marginal units somewhat less strongly developed (Fig. 39, 40 and 159: 13).

NATAL.—Estcourt: Acocks 11431. Bergville: Edwards 570 and 642; Killick 1258; 1382; 1951; 1915; 1000 and 1056; Meebold s.n. (NH 15728); Mogg s.n. (H. 20634) (isopleth). Weenen: Pillans 15487.

DISTRIBUTION.—(See Fig. 73.)

Related to *A. aequiglumis* and *A. transvaalensis* but distinguished from both these species by the creeping rhizome. The presence of a well developed rhizome in *Aristida* is very rare. A species of local occurrence in the Drakensberg in the Bergville and Estcourt districts of Natal and remarkable for its preference for moist situations such as stream-banks and seepage areas on steep slopes.

In anatomical characteristics very close to *A. transvaalensis* and *A. aequiglumis*, this character together with many organographic similarities indicating a close relationship.

Theron (1936; p. 21) investigated this species anatomically but gives no drawing. His description agrees in main details with the author's observations.



FIG. 41.—A. junciformis subsp. junciformis: cross section of the leaf-blade (Baker 19).



FIG. 42.—A. junciformis subsp. junciformis: abaxial epidermis of the leaf-blade.

14. A. junciformis Trin. & Rupr., Gram. Stip. 143 (1842)

Perennial usually densely caespitose up to 60 cm high, with a fascicled base and very thick almost spongy roots. Culms erect, simple or sparingly branched, wiry, 3-4-

noded; nodes glabrous, internodes glabrous; compressed below the nodes. *Leaf-sheaths* glabrous or sparsely woolly. *Leaf-blades* narrow, gradually passing into the sheaths, sub-setaceous, folded, up to 30 cm long and 1 mm wide. *Panicle* narrow, contracted or rather lax, up to 20 cm long and 1-8 cm wide, erect or somewhat nodding; branches with spikelets congested towards the ends. *Glumes* unequal, linear-lanceolate; glabrous or minutely pubescent, subacute, or acute and awned; lower 4-9 mm long: upper 8-12 mm long. *Lemma* up to 9 cm including the column, smooth or scaberulous upwards; column well developed or practically absent; central awn 12-35 mm long; lateral awns 9-28 mm long; callus bearded, obtuse. *Caryopsis* linear, terete.



FIG. 43 .- Distribution of OA. Junciformia subsp. junciformis; #A. parvula.

ANATOMY (Fig. 41, 42 and 159: 14).

Leaf-blade V-shaped in transverse section, keel not protruding; adaxial surface with the bundle units projecting strongly, furnished with short bristly hairs adjacent to the stereome strands; abaxial surface, smooth and practically hairless; margins subacute to obtuse. Abaxial epidermis: stomatal zones of 6-9 rows of rectangular narrowly-oblong ripple-walled cells alternating with transversely narrowly-oblong short elements and with one to four rows of stomata; silicified cell zones with few to many rows of dumb-bell-shaped silicified cells alternating with short, thin-walled, transversely oblong to oblong suberized cells with undulate walls; unicellular hairs not observed; bi-cellular hairs present in, or flanking the stomatal zones, or occasionally even in the silicified cell zones. Vascular bundle units more or less oblong in outline: first order units 3, midrib flanked by three third order bundles, all units approximately equal in height, gradually diminishing in size towards the midrib which usually is slightly smaller than the other bundles, and ovate to circular in outline. Stereome strands present abaxially opposite the motor cell groups as well as the bundles except for the two third order bundles on either side of the midrib; the strands of the motor cells flanking the third order bundle units inside the marginal first order bundle, usually fused to form a single strand subtending the two motor cell groups as well as the bundle; the adaxial strand fairly strongly developed opposite the bundles, or consisting only of small groups of fibres. Triangular or oblong *motor cell* groups present and alternating with all the bundles; the groups on either side of the third bundle from the midrib at times fused laterally to form a compound unit enclosing the bundle abaxially.

Culms 2-4-noded, forming strictly erect tufts, often quite tall and not very densely leafy at the base; panicles usually rather robust.....subsp. junciformis

Culms usually 1-noded rarely some 2-noded forming small leafy tufts; panicles rather small subsp. galpinii

(a) subsp. junciformis.

A. junciformis Trin. & Rupr., Gram. Stip. 143 (1842). A. welwitschii Rendle, Cat. Pl. Welw. 2, 1: 202 (1899). A. angustata Stapf, in F.C. 7: 556 (1899).

Culms two or more-noded; panicles usually contracted; peduncles of the spikelets short; often tall, strictly erect tufts, with fine leaves and short branched rhizomes.

CAPE.—George: Baker 19. Somerset East: Acocks 15742. Ceres: Adamson D 25. Somerset West: van Rensburg 192. Fort Beaufort: Killick 864.

ORANGE FREE STATE.—Senekal: Goossens 889. Bethlehem: Potts 4517. Kroonstad: Goossens 1179.

NATAL.—Underberg: McClean 607. Maritzburg: McClean 198. Durban: Schweickerdt 1351. Melmoth: Tinley 14. Hlabisa: Michelmore 15. TRANSVAAL.—Ermelo: Burtt Davy 9320. Heidelberg: Burtt Davy 9185. Pretoria:

TRANSVAAL.—Ermelo: Burtt Davy 9320. Heidelberg: Burtt Davy 9185. Pretoria: Pole Evans H 17587. Waterberg: de Winter 735. Pietersburg: v.d. Schijff 5396; Strey & Schlieben 8524. Soutpansberg: Codd 6565. SOUTH WEST AFRICA.—Okavango: de Winter 5043.

DISTRIBUTION.—(See Fig. 43.)



FIG. 44.—A. junciformis subsp. galpinii: cross section of the leaf-blade (Galpin 6900).



FIG. 45.—A. junciformis subsp. galpinii: abaxial epidermis of the leaf-blade.



FIG. 46.—A. recta: cross section of the leaf-blade (Schweickerdt 1677).

A variable and very widely distributed subspecies. An aggressive plant in areas where the rainfall is high and selective overgrazing takes place, such as in the sour mountain grasslands in parts of Natal. In areas with a lower rainfall it occurs mainly in depressions where water collects during the rainy season. Its very tough roots, covered by a spongy white outer layer, makes it very difficult to remove from the soil. The bases of the erect, hard tufts are branched and often produce short rhizomes.

(b) subsp. galpinii (Stapf) de Winter in Kirkia 3: 132 (1963).

A. galpinii Stapf in Kew Bull. 1910: 130 (1910).

Culms one-noded or rarely 2-noded; panicles contracted but laxly branched; peduncles often longer than the spikelets. Low very densely leafy tufts with a distinctly rhizomatous base.

CAPE.—Port Elizabeth: Liebenberg 5388. King William's Town: Dyer 257. Keiskamahoek: Story 3429; 3789; 3287. Mt. Currie: Acocks 13283. Barkly East: Acocks 20148. Cathcart: Galpin 2417; Liebenberg 5367. Kokstad: Mogg 5013. BASUTOLAND.—Pole Evans 14; 19; 66; 2; 98; Guillarmod 695; Staples 112. NATAL.—Bergville: Killick 1246; 1247; 1235; Bayer & McClean 24; Nkand¹a: Fisher and Schweickerdt 122.

This subspecies is confined to high altitudes in the mountainous areas of the Cape, Basutoland and Natal. No specimens have been collected below 3,000 feet and in Basutoland it occurs up to 8,500 feet and probably at even higher altitudes.

The two subsp. of *A. junciformis* can be distinguished by the habit as given in the key. Anatomically they are very similar and only distinguishable by the more robust development of the leaf-blades of subsp. *junciformis* (cf. Fig. 41, 44 and 42, 45). Anatomically *A. junciformis* is similar only to *A. recta* (see p. 273) and is easily distinguished from all the other species examined as set out in the key on p. 241.



FIG. 47.-A. recta: abaxial epidermis of the leaf-blade.

15. A. recta Franch. in Bull. Soc. d'Autun 8: 365 (1896) A. atroviolacea Hack. apud Schinz in Bull. Herb. Boiss 2, 6: 707 (1906). A. gossweileri Pilger in Engl. Bot. Jahrb. 39: 598 (1907). A. hockii De Wild. in Bull. Jard. Bot. Brux. 6: 39 (1919).

Perennial, caespitose, 10–30 cm high with the persistent basal leaf-sheaths breaking up into fibres, forming a dense tuft at the base of the culms. *Culms* erect, 1–(2)-noded. *Leaf-sheaths* striate glabrous; auricles bearded. *Leaf-blades* mostly basal, setaceous,

folded, up to 20 cm long and 1 mm wide. *Panicle* ovate-lanceolate in outline, up to 8 cm long and 4 cm wide, lax but not much branched or diffuse. *Spikelets* contracted towards the ends of the branches, brownish-purple to deep purple. *Glumes* subequal to unequal, 1-nerved, glabrous or scabrid on the keels; lower lanceolate shortly awned, 3-keeled, $2 \cdot 5-6$ mm long; upper linear-lanceolate, shortly awned $5-7 \cdot 5$ mm long. *Lemma* 4-5 mm long narrowed into a very short column, scaberulous below the awns; awns subequal scabrid, usually loosely spirally contorted at the base; callus 0.25 mm long, rounded obtuse, bearded. *Caryopsis* not seen.



FIG. 48.—Distribution of A. recta; A. spectabilis.

ANATOMY (Fig. 46, 47 and 159: 15)

Leaf-blade V-shaped in transverse section, keel not protruding; adaxial surface with the bundles strongly protruding, furnished with very short almost papillose hairs opposite the stereome strands; abaxial surface smooth and practically glabrous; margins subacute. Abaxial epidermis: stomatal zones of 4–9 rows of rectangular, narrowly-oblong ripple-walled cells alternating with transversely narrowly-oblong short elements and with 1–2 (rarely 3–4) rows of stomata; silicified cell zones with 1–3 files of dumb-bell-shaped silicified cells alternating with short thin-walled rectangular or very broadly oblong suberized cells with undulate walls; unicellular hairs very rare, short and acute; bicellular hairs short and thin-walled present in the transitional area between the zones. Vascular bundle units more or less oblong in outline; first order units 3; midrib flanked by three third order units; all units more or less equal in height, gradually diminishing in size towards the midrib which usually is somewhat smaller than the other units. Stereome strands present abaxially opposite the motor cell groups as well as the bundle units except for the pairs of third order bundles flanking the midrib; the strands subtending the motor cell groups flanking the bundle as well as the two motor cell groups; adaxially replaced by a single row of large parenchyma cells opposite the bundles, except in the margin where a small group of fibres is present. Motor cell groups alternating with all bundles.



FIG. 49.-A. sciurus: cross section of the leaf-blade (Pentz & Acocks 10314).



FIG. 50.—A. sciurus: abaxial epidermis of the leaf-blade.

TRANSVAAL.—Bronkhorstspruit: Schweickerdt 1677; 1656. Ermelo: Norval 24. Carolina: Codd 577. Pilgrim's Rest: de Winter and Codd 222. Soutpansberg: Codd 3047.

SWAZILAND.—Mbabane: Dlamini s.n.

DISTRIBUTION.—(See Fig. 48.)

A distinct species recognized by its small stature, dense fibrous base, and small brown or purple spikelets with usually laxly spirally contorted awns. The probably distantly related *A. junciformis* is a more robust plant which tends to develop short rhizomes and lacks the fibrous basal leaf-sheaths typical of *A. recta*. *A. recta* is found mainly in seepage areas in sour mountain grassland and, together with *A. monticola* and *A. junciformis*, is exceptional for the genus in preferring moist habitats.

It is widely distributed in tropical Africa from the Rhodesias to Ghana and East Africa. The specimens from tropical Africa agree very well with the South African material.

Anatomically similar to *A. junciformis* but differing from this species in the very large epidermal cells which equal or even exceed the bundle sheath cells in size.

16. A. sciurus Stapf in Fl. Cap. 7: 557 (1899)

Perennial, very robust and erect, up to 140 cm high. Culms arising from a short rhizome, 4-5-noded, simple; internodes adpressedly woolly just below the nodes, glabrescent, terete; nodes glabrous inconspicuous. Leaf-sheaths crowded near the base, glabrous or more or less fugaciously woolly; ligule a fringe of short hairs hidden by a tuft of wool at the mouth of the sheath which may disappear with age. Leaf-blades linear, folded, up to 60 cm long or rarely longer, up to 5 mm wide at the base. Panicle dense, contracted to almost spike-like, up to 45 cm long. Spikelets pallid or tinged with purple. Glumes 1-nerved, very unequal, thin; lower lanceolate, acute, minutely scaberulous upwards and on the keels, 5-7 mm long; upper linear-oblong, 11-13 mm long mucronate. Lemma glabrous, up to 12 mm long; column absent; awns subequal central up to 23 mm, lateral up to 20 mm long; callus 1-1.5 mm long, rounded-obtuse, bearded. Caryopsis linear, terete.

ANATOMY (Fig. 49, 50 and 159: 16)

Leaf-blade V-shaped in transverse section; abaxial surface smooth, glabrous; adaxial surface with deep grooves between the strongly projecting first order bundle units, covered with short papilla-like unicellular hairs opposite the bundles; margins subacute to obtuse. Abaxial epidermis consisting almost exclusively of long elongate-rectangular cells with deeply and compactly undulate walls, alternating with transversely elongate short elements (suberized cells); stomata very few or absent. Silicified zones few and usually reduced to 1–2 files of silicified cells which are solitary, or accompanied by suberized cells alternating with short ripple-walled cells; silicified cells variable in shape, circular, transversely-oblong, kidney-shaped or dumb-bell-shaped; no hairs observed in the abaxial epidermis. Vascular bundle units: first order units obvate in outline; the ovate third order units being only one third to half of the height and much narrower than, and completely overtopped by the first order units; midrib smaller than the other first order bundles, not projecting abaxially. Stereome strands abaxially fused to form a practically continuous hypodermal band $\pm 1-5$ cell-layers thick, multi-layered opposite the bundles and forming rather narrow projections which enter the bundles, consisting of typical fibres (very strongly thickened walls); adaxial stereome consisting of large cells with large lumen and relatively thin though distinctly lignified walls, large anchor-shaped strands opposite the first order bundles. Motor cells in many-celled triangular groups alternating with all the bundles.

TRANSVAAL.—Potgietersrust: de Winter 2321. Carolina: Mundy H. 4292 A.; Burtt-Davy 1418; Pole Evans 1967. Belfast: Schweickerdt 1914; Pole Evans 3688. Lydenburg: Burtt-Davy 1449; Story 3897. SWAZILAND.—Mbabane: Compton 30594; 25712; Codd and Muller 330. NATAL.—Estcourt: Edwards 2049; 2051. Ngutu: West 755.

DISTRIBUTION.—(See Fig. 20.)

A robust *perennial* vegetatively strongly resembling species belonging to the section *Arthratherum* in stature and in the woolly indumentum of the internodes and mouth of the sheaths. The spikelets are, however, fairly typical of the section *Aristida*. The anatomy resembles that of *A. diffusa* and *A. dasydesmis*. The leaf-blade is V-shaped

in transverse section and the first order bundle units protrude very strongly, characteristics not found in any other species of the section *Aristida*. This species may represent a link between the sections *Aristida* and *Arthratherum* and has no obvious close relatives.



FIG. 52.-A. dasydesmis: abaxial epidermis of the leaf-blade.

A species found mainly in mountain sourveld in the eastern Transvaal, Swaziland and Natal. A specimen was also collected in the mountains near Potgietersrust in the Transvaal bushveld.

17. A. dasydesmis Mez in Fedde Rep. 17: 148 (1921) A. vestita var. parviflora Trin. & Rupr., Gram. Stip. 158 (1842)

Perennial, much branched, caespitose up to 70 cm high. *Culms* many-noded, fascicled from the lower nodes; nodes and internodes glabrous. *Leaf-sheaths* glabrous, lax; auricles pubescent. *Leaf-blades* stiffly erect, semiterete, smooth sub-pungent, about 1 mm wide. *Panicle* somewhat contracted in young specimens but lax and effusely branched up to 10 cm long and 6 cm wide. *Glumes* unequal, glabrous 1-nerved, lower about 5 mm long; upper up to 8 mm long. *Lemma* glabrous, including the callus up to 8 mm long; column of awns twisted, about 5 mm long; awns slightly unequal; central up to 25 mm, the lateral up to 20 mm long. *Caryopsis* not seen.

ANATOMY (Fig. 51, 52 and 159: 17)

Leaf-balde horseshoe-shaped in transverse section; abaxial surface smooth and practically glabrous; adaxial surface deeply grooved due to the strongly projecting bundle units, with numerous hairs opposite the bundles. Abaxial epidermis: stomatal zones with one row of stomata, ripple-walled cells elongate-rectangular, with thickened, strongly and compactly undulate walls, usually with a few solitary short elements scattered amongst them; silicified cell zones with the silicified cells subcircular and usually accompanied by a very short, more or less square to elongate-rectangular, thin-walled suberized cell with undulate walls, ripple-walled cells narrower, and with thinner more finely undulate walls. Vascular bundle units: first order units 5, midrib slightly smaller than the adjacent first order bundle units, more or less ovate in shape, the other units oblong with rounded adaxial surfaces; third order units ovate, half or less than half the length of those of first order. Stereome strands very well developed abaxially opposite all the bundles, as well as the motor cell groups; adaxially very strongly developed opposite the first order bundles and less so opposite the second order bundles, consisting of small very thick-walled fibres, or of rather large cells with large lumen, or of a mixture of both types. Motor cells in oblong or obtusely triangular groups, occupying the whole thickness of the leaf.

CAPE.—Namaqualand: Schlechter 11228 (lectotype!); Pearson 2952 and 3487; Drege s.n. (Zilverfontein); Acocks 19518. Vanrhynsdorp: Stokoe 8399.

DISTRIBUTION.—(See Fig. 29.)

A species closely related to A. vestita and A. diffusa but with smaller spikelets and branched fascicled culms, an obtuse truncate or emarginate not distinctly bifid callus, and wiry, erect and sub-terete leaf-blades. It may have arisen as an adaptation of a form of A. vestita to extremely arid conditions. Its distribution is restricted to the desert areas of the north western Cape. Anatomically similar to A. diffusa var. diffusa but the leaf-blade sub-terete. Also similar to A. sciurus in leaf anatomy (cf. Fig. 159: 16 and 17) the latter species, however, always lacks an articulation in the lemma and has a subacute or obtuse callus, while the column is absent. Whereas in some specimens of A. dasydesmis the articulation of the lemma is very inconspicuous, it is clearly visible in others. Theron (1936; p. 23) investigated the leaf anatomy of one specimen of this species, namely Schlechter 11228. His description agrees fairly well with the one given above but no drawing is available for comparison.

18. A. diffusa Trin. in Mem. Acad. Imp. Sc. Petrop. 6, 1: 86 (1830)

Perennial, densely caespitose, up to 75 cm high. *Culms* simple or rarely branched, erect, often wiry, smooth, one to several-noded, internodes terete, glabrous; nodes glabrous. *Leaf-sheaths* glabrous or lower ones covered with a fugacious wool; auricles pubescent or glabrous. *Leaf-blades* convolute, rather robust to setaceous up to 30 cm, rarely longer. *Panicle* up to 30 cm, rarely longer, very effuse and open, or somewhat dense but much branched. *Spikelets* yellow-brown to pallid, nodding. *Glumes* unequal, glabrous; lower up to 4–10 mm long, obtuse; upper 11–18 mm long; somewhat involute and curved. *Lemma* including the callus 10–14 mm long, almost smooth to

scaberulous upwards; column from almost absent to 6 mm long; awns subequal to unequal, central up to 35 mm long but usually shorter; callus bifid, densely bearded. *Caryopsis* linear, terete.



FIG. 53.—A. diffusa var. diffusa: cross section of the leaf-blade (Schlechter 9138).



FIG. 54.--A. diffusa var. diffusa: abaxial epidermis of the leaf.

ANATOMY (Fig. 53, 54 and 159: 18)

Leaf-blade somewhat crescent-shaped in transverse section; abaxial surface usually quite flat or only slightly undulate, midrib not protruding, and leaf without a keel; adaxial surface deeply grooved between the very strongly protruding first order bundle units, usually densely covered with hairs opposite the bundles. Abaxial epidermis: stomatal zones with one row of stomata and a few rows of long ripple-walled cells, elongate-rectangular in shape and with finely and compactly undulate walls (in var. diffusa stomata sometimes absent and abaxial epidermis consisting of a series o? silicified zones); silicified zones: silicified cells small, dumb-bell-shaped, shorter than or exceeding the stomata in length (in var. diffusa some cells circular, each accompanied by a kidney-shaped or rectangular suberized cell), long ripple-walled cells with compactly and finely undulate walls. Stereome strands strongly developed adaxially opposite the first order bundle units; abaxially also present opposite, and in contact with the second order bundles as well as the motor cell groups, or forming a continuous band below the epidermis; adaxially well developed opposite the first order bundles and in the var. diffusa also in small groups laterally situated on the flanks of these units, present also opposite the second order bundles. Motor cells in triangular to broadly oblong groups occupying most of the leaf thickness.

Culms 1–2-noded; lemma usually about 12–14 mm long; southern Cape.....var. diffusa Culms several-noded, very rarely 2-noded; lemma usually 12 mm or less; widespread in the summer rainfall areas.....var. burkei

(a) var. diffusa.

A. hystrix sensu Thunb., Prod. 19 (1794) non L.f. (1781). A. diffusa Trin. in Mem. Acad. Imp. Petrop. 6, 1: 86 (1830). A. vestita Thunb. var. brevistipitata Trin. & Rupr., Gram. Stip. 158 (1842). A. vestita Thunb. var. densa Trin. & Rupr., Gram. Stip. 158 (1842). A. vestita Thunb. var. pseudo-hystrix Trin. & Rupr., Gram. Stip. 158 (1842). A. vestita Thunb. var. pseudo-hystrix Trin. & Rupr., Gram. Stip. 158 (1842). A. vestita Thunb. var. schraderiana Trin. & Rupr., Gram. Stip. 158 (1842). A. vestita Thunb. var. schraderiana Trin. & Rupr., Gram. Stip. 158 (1842). A. vestita Thunb. var. diffusa (Trin.) Walp., Ann. Bot. 3: 747 (1852). A. pseudo-hystrix (Trin. & Rupr.) Steud., Syn. Pl. Glum, 1: 142 (1854). A. diffusa Trin. var. brevistipitata (Trin. & Rupr.) Henrard, Crit. Rev. Aristida 3: 665 (1928). A. diffusa Trin. var. densa (Trin. & Rupr.) Henrard, Crit. Rev. Aristida 3: 665 (1928). A. diffusa Trin. var. eckloniana (Tiin. & Rupr.) Henrard, Crit. Rev. Aristida 3: 666 (1928). A. diffusa Trin. var. schraderiana (Trin. & Rupr.) Henrard, Crit. Rev. Aristida 3: 666 (1928). A. diffusa Trin. var. genuina Henrard, Monogr. Aristida 1: 97 (1929).

Densely caespitose plants; culms usually one- rarely two-noded. *Panicle* effuse or somewhat contracted, up to 15 cm long. *Spikelets* purple, purplish-brown or brown. *Glumes* unequal; lower obtuse, 4–10 mm long; upper up to 18 mm long but usually shorter. *Lemma* including the callus up to 14 mm long; column of the awns 2–5 mm long.

CAPE.—Paarl: Schlechter 9138. Caledon: de Villiers 16. Uitenhage: Zeyher 4004: Ecklon & Zeyher 447. Malmesbury: Liebenberg 4240. Stellenbosch: van Rensburg 193; Sandwith 154. Tulbagh: Zeyher s.n., NH. No. 8685.

DISTRIBUTION.—(See Fig. 55.)

This variety is limited to the southern Cape, but partly overlaps with var. *burkei* in distribution. Intermediates between these two varieties are not uncommon. Anatomically it differs very little from var. *burkei*. Fig. 159: 18 and 18a depict a very robust and a less robust leaf, in cross-section, showing the variation possible within this variety.

(b) va1. burkei (Stapf) Schweikerdt in Notizbl. Bot. Gart. & Mus. Berlin 14: 122 and 195 (1938).

A. burkei Stapf in Fl. Cap. 7: 577 (1899).

Densely to laxly caespitose plants. *Culms* 3 to several-noded, rarely 2-noded. *Panicle* lax and effuse, up to 30 cm long but often much smaller. *Spikelets* yellow-brown to pallid. *Glumes* unequal; lower obtuse, up to 6 mm long; upper usually about 12 mm long. *Lemma* about 12 mm long including the callus; column of the awns 2-5 mm long.

CAPE.—Queenstown: Galpin 2383; Everett 50. Middelburg: Comins 699; Theron 720. Somerset East: Theron 716. Komga: Flanagan 1780. Aliwal North: Flanagan 2305. Tarka: Story 4501. Colesberg: Liebenberg 9.

BASUTOLAND.—Leribe: Dieterlen 199a. Mamathes: Guillarmod 858. Malutis: Staples 29 and 131.

ORANGE FREE STATE.—Heilbron: Goossens 547. Senekal: Goossens 958. Bethlehem: Potts 4519. Fauresmith: Smith 4168; Pole Evans 1573.

NATAL.—Utrecht: Codd 2533. Estcourt: West 1778. Pietermaritzburg: Comins 205. Weenen: Acocks 10115. Umvoti: Edwards 1255.

TRANSVAAL.—Heidelberg: Burtt-Davy 9161. Ermelo: Henrici 1524. Pretoria: de Winter 795; Mogg 15, 979; Pole Evans 369. Waterberg: Codd 970. Potgietersrust: Codd 6578. Pietersburg: Gerstner 5354. Lydenburg: Strey 3728.

DISTRIBUTION.—(See Fig. 55.)



FIG. 55.-Distribution of A. diffusa; Ovar. diffusa; Ovar. burkei; MA. hordeacea.

The var. *burkei* grades into the var. *diffusa* in certain areas of the Cape but on the whole is fairly distinct, the culms usually being more than 2-noded and the spikelets smaller and more graceful. The extremes of both varieties are very easily distinguished and for this reason var. *burkei* is retained. Geographically var. *diffusa* has a rather limited distribution while var. *burkei* is very widespread, covering most of South Africa

Anatomically it is very similar to var. *diffusa* but the leaves are usually less robust. The stereome consists of separate strands which abaxially never form a continuous layer, as is the case *in some specimens of var. diffusa*.

19. A. vestita Thunb., Prodr. 19 (1794)

A. lanuginosa Burchell, Travels 2: 226 (1824). A. vestita forma amplior Hack. in Engl. Bot. Jahrb. 11: 400 (1889). A. flocciculmis Mez, in Fedde Rep. 17: 147 (1921). Chaetaria vestita (Thunb.) Beauv. Agrost. 30 (1812). Arthratherum vestitum (Thunb.) Nees, Fl. Afr. Austr. 174 (1841).

Perennial densely caespitose, up to 85 cm high. Culms 3-5-noded rigid, simple or rarely branched; internodes, or at least the lower, densely to sparsely pubescent; nodes glabious. Lower *leaf-sheaths* woolly or glabrescent; auricles with a flake of wool. Leaf-blades linear, up to 24 cm long and 4 mm wide, expanded or rolled. Panicles pyramidal, effuse and open, up to 20 cm long and 12 cm wide, laxly contracted when young. Spikelets light brown or pallid. Glumes firm, 1-nerved, unequal: lower lanceolate $4 \cdot 5-7$ mm long, rounded at the apex; upper narrowly lanceolate 9-13 mm long. Lemma glabrous, 7-11 mm long including the callus, often mottled with purple; column variable 2-7 mm long, twisted, awns unequal, the central up to 35 mm long, the lateral shorter; callus bifid about $1 \cdot 5$ mm long, bearded. Caryopsis linea1, terete.

ANATOMY (Fig. 57 and 159: 19)

Leaf-blade in transverse section expanded; adaxial surface with the bundles protruding about one third of their height; numerous unicellular bristle-like hairs present opposite the stereome strands; abaxial surface flat, smooth and almost glabrous. Abaxial epidermis cells with very strongly thickened outer walls; anticlinal walls much thinner; stomatal zones usually with one row of stomata and one to four rows of long ripple-walled cells with strongly undulating walls, the undulations approximate, and viewed under low magnification the walls often apparently thick and smooth; a few paired short elements present; silicified cell zones consisting of 1 to 9 files of silicified cells alternating with rows of narrow finely ripple-walled cells; silicified cells dumb-bell-shaped and usually accompanied by oblong to rectangular suberized cells with slightly undulate walls; very few unicellular sharp-pointed and linear bicellular hairs present. Vascular bundle units: first order units 5-7, square in outline, only slightly exceeding the third order units in height; third order units ovate in outline, alternating with the first order bundles in pairs or as single units; midrib similar to other first order bundles (occasionally somewhat smaller). Stereome strands usually well developed abaxially, and present opposite all the bundles as well as at least some of the motor cell groups. Motor cells in oblong to triangular groups occupying about two thirds of the leaf width, alternating with all except occasionally the marginal bundles.



FIG. 55.—A. diffusa var. burkei: cross section of the leaf-blade (de Winter 795).



FIG. 57.-A. vestita: abaxial epidermis of the leaf-blade (de Winter 3584).

CAPE.—Sutherland: Acocks 16911. Hanover: Sim (Galpin Herb. No. 6260). Kenhardt: Pole Evans 2182; Liebenberg 5363. Hay: Esterhuyzen 2293; Brueckner 1042. Gordonia: de Winter 3584. Kuruman: Pole Evans 2097. Kimberley: Acocks 2346. Barkly West: Brueckner 834.

ORANGE FREE STATE.—Boshof: Wolff 17.

TRANSVAAL.—Christiana: Theron 599; Burtt-Davy 13030. Lichtenburg: Kinges 1412.

DISTRIBUTION.—(See Fig. 36.)

Occurs on limestone, dolorite and ironstone formations as well as on red loamy and sandy soils.



FIG. 58.-A. engleri: cross section of the leaf-blade (Pole Evans 80).

Closely allied to *A. diffusa* which it resembles very strongly in spikelet characters, the main differences being the slightly smaller spikelets, the more scabrid lemmas, and the woolly lower internodes of the culms. Anatomically it can be distinguished by the more or less square, less protruding first order bundle units which do not much exceed those of the third order. In *A. diffusa* the first order units protrude strongly and much exceed those of the third order in height. Difficulties experienced in distinguishing this species from *A. diffusa* var. *burkei* in the veld may indicate that it could be regarded as a variety of *A. diffusa* but the anatomical differences, together with the difference in spikelet size, seem to indicate a higher category, particularly since they overlap in distribution.



FIG. 59.—A. engleri: abaxial epidermis of the leaf-blade.

20. A. engleri Mez in Fedde Rep. 17: 147 (1921)

Perennial, caespitose and erect to lax and sprawling up to 70 cm high. Culms many-noded, simple or much branched from the nodes, nodes glabrous; internodes glabrous, thin and wiry to fairly robust. Leaf-sheaths glabrous; auricles pubescent. Leaf-blades expanded or involute, narrow, up to 15 cm long. Panicle effuse and open, or rather narrow and much longer than broad, the branches short and somewhat contracted. Spikelets brownish or pallid. Glumes unequal, glabrous or scaberulous, up to 6 mm long, sub-obtuse; upper 9–10 mm long. Lemma 5–8 mm long, scabrid upwards; column about 4.5 mm long; awns slightly unequal; central about 20 mm long, lateral about 15 mm long; callus bifid, bearded. Caryopsis linear, terete.

ANATOMY of the leaf-blade is mainly as described for A. vestita (see also Fig. 58, 59 and 159: 20).

Culms not branched or rarely branched from the upper nodes; panicle much longer than wide and rather contracted.....var. engleri Culms much branched; panicle not much longer than wide, rather open......var. ramosissima

(a) var. engleri.

A. engleri Mez in Fedde Rep. 17: 147 (1921).

Erect tufted perennials, usually with simple culms or rarely branched from the upper nodes; panicles much longer than wide or if rather wide the branches contracted and dense.

CAPE.—Kenhardt: Acocks 16366; 14278, and 16374; Leistner 2422; Wasserfall 1051. Gordonia: de Winter 3585. SOUTH WEST AFRICA.—Warmbad: Theron 1972. Keetmanshoop: de Winter 3416; 3274; 3307 and 3369. Luderitz: Kinges 2268; Giess and van Vuuren 749; Giess 2382. Bethanien: Kinges 2194. Maltahohe: Louw 283. Rehoboth: Volk 2522 and 2541.

DISTRIBUTION.—(See Fig. 33.)

Related to A. diffusa and A. vestita but differing from A. diffusa by the narrow somewhat contracted panicles and somewhat smaller spikelets, and from A. vestita by the glabrous lower internodes of the culms. Distinguished from A. dasydesmis by the rolled or expanded, not stiff subterete leaves. Found mainly on rocky outcrops near the Orange River and further northwards in South West Africa. Anatomically very similar to A. vestita.

(b) var. ramosissima de Winter in Kirkia 3: 132 (1963). Type: Cape, Gordonia, ± 15 m. N.N.W. of Winstead, Acocks 2053 (PRE, holo.!).

A. engleri Mez sensu Schweickerdt Bothalia 4, 1: 165 (1941) pro minore parte.

A variety characterized by the much branched slender often fascicled culms, and small usually elongate but rather lax and open panicles. Indistinguishable from var. *engleri* on floral characteristics.

CAPE.—Hay: Esterhuyzen 2359; Acocks 2053. Gordonia: Leistner 2042. Kuruman: Cooke s.n. (McGreg. Mus. No. 6355). Postmasburg: Leistner 1599; 1719. SOUTH WEST AFRICA.—Keetmanshoop: Liebenberg 5228. Luderitz: Kinges 2365.

DISTRIBUTION.—(See Fig. 33.)

This variety is not always clearly distinguishable from var. *engleri*. Both occur in the Karasberg in South West Africa. The typical forms are, however, very easily separated: the stereome is usually less developed and hence the leaf-blades tend to be softer than those of the var. *engleri*.



FIG. 60.—A. spectabilis: cross section of the leaf-blade (de Winter 773).

Due to the mixed gathering on sheet 2 of Pearson 3487 (PRE), collected at "Alewyns Fontein" (Aalwynsfontein) in Namaqualand this collection is quoted under both *A. engleri* and *A. dasydesmis* by Schweickerdt. The loose inflorescence on sheet 2 clearly belongs to *A. engleri* whereas the other two fragments agree with sheet 1 of Pearson 3487. This explains Schweickerdt's remark under *A. engleri* where he states that the facies of the two species are identical. *A. dasydesmis*, with branched and fascicled culms and stiffly erect subterete very firm leaf-blades, is easily distinguished from *A. engleri*, which is a densely tufted plant often with branched but not fascicled culms, and with expanded or rolled, but never subterete leaves. *A. engleri* also occurs further northwards and more inland, and does not overlap in distribution with *A. dasydesmis* (as far as known at present).

A. engleri is very closely allied to A. diffusa var. burkei and A. vestita and intermediates are not uncommon. These intermediates may represent hybrids.

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21. A. spectabilis Hack. in Bull. Herb. Boiss. 3, 8: 380 (1895)

Perennial, densely caespitose, robust up to 1.75 m high. *Culms* stout, erect, simple terete. *Leaf-sheaths* well developed and exceeding the internodes, glabrous, often with a flake of wool at the mouth of the sheath, and somewhat woolly on the margins downwards. *Leaf-blades* linear, involute or expanded, up to 60 cm long and 4–5 mm wide at the base. *Panicle* lax and effuse, nodding, 30–40 cm long and up to 25 cm wide. *Spikelets* glabrous, pallid. *Glumes* linear lanceolate, acute, firm below and with membranous hyaline tips, 1-nerved, subequal, about 10–12 mm long. *Lemma* linear, $6 \cdot 5-7-5 \text{ mm}$ long including the callus, smooth or minutely scaberulous upwards; column twisted, 5–6 mm long; awns unequal, central up to 44 mm long, lateral up to 28 mm long; callus up to 1 mm long, bearded, bifid. *Caryopsis* not seen.

ANATOMY (Fig. 60, 61 and 159: 21)

Leaf-blade in transverse section expanded; adaxial surface with the bundle units protruding, and with grooves extending about one third of the leaf thickness between the bundles; bristle-like, unicellular sharp hairs present adjacent to the stereome strands; abaxial surface flat, unicellular hairs practically absent; margins obtuse or obliquely truncate. Abaxial epidermis cells with very strongly thickened walls; stomatal zones usually with a single row of stomata and one to three rows of long ripple-walled cells, undulations very deep and approximate, clearly visiable only when strongly magnified; short elements more or less transversely oblong in outline; silicified cell zones of one to three files of short elements alternating with files of ripple-walled elements opposite the third order bundles and motor cells, and six to seven files of short elements alternating with files of long ripplewalled cells opposite the first order bundles; silicified cell suberized cell or an oblong suberized cell with undulate thin walls; both the unicellular and bicellular type of hair very rare or absent. Vascular bundle units: first order units 5–9, square in outline, the second and third order units projecting only slightly less than those of the first order and ovate to ovate-oblong in outline, usually in pairs between the first order units, but single adjacent to the marginal first order unit; midrib like the other first order bundles. *Stereome* strands abaxially well developed opposite all bundles as well as the motor cell groups, slightly projecting into the first order bundles and in contact with the other bundles; adaxially in contact with the first order bundles and free from the other bundles. *Motor cells* in more or less equally wide, elongate groups of thin-walled cells, occupying almost the whole width of the leaf-blade.

CAPE.—Mafeking: Brueckner 381.

TRANSVAAL.—Potchefstroom: Louw 1390. Pretoria: Schweickerdt 1339; de Winter 773. Brits: Mogg 14985. Rustenburg: Codd 1046.

DISTRIBUTION.—(See Fig. 48).

A species which occasionally superficially resembles *A. diffusa* var. *burkei* but much more robust and with subequal glumes which are hyaline at the tips. Related to *A. meridionalis* but distinguished from this species by the denser pallid inflorescence, and subequal glumes with hyaline tips.

A. spectabilis exhibits a marked preference for acid soils derived from quartzite and occurs mainly on the summits and stony slopes of mountains, usually only on northern aspects. Apparently a rather rare species.

22. A. meridionalis Henrard, Crit. Rev. Aristida 2: 344 (1927) A. stipoides Lam. var. meridionalis Stapf in Fl. Cap. 7: 562 (1899)

Perennial compactly caespitose, very robust, up to 2 m high. Culms erect, simple or somewhat branched, 2–3-noded; internodes glabrous; nodes often dark coloured, glabrous. Leaf-sheaths densely woolly or glabrescent those of the culms glabrous; auricles with a dense flake of wool. Leaf-blades narrow, involute, up to 50 cm long and 5 mm wide. Panicle large, lax and effuse, often nodding, up to 80 cm long and over 20 cm wide. Glumes unequal, glabrous; lower 5–7 mm; upper 10–15 mm. Lemma 7–9 mm long, mottled with purple, smooth or slightly punctulate and scaberulous upwards; column slender, twisted, up to 2 cm long; awns subequal, up to 5 cm long; callus 1.5-2 mm long, bearded, distinctly bifid. Caryopsis linear terete.

ANATOMY (Fig. 62 and 159: 22)

Anatomy of the leaf-blade in general details similar to that of *A. spectabilis* but with a distinct tendency towards the development of more second order bundles which alternate with those of the first order.

CAPE.—Mafeking: Pole Evans 2390. Kimberley: Esterhuyzen 1048. ORANGE FREE STATE.—Boshof: Wolff 25. TRANSVAAL.—Waterberg: Codd 4879. Potgietersrust: Galpin M617. Zoutpansberg: de Winter & Codd 336. SOUTH WEST AFRICA.—Otavi: Dinter 5767. Okavango: Maguire 2492.

DISTRIBUTION.—(See Fig. 63.)

A species occurring mainly in the warm, dry, sandy areas of South Africa. The large divaricate open inflorescence together with the flake of wool at the mouth of the leaf-sheath makes this species easily recognizable. *A. meridionalis* is related to *A. stipoides* from which it can be distinguished by the perennial habit and, on the whole, shorter column of the awns. *A. spectabilis* which may be confused with *A. meridionalis* has usually more dense inflorescences, pallid spikelets and membranous-tipped glumes.

A number of specimens in the National Herbarium collected in Southern Rhodesia viz. Goldsmith 138/36, Chase s.n. and Fisher 1402 agree in most respects with the above species, except for the densely lanate internodes of the culms, and could be described as a new variety of A. meridionalis (see also notes under A. mollissima).



FIG. 62.-A. meridionalis: abaxial epidermis of the leaf-blade [Pole Evans 3307 (3)].



FIG. 63.—Distribution of A. meridionalis.

The tendency to develop second order bundles which alternate with first order bundles, is the only feature by which this species can be distinguished from *A. spectabilis* on anatomical grounds. This tendency is also noticeable in the related though annual, *A. stipoides*. In the other species of the section *Arthratherum* the bundles (or groups of bundles) alternating with those of the first order are invariably of the third order. 23. A. stipoides Lam., Encycl. Method. 157 (1791).

A. gracillima Oliv. in Trans. Linn. Soc. 29: 173 (1875). A. lamarkii (R. & S.) Steud., Nom. Bot. 1: 69 (1821). Chaetaria lamarkii R. & S., Syst. Veg. Ed. 2: 393 (1817). A. fontismagni Schweick. in Bot. Jahrb. 76, 2: 220 (1954).

Annual, laxly caespitose, up to 1.5 m high; internodes and nodes glabrous. Leafsheaths glabrous; auricles with a dense flake of wool. Leaf-blades narrow, expanded or involute, up to 30 cm long and 3-5 mm wide. Panicle effuse and very lax, often nodding, up to 50 cm long, the spikelets spreading. Glumes usually purplish, very unequal, glabrous, 1-nerved; lower lanceolate, up to 7 mm long; lower linear-lanceolate, 15-20 mm long, mucronate from a bifid apex. Lemma including the callus up to 9 mm long, smooth below, punctulate upwards; column 2-3 cm long; awns subequal, scabrous, up to 5.5 cm long; callus slender, about 2 mm long, bearded, distinctly bifid. Caryopsis linear, terete.



FIG. 64.—A. stipoides: cross section of the leaf-blade (Schweickerdt 2129).



FIG. 65.—A. stipoides: abaxial epidermis of the leaf-blade.

Anatomically very similar to *A. meridionalis* and distinguishable only by the slightly weaker stereome strands; only distinguishable from *A. spectabilis*, and some other species of the section, by the development of second order bundles alternating with the first order bundles especially next to the midrib.

SOUTH WEST AFRICA.—Ovamboland: de Winter and Giess 7041. Okavango: Maguire 2307; de Winter and Marais 4654; le Roux 1007; Volk 1790 and 1203. Grootfontein: Schweickerdt 2129 and 2131. Gobabis: Liebenberg 4630.

DISTRIBUTION.—(See Fig. 21.)

Though described by Schweickerdt as a robust perennial in his revision of Aristida (1941; p. 161) specimens from Senegal studied by the author, as well as the two Barnard specimens cited by Schweickerdt, are all very robust annuals lacking, or rarely with a few, innovation shoots. Henrard also makes use of the annual habit of A. stipoides in order to distinguish between this species and A. meridionalis. Barnard 42 and 815 moreover agree with the type of A. fontismagni which is here placed in synonymy under A. stipoides. A. stipoides and A. meridionalis are undoubtedly closely related and are both organographically, and anatomically very similar, the only anatomical difference being the weaker development of the stereome in the annual A. stipoides.

This species, like *A. meridionalis*, is found mainly in sandy, dry and warm areas but is less widely spread in southern Africa than the latter. It occurs in suitable habitats from South West Africa northwards to Senegal and apparently is not found in the eastern parts of tropical Africa where, however, *A. meridionalis* is fairly common.

For the discussion of the anatomy the reader is referred to the previous species.

24. A. mollissima *Pilger* in Engl. Bot. Jahrb. 40: 80 (1908) A. elymoides Mez in Fedde Rep. 17: 148 (1921).



FIG. 66.—A. mollissima: abaxial epidermis of the leaf-blade (Murray 2).: CC, suberized cell; OH one celled hair; LC, long ripple-walled cell; SC, silified cell; ST stoma.

Perennial, densely caespitose, up to 85 cm high. *Culms* erect, many-noded simple or rarely branched upwards; nodes glabrous; internodes densely lanate-tomentose. *Leaf-sheaths* lanate tomentose to glabrescent; auricles ciliate or furnished with a flake of wool. *Leaf-blades* linear to filiform, up to 30 cm long and 3 mm wide. *Panicle* narrow, very dense and spike-like, up to 20 cm long and 5 cm wide, axis lanate.

Spikelets almost sessile, glabrous. Glumes very unequal, shortly awned, narrowly lanceolate, 1-nerved, scabrid on the keel, and finely scaberulous upwards; lower 10–14 mm long; upper 17.5-24 mm long. Lemma, including the callus and up to the articulation, 8–10 mm long, minutely granular; column 16–27 mm long, scabrid, twisted; awns subequal 2.8-5.5 cm long; callus 2-2.5 mm long, acuminate, bearded. Caryopsis linear, terete.

ANATOMY (Fig. 66 and 159: 24)

Practically indistuinguishable from A. spectabilis in the anatomy of the leaf-blade. The slight difference which can be detected in individual leaves are not constant.

CAPE.—Kimberley: Wilman s.n. (McGr. Mus. 4089). Mafeking: Pole Evans 2435-Vryburg: Murray 2. Kuruman: Codd 1285; Esterhuyzen 2236; Leistner 1065. ORANGE FREE STATE.—Kroonstad: Goossens 1175. Hertzogville: Serfontein 9. TRANSVAAL.—Christiana: Strey 407; Schweickerdt 1465. Lichtenburg: Kinges 1410. SOUTH WEST AFRICA.—Otjiwarongo: Volk 2337. Okavango: Volk 1741; Story 6474.

DISTRIBUTION.—(See Fig. 67.)



FIG. 67.—Distribution of A. mollissima; A. argentea.

A. mollissima is virtually indistinguishable from A. stipitata var. stipitata except for the densely woolly internodes of the culms. It could be regarded as a "form" of the latter and has a distribution which coincides almost completely with that of the var. stipitata. The same may apply to A. argentea which has woolly culms, and A. stipitata var. graciliflora, with glabrous culms. A number of specimens indistinguishable from A. meridionalis, except for the densely lanate internodes, have been collected in Rhodesia but have not yet been described. The forms differing from each other solely on basis of indumentum as far as the internodes are concerned should not be regarded as independent species, but preferably as taxa worthy only of infraspecific rank. Before deciding on such changes the problem should, however, be investigated thoroughly on a much wider scale than was possible here.

25. A. argentea Schweick. in Engl. Bot. Jahrb. 76, 2: 218 (1954). Type: Transvaal, 50 m N.W. of Potgietersrust to rd. to Maalstroom, Schweickerdt 1806. (holo! UPR; iso!, PRE).



FIG. 68.—A. argentea: cross section of the leaf-blade (Schweickerdt 1806).



FIG. 69.—A. argentea: abaxial epidermis of the leaf-blade.

Perennial, caespitose, up to 90 cm high. *Culms* erect or somewhat geniculate, branched from the nodes or simple, 3-many-noded; nodes glabrous; internodes densely to sparsely lanate-tomentose. *Leaf-sheaths* lanate to glabrescent, rather lax; auricles ciliate to somewhat woolly. *Leaf-blades* linear to filiform, up to 30 cm long and 4 mm wide. *Panicle* erect, lax, narrow, up to 30 cm long, occasionally contracted. Spikelets glabrous, pallid or purplish. *Glumes* very unequal, glabrous; lower 1–2-nerved, 10–13 mm long, keel scabrid; upper 1-nerved, 18–20 mm long, awned, keel scabrid. *Lemma* minutely granular, 9–11 mm long; column twisted, 13–16 mm long; awns more or less unequal, up to 6 cm long but usually shorter; callus about 2.5 mm long, very acute, bearded. *Caryopsis* linear, terete.

ANATOMY (Fig. 68, 69 and 159: 25)

Only differing from A. spectabilis in the first order vascular bundle units which protrude slightly more than in the latter species.

TRANSVAAL.—Warmbad: Schweickerdt 2035; de Winter 693. Soutpansberg: de Winter and Codd 664. Nelspruit: van der Schijff 4189.

DISTRIBUTION.—(See Fig. 67.)

Related to A. stipitata var. graciliflora but with the internodes of the culms densely woolly and a more openly branched inflorescence. (See also note under A. mollissima.)

Usually found in sandy soil in open bushveld.

26. A. stipitata Hack. apud Schinz in Verh. Bot. Ver. Prov. Brandenburg 30. 143 (1888)

Perennial, laxly to densely caespitose, 30-150 cm high. Culms erect, usually branched from the upper nodes, rarely some culms simple; internodes and nodes glabrous. Leaf-sheaths usually lax, glabrous; auricles pubescent, long bearded. Leafblades variable in length, up to 30 cm long but often much shorter, involute or expanded and up to 4 mm wide, borne mainly on the culms. Panicles usually erect and stiff or rarely somewhat drooping, several borne at the ends of fascicled branches or solitary at the ends of robust culms, spike-like, many-flowered and dense, or lax open and few-flowered, often interrupted when spike-like. Glumes unequal, chartaceous, narrowly lanceolate, 1-nerved, glabrous and smooth with scabrid or scaberulous keels; lower up to 13 mm long, tapering to a fine point, midnerve often excurrent into a short awn; upper up to 22 mm long tapering to a very fine acuminate apex, often shortly awned from between two hyaline lacerate lobes. Lemma including the callus up to 11 mm long, mottled or pallid, finely punctulate, distinctly articulated; column very variable 12-40 mm long, usually about 16-25 mm long; awns very variable in length, subequal, 25-60 mm long; callus acuminate, densely bearded, 2-3 mm long. Caryopsis linear, terete.

ANATOMY (Fig. 159: 26 and 26a)

In leaf anatomy practically identical with A. spectabilis.

Tall strictly erect robust plants 70–150 cm high; culms usually simple or rarely branched from some of the upper nodes:

Panicles narrow but loosely branched and rather lax and interrupted..... var. graciliflora
(a) var. stipitata.

Very tall, strictly erect, robust *perennials* with dense spike-like inflorescences and mostly pallid spikelets. *Culms* usually simple or with some culms branched from the upper nodes, 70–150 cm high, in very tall plants almost reed-like and up to 3.5 mm thick.



FIG. 70.—Distribution of A. stipitata: \bigcirc var. stipitata; \bigcirc var. robusta; \otimes var. spicata, \bigcirc var. gracilifora.

ORANGE FREE STATE.—Bothaville: Acocks 19120.

TRANSVAAL.—Pretoria: Smith 6573; Schweickerdt 1695. Warmbad: Pole Evans and Smuts 679. Waterberg: de Winter 752; Codd 971. Potgietersrust: de Winter 2280. SOUTH WEST AFRICA.—Gobabis: de Winter 2458. Ovamboland: de Winter and Giess 7038. Okavango: de Winter and Wiss 4400.

DISTRIBUTION.—(See Fig. 70.)

This variety cocurs mainly in areas characterized by deep white sandy soil. The type, collected by Schinz at Omatope in South West Africa, has the columns of the awns up to 40 mm long but in most other gatherings they rarely exceed 30 mm. The length of the column is not correlated with other characteristics that could be used to distinguish var. *stipitata* from the other varieties of *A. stipitata* and must be regarded as variable.

(b) var. robusta (Stent & Rattray) de Winter in Kirkia 3: 133 (1963). A. graciliflora var. robusta Stent & Rattray in Proc. Rhod. Sci. Ass. 32: 44 (1933) Practically indistinguishable from var. *stipitata* except for the branches of the narrow panicle which are spreading and rather lax, i.e. not dense and appressed. Intermediates between these two varieties are not uncommon.

BECHUANALAND.—de Winter 7394. SOUTH WEST AFRICA.—Okavango: de Winter & Marais 4607; Maguire 2333 and 2453; Story 6421 and 6477. Otjiwarongo: Volk 1087 and 1002.

DISTRIBUTION.—(See Fig. 70.)

Maguire, who collected this variety in the Okavango Native Reserve, reports that it grades into the var. *stipitata*. This observation supports the author's view that *A. stipitata* and *A. graciliflora* cannot be regarded as distinct species. Schweickerdt cited several specimens of var. *robusta* under *A. graciliflora*, from which it can be distinguished only on size. Occurs on deep sandy soils in the Kalahari.

(c) var. spicata de Winter in Kirkia 3: 133 (1963). Type: Bechuanaland, Tsabong, de Winter 7485 (PRE, holo.!).

Erect, lax to dense, usually much-branched plants rarely exceeding 60 cm in height, with dense pallid spike-like panicles often borne in terminal fascicles or pairs.

ORANGE FREE STATE.—Bothaville: Acocks 18711. Heilbron: Brandmuller 118. CAPE.—Gordonia: Leistner 2033; 2164 and 1136; Barnard 814. Hay: Acocks 2159. Barkly West: Ferrar 2. Kuruman: Acocks 458. SOUTH WEST AFRICA.—Gibeon: van Vuuren & Giess 1119. BECHUANALAND.—Tsabong: de Winter 7485.

DISTRIBUTION.—(See Fig. 70.)

Prefers sandy soils associated with rocky outcrops. Intermediates between var. *spicata* and var. *graciliflora* occur fairly frequently.

(d) var. graciliflora (Pilger) de Winter in Kirkia 3: 133 (1963).

A. graciliflora Pilger in Engl. Bot. Jahrb. 53: 599 (1907).

Erect, rather lax, much branched plants only occasionally exceeding 60 cm in height, with narrow but lax, often effuse, purplish panicles.

CAPE.—Kimberley: Acocks 1605. Barkly West: Acocks 1432.

ORANGE FREE STATE.—Hoopstad: Goossens 1250. Kroonstad: Goossens 1152.

TRANSVAAL.—Wolmaransstad: Liebenberg 2355. Bloemhof: Burtt-Davy 13030A. Ventersdorp: Pole Evans 3144. Potchefstroom: Theron 4. Pretoria: Smith 6567. Brits: de Winter 2194. Rustenburg: van Nouhuys 22. Waterberg: de Winter 752. Warmbad: de Winter 6017. Potgietersrust: Galpin 425. Nelspruit: van der Schijff 213 and 1332.

SWAZILAND.—Acocks 15339.

NATAL.—Ubombo: Tinley 609.

BECHUANALAND.—Liebenberg 5485; Hillary & Robertson 565.

DISTRIBUTION.—(See Fig. 70.)

The var. graciliflora is the most widespread and most common of the varieties and, although frequently associated with sand, can also be found on red loamy soils, frequently in rocky situations.

The varieties now included in *A. stipitata* show no anatomical differences in the structure of the leaf-blade and differ only in size: the leaf-blades of the larger plants being more robust. The curved leaf-blade of var. *graciliflora* depicted in Fig. 159: 26a is not characteristic since in the majority of cases the leaves are fully expanded.









27. A. pilgeri Henrard, Crit. Rev. Aristida 2: 443 (1927)

Perennial, caespitose, robust, up to 1.5 m high. Culms erect, simple, 3-6-noded; internodes and nodes glabrous. Leaf-sheaths tight, pallid, margins ciliolate; auticles glabrous or bearded. Leaf-blades linear, expanded at the base and usually laxly involute upwards, up to 35 cm long. Panicle usually dense, more or less contracted, at times subspicate, up to 40 cm long and 5 cm wide; branches up to 11 cm long, solitary. Spikelets congested, shortly pedicelled. Glumes slightly unequal, lanceolate to linear-lanceolate, awned; lower 7.5-9 mm long including the 1.5-2 mm long awn:

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the upper 10-12 mm long including the 2 mm long awn. Lemma 6-7 mm long including the column, finely punctulate, scaberulous upwards; column about 1.5 mm long twisted; awns subequal, 10-12 mm long; callus 1.5 mm long, bearded, acuminate. Caryopsis linear, terete.

ANATOMY (Fig. 71, 72 and 159: 27)

Leaf-blades flat or slightly curved in transverse section; abaxial surface flat; adaxial surface grooved between the shortly protruding bundle units, covered with short bristle-like hairs opposite the vascular bundles; midrib not projecting abaxially. Abaxial epidermis: stomatal zones with one to two rows of stomata, ripple-walled cells elongate-rectangular, with strongly and deeply undulate, slightly thickened walls with short, paired or unpaired elements scattered amongst them as well as some bi-cellular hairs: silicified zones: silicified cells dumb-bell-shaped, kidney-shaped or circular, usually accompanied by a square to elongate-rectangular thin-walled suberized cell with undulate walls; ripple-walled cells mostly very strongly thickened, the undulate walls apparently almost solid due to the approximate ripples, this zone flanked by unicellular very sharp-pointed retrorse hairs projecting obliquely over the stomatal zones. Vascular bundle units: first order units 7, square to very broadily oblong with truncate apices; second order units only very slightly smaller than the first order units; the leaf of approximately the same width throughout; midrib similar to the other first order units. Motor cells in Y-shaped groups one to two cells wide, and occupying the whole width of the leaf, present and alternating with all but the two marginal bundles.

TRANSVAAL.—Pretoria: Schweickerdt 2036. Potgietersrust: Liebenberg 4418. SOUTH WEST AFRICA.—Otjiwarongo: de Winter 2730; Liebenberg 4801. Grootfontein: Giess 2250; Schweickerdt 2055. Okavango: Volk 1706; 1831 and 2156; Story 5246.



DISTRIBUTION.—(See Fig. 73.)

FIG. 73.—Distribution of A. pilgeri; A. monticola.

Of the South African species this is the most distinctive taxon in the section *Pseudarthratherum.* It is more robust than most of the other species, often being up to 150 cm high and differing in the structure of the inflorescence from all the others. The panicle in this species is contracted but much branched, the branches solitary, up to 11 cm long and with the spikelets appressed. The other species have spike-like, very dense, or very narrow and interrupted inflorescences with short branches, or if the inflorescence is divaricate then the branches bear spike-like clusters at their apices. In *A. pilgeri* the column of the lemma is relatively short and not much twisted. Less robust plants often resemble *A. canescens* so closely that an examination of the articulation of the lemma and the nervation of the leaves is necessary before a correct determination is possible.



FIG. 74.-A. congesta subsp. congesta: cross section of the leaf-blade (de Winter 5986).



FIG. 75.—A. congesta subsp. congesta: abaxial epidermis of the leaf-blade.

Anatomically it agrees so closely with the other species of the section that it cannot be distinguished without the use of additional organographic characteristics. It is not particularly closely related to any of the other species included in the section *Pseudarthratherum*.



FIG. 76.—Distribution of A. congesta: Osubsp. congesta; Osubsp. barbicollis.

28. A. congesta R. & S., Syst. Veg. 2: 401 (1817)

Perennial, densely tufted, up to 75 cm high, or in desert areas reduced to a small annual. *Culms* simple or branched from the lower nodes, erect or geniculate, severalnoded; internodes usually somewhat compressed, glabrous; nodes glabrous. *Leafsheaths* compressed, glabrous or scaberulous upwards, lower strongly keeled the upper less so; auricles bearded or glabrous. *Leaf-blades* linear, up to 20 cm long, folded or convolute. *Panicle* dense, spike-like, often interrupted towards the base, or composed of many peduncled, false spikes in a spreading and divaricate inflorescence; up to 20 cm long. *Glumes* unequal, sub-hyaline; lower lanceolate, scaberulous on the keel, and often minutely scaberulous on the flanks upwards, up to 8 mm long, awned; upper 10 mm long, scaberulous on the keel upwards, shortly awned. *Lemma* 7–10 mm long including the callus and column; scabrid to coarsely scabrid upwards; column up to 5 mm long; awns subequal, up to 25 mm long but usually shorter; callus 1 mm long, bearded, acuminate. *Caryopsis* linear, terete.

ANATOMY (Fig. 74, 75 and 159: 28)

Anatomically practically indistinguishable from A. pilgeri.

Inflorescence subspicate, very dense and contracted, occasionally with one or two subspicate peduncled branches at the base..... subsp. congesta

Inflorescence composed of several to many peduncled spike-like branches arranged in an open divaricate panicle...... subsp. barbicollis

(a) subsp. congesta.

A. congesta R. & S., Syst. Veg. 2: 401 (1817). A. congesta var. genuina Choiv., Fl. Erit. 383 (1899). A. rangei Pilger in Engl. Bot. Jahrb. 48: 344 (1912). A. longicauda Hack. ap. Henriques Bol. Soc. Brot 6: 143 (1883). A. alopecuroides Hack. in Verh. Bot. Ver., Prov. Brandenb. 30: 114 (1888). A. congesta var. megalostachya Henrard, Mon. Aristida 1: 126 (1929).

Chaetaria congesta (R. & S.) Nees, Fl. Afr. Austr. 189 (1841).

Inflorescence dense and spike-like, occasionally with one or two peduncled spikelike branches at the base; lemma scaberulous upwards.



FIG. 77.-A. congesta subsp. barbicollis: cross section of the leaf-blade (de Winter 791).



0.1 mm

FIG. 78.—A. congesta subsp. barbicollis: abaxial epidermis of the leaf-bladc.

CAPE.—Komga: Flanagan 2317. Graaff-Reinet: Galpin 10588. Gordonia: Pole Evans 2173. BASUTOLAND.—Staples 142.

ORANGE FREE STATE.—Senekal: Goossens 933.

TRANSVAAL.—Pretoria: Codd 860. Waterberg: Burtt-Davy 1112.

NATAL.—Estcourt: Pentz 79. Dundee: Acocks 10273.

SOUTH WEST AFRICA.—Gobabis: de Winter 2439. Windhoek: de Winter & Giess 7142. Ovamboland: Schinz (H. Vindob. No. 15847). Okavango: Maguire 2480.

DISTRIBUTION.—(See Fig. 76.)

In the drier areas of the Cape and South West Africa this variety tends to behave as an annual. This annual form was described by Pilger as *A. rangei*. Since a gradual transition from the annual to the perennial habit can be traced in specimens from these areas, *A. rangei* cannot be regarded as a distinct species.

The South African specimen cited by Schweickerdt as A. longicauda (Moss & Rogers 608) cannot, in the author's opinion, be regarded as specifically distinct from A. congesta sens. lat. It is likely that A. longicauda also merely is a form of A. congesta since the inflorescence fragment of the type in PRE (from Mozambique) differs so little from the South African material as to be indistinguishable.

(b) subsp. barbicollis (Trin. & Rupr.) de Winter in Bothalia 8:173 (1964). A. barbicollis Trin. & Rupr., Gtam. Stip. 135 (1842).

A. barbicollis var. conglomerata Henrard, Crit. Rev. Aristida, Suppl. 705 (1933).

Inflorescence composed of several to many peduncled spikes arranged in an open divaricate panicle. Otherwise similar to subsp. *congesta* both in floral and vegetative characteristics.

ANATOMY practically identical with that of the subsp. congesta (Fig. 77, 78 and 159: 28a)

CAPE.—Albany: Dyer 1365. Mount Frere: Story 935.

TRANSVAAL.—Bloemhof: Leistner 125. Pretoria: de Winter 7511. Potgietersrust: Galpin 422. Nelspluit: v.d. Schijff 309.

SWAZILAND.—Pole Evans 3446.

NATAL.—Pietermaritzburg: Goossens 153. Estcourt: West 1560. Hlabisa: Ward 2435.

DISTRIBUTION.—(See Fig. 76.)

No difference in the structure of the spikelets of subsp. *barbicollis* and subsp. *congesta* could be found and some plants cannot be referred with certainty to either subspecies, not even on the characteristics of the inflorescence. The majority of specimens are comparatively easily distinguished. Subspecies *barbicollis* is much more limited in distribution than subsp. *congesta*.

2.7.8. RELATIONSHIP AND DERIVATION OF THE SECTIONS

The probable derivation of the sections of *Aristida* and *Stipagrostis* is graphically presented in Fig. 79.

Of the six sections of Aristida, the section Aristida (Chaetaria) has the widest distribution and the simplest floral structure. As pointed out by Pilger (1956, p. 119 Footnote III) in a discussion of the awns of the genus, those lemmas possessing no column can be regarded as having a simple tri-lobed apex, the lobes being very narrow and awn-like. The development of a column by the elongation and twisting of the apex of the lemma, as well as the acquisition of an articulation, must be regarded as progressive steps in the evolution of the group. The section Aristida consists of species in which the lemmas either lack a column or possess a column. The column may be weakly to well developed. None of these species, however, has articulated lemmas. It seems reasonable, therefore, on basis of the relatively primitive structure of its

lemmas, to regard it as the oldest or most primitive of the sections. It is probable that most of the other sections were derived, by slight modifications, from this section. The section *Pseudarthratherum*, for instance, may be distinguished from the section Aristida by the presence of an articulation at the summit of the column just below the branching point of the awns. A. burkei was placed in the section Aristida (Chaetaria) by Henrard. Schweickerdt (1941, p. 169) however, found that in A. burkei an articulation was sometimes present, and also pointed out that the callus was bifid, and not obtuse or acute as in the section Aristida. On this evidence he placed it in the section Arthratherum as a variety of A. diffusa. This decision is supported by the anatomical evidence presented in the present paper. A. sericans, a species with plumose awns, was placed by Henrard and Schweickerdt in the section Aristida (Chaetaria) because of the absence of an articulation. A. sericans is extremely similar to A. copensis var. dieterleniana (Stipagrostis zeyheri var. sericans). Examination of a wide range of material of both these taxa has proved that intermediates between non-articulated and distinctly articulated lemmas exist. Anatomical investigation has furnished additional evidence that A. sericans must be considered to be a representative of the genus *Stipagrostis* which, with the exception of the species just mentioned, invariably has a pronounced articulation. The presence of plumose awns must, therefore, be regarded as taxonomically more important than the absence or presence of an articulation. Another good example of relationships which cut across the division into sections based on the presence or absence, as well as the position of the articulation, is found in the species characterized by having ventrally furrowed florets. A. hordeacea, the only South African member of the section Pseudochaetaria, has a ventrally-furrowed lemma with an articulation situated at the base of the awns. A. hubbardiana, a South West African species, and A. elliptica from South America, are closely related to A. hordeacea but lack an articulation, yet possess ventrally-furrowed florets. The two species A. hordeacea and A. hubbardiana likewise show similarity in the anatomical structure of the leaf-blade. It therefore seems probable that, in spite of having been placed in two separate sections, these species are more closely related to each other than to many of the other species in the sections to which they were relegated. The exclusive use of the absence or presence (combined with the position) of the articulation for subdividing the genus Aristida into sections, although of great practical value, cannot be regarded as entirely satisfactory from the taxonomic point of view.

The section *Streptachne* occurs in most areas where the section *Aristida* is represented, except for South America, West Africa, Southern Africa and China. A pronounced articulation is lacking and the known species exhibit all stages from short lateral awns to a complete suppression of the lateral awns. The species of the section *Streptachne* do not form a natural coherent group and the probable explanation seems to be, that they developed independently from different members of the section *Aristida* in (or in the vicinity of) the areas in which they occur today. A tendency towards the reduction of the lateral awns can be seen in a number of species placed in the section *Aristida*, e.g. in *A. transvaalensis* where the lateral awns are practically absent could, technically, be referred to the section *Streptachne*.

A South West African species which was previously referred to *Stipa* is transferred to *Aristida* on both organographic and anatomical grounds: *Aristida parvula* (*Stipa parvula*) has lemmas with a single awn, but this awn is *deciduous*, conspicuously twice geniculate and the articulation is situated between the foot of the column and the apex of the lemma; in addition to the above the rounded callus is conspicuously *long-bearded*. None of the species of the section *Streptachne* has deciduous or conspicuously twice geniculate awns, even though signs of an articulation may be present. For this reason *A. parvula* is placed in a separate section *Schizachne*. *Aristida parvula* is an annual and seems to be allied to annual species of the section *Aristida* such as *A. effusa*, which it resembles greatly in habit. It does not seem to be related to any of the species

of the section *Arthratherum*, which have similar articulations, but possess three awns, larger spikelets, acute or bifid calli, and are usually all perennials. In *Aristida parvula* the callus is obtuse as in the species of the section *Aristida*. It seems most likely that it was derived from one of the annual species of the latter section by reduction of the lateral awns and the acquisition of an articulation.



FIG. 79.-Relationships of Aristida, Stipagrostis and their sections.

The section *Pseudochaetaria* is composed of three species: only *A. hordeacea* is represented in Southern Africa. This section is probably also a derivative of the section *Aristida*. As stated earlier in this discussion, *A. hordeacea* is undoubtedly related to *A. hubbardiana*, a member of the section *Aristida*. The latter would become a typical member of *Pseudochaetaria* by the acquisition of an articulation between the base of the awns (no column present) and the apex of the lemma.

The derivation of the section Arthratherum presents more difficulty. The species in this section have, on the whole, larger spikelets and are often more robust plants than those in the section Aristida. The calli are either bifid, or very acute and long. A. sciurus, the only very robust South African representative of the section Aristida, strongly resembles some of the species of Arthratherum in vegetative characteristics. In leaf anatomy A. sciurus approaches A. diffusa (section Arthratherum) more closely than any of the South African representatives of the section Aristida. The spikelets, however, agree with those of species of the latter section in most details. Some of the species at present placed in the section Aristida eventually may prove to belong to the section Arthratherum, as was found to be the case in A. diffusa var. burkei. Except for A. diffusa var. burkei, the only other species with a bifid callus placed in the section Aristida by Henrard is A. riparia Trin.: the large spikelets and 15 mm long column suggests that A. riparia may also belong to the section Arthratherum. Should this suspicion prove to be correct, this will be the first record for the section Arthratherum from South America. It seems unlikely that Arthratherum could have been derived from Pseudarthratherum which is a smaller, less widespread, section than the former. The section Pseudarthratherum is absent from North America, where five species belonging to the section Arthratherum occur, and is represented by two species in South America where the section Arthratherum is absent. All the characteristics combined in the section Arthratherum are present in the section Aristida, except for the bifid callus found in a number of African species, and the articulation. It therefore seems probable that Arthratherum was also derived from some ancestor belonging to the section Aristida and was probably not derived from any of the other sections.

It is fully realized that the placing of related species in different sections is taxonomically inaccurate, but for practical reasons, i.e. the ease of determination and reference, it is probably advisable to retain the basic arrangement presented by Henrard although in a somewhat modified form.

2.7.9. INTERRELATIONSHIP OF THE SOUTH AFRICAN SPECIES

The affinities of the various species are discussed in the descriptions.

In Fig. 80 the possible interrelationship of the species is graphically presented. Unbroken double lines indicate very close affinity, unbroken single lines, close affinity and dotted lines more distant affinity.

Certain points are evident when this diagram is studied. The annuals form groups of inter-related species; links with the perennial species, even within the same section, appear to be absent. The absence of a column seems to be associated mainly with an annual habit, but exceptions occur, such as the perennial *A. canescens*, which has no column, and *A. parvula*, an annual with both a column and an articulation.

The species of the section Aristida fall into five groups: 1. The annual group typified by A. adscensionis, including the sub-perennial A. bipartita, consists of relatively small plants occurring mainly in disturbed soils. All of these are without a column and agree with each other closely in leaf anatomy, shape of grain and general characteristics of the spikelet. 2. The second group contains two species: A. rhiniochloa and A. hubbardiana. These two species are not very closely related but agree in the rather broad ventrally furrowed grain which adheres to the palea, and the scabrid surface of the whole lemma, which is narrowed towards the apex, as well as in the anatomical structure of the leaf. In all these characteristics they agree with A. hordeacea which, however, is placed in a distinct section due to the presence of an articulation at the apex of the lemma. 3. A. transvaalensis, A. aequiglumis and A. monticola are grouped together on the characteristic anatomy of the leaf-blades, the similarity in the structure of the spikelet, as well as the branched culms. A. canescens, although somewhat divergent, should be linked with this group. 4. The fourth group consists of two species typified, anatomically, by leaf-blades which are V-shaped in crosssection: A. recta, although very distinct from A. junciformis, is probably best placed near it. Both species show a marked preference for habitats which provide moist summer conditions. 5. A. sciurus occupies a somewhat intermediate and isolated position. In the characters of the spikelet it belongs to the section Aristida, but anatomically, and in habit it approaches species such as A. diffusa and A. dasydesmis of the section Arthratherum.





The section Arthratherum falls roughly into three groups:---

- (1) A. diffusa and its allies, including those species with a bifid callus, a rather short column to the awns, and strongly to slightly projecting bundle units as seen in cross-sections of the leaf-blades.
- (2) A. meridionalis, A. spectabilis and A. stipoides form a second group, characterized by large open graceful inflorescences with numerous spikelets, a tuft of wool at the mouth of the sheath, as well as a *bifid* callus; anatomically they are very similar, the bundle units being nearly equal in height as seen in cross-section.
- (3) A. mollissima and its allies, are anatomically indistinguishable from group 2 above but the inflorescences are less copious, the spikelets rather 10bust, the calli acute, pungent and well developed, and the culms often branched.

The section *Pseudarthratherum* consists of a number of taxa so closely allied that specific identification is often very difficult. *A. pilgeri* is practically the only species where intermediate links with the other species are absent. Due to its robustness it often resembles, in habit, species belonging to the section *Arthratherum*.

As discussed previously the genus *Sartidia* is very distinct anatomically and no evidence of close affinities with any of the sections of *Aristida* could be found.

This anatomical study has, therefore, confirmed that the classification based on organographic characters, is, with a few exceptions basically sound. Furthermore on the basis of anatomical structure, it is now possible to recognize groups of related species within the sections more clearly than was hitherto possible on purely organographic grounds. Moreover anatomical study indicated the existence of an anomalous group of species, i.e. the genus *Sartidia*, which shows little affinity with *Aristida* in spite of a great organographic similarity.

From the above it may be inferred that an anatomical study of *all* the species of *Aristida* should provide valuable data for a refinement of the classification as well as the clarification of possible relationships within and between the sections.



FIG. 81.—World distribution of the genus Stipagrostis.

THE GENUS STIPAGROSTIS

2.8.1. HISTORY

The genus *Stipagrostis*, described by Nees in Linnaea 7: 290 (1832), was based on a single species, *S. capensis* Nees. Since *S. capensis* is a synonym of *Aristida obtusa* Del. the latter must be regarded as the type species of the genus. Kunth (1833, p. 197) accepted Nees's genus and included only the type species.

In 1841 Nees enlarged the genus to include two more species: S. dregeana and S. geminifolia. Apparently he did not regard the plumose awn(s) as an important characteristic, since all the other plumose species then known were accommodated by him in the genus Arthratherum. The diagnostic character used to distinguish Stipagrostis was the presence of two small lobes flanking the column at the apex of the lemma. This character has subsequently proved to be of little value. Trinius and Ruprecht in 1842 reduced Stipagrostis to a section of Aristida including in it all the species with plumose awns known to them, totalling seventeen species. Nine years later Figari and Denotaris dscribed the genus Schistachne based on Aristida ciliata Desf. Henrard in his monograph of the genus Arisida regarded both Stipagrostis and Schistachne as sections of Aristida: Schistachne containing all the species which have plumose awns and an articulation at or near the middle of the lemma, and Stipagrostis all those with plumose awns articulated at the apex of the lemma, except for A. sericans which has no articulation and therefore was placed in Chaetaria.

Schweickerdt's account of the South African species is basically the same as that of Henrard except for the clarification of the status of some of the species. The latest account is that given by Chippendall (1955) which is an abbreviated account based on Schweickerdt's revision.

2.8.2. DISTRIBUTION AND ECOLOGY

In contrast to Aristida, which is pantropical in distribution, Stipagrostis occurs only in the Old World where it is limited to the drier areas of Africa and the Middle East (Fig. 81). The majority of the species of Stipagrostis occur in desert or semi-desert areas and the general distribution of the genus coincides with areas with an average annual rainfall of less than 250 mm. The only deviation from this pattern is found in Asiatic Russia which has vast areas with a rainfall of under 250 mm, but where no species of Stipagrostis occur. The scant data from which the distribution in this area was plotted may be the reason for this apparent deviation. It seems as if temperature, which in many cases plays such an important role in the distribution of the Gramineae (Hartley, 1958), is not of great importance here. This is clear from a study of the map, where many of the areas which support no species of Stipagrostis are subject to conditions of temperature similar to those areas supporting many species. This phenomenon probably is explained by the higher annual rainfall (500 to 1,500 mm) of the areas where no species occur.

The disjunct distribution of *Stipagrostis* (Fig. 81) is not unique and other examples have come to the attention of the present author, additional to those which have already been noted by Engler in Die Pflanzenwelt Afrikas (1921, p. 851). It is interesting to note that a large number of species are disrupted in distribution, many without showing any signs of having undergone changes recognizable in the taxonomic sense, while others have developed varieties or subspecies in the different areas. As pointed out by Engler, there evidently must have been a connection between these widely separated floras in the past, probably during a drier geological period in Africa.

It is reasonably certain that the Namib Desert along the West Coast of South West Africa and Angola is geologically an extremely old area. In this desert belt, averaging 60 to 80 miles in width and about 900 miles in length, the majority of the

2.8.

species of *Stipagrostis* are concentrated, many of them endemics, occupying extremely limited distributional areas. It seems possible that many of these species originated in this area, since they do not occur in the northern areas of the generic distribution, although suitable habitats exist there. *S. hirtigluma*, *S. ciliata* and *S. obtusa* occur both in Northern and Southern Africa, while all the other species are either southern or northern in distribution.

As could be expected, the whole group is characterized by adaptation to extremes of temperature and low rainfall. These adaptations can be divided, into three categories:—

- (a) avoidance of the driest periods by the adoption of an annual habit;
- (b) reduction of vulnerable parts (leaves) and transfer of function of these parts to less vulnerable organs (culms);
- (c) protection of the vulnerable parts by extreme thickening of the cell walls.

The annual habit is found in only a few species and probably has to be regarded as a secondary development in this predominantly perennial genus. Species such as *S. hermannii* and *S. subacaulis*, which occur in the drier parts of the Namib Desert, are dwarf annuals only a few centimetres high, capable of reaching maturity and producing seed a few weeks after germination. All the parts are soft, the cells relatively thin-walled and the plants die off as soon as conditions become unfavourable. The seeds of these plants are apparently very resistant to desiccation and remain viable for long periods. No experiments have, however, been carried out to test the longevity of the seeds of grasses occurring in the Namib areas. That a source of viable seed is normally available in the soil after several years of drought can be seen after good rains, when otherwise bare flats are covered by waving grass within a few weeks. Sight should not be lost, however, of the fact that after very slight showers small plants, easily overlooked, are present, which although very depauperate, will produce a few viable seeds and thus replenish the supply.

It is striking that the annual species of *Stipagrostis* are found mainly in the drier areas, and that, even within a species, the annual varieties are desert forms, while the longer-lived forms are found further inland where the rainfall is higher. Examples of these transitions are found in species such as *S. hirtigluma*, where the variety *patula* is more or less perennial and requires a higher rainfall, whereas the var. *pearsonii* is annual, and occurs in the more arid areas. In *S. uniplumis* the forms of the typical variety occurring near the dry coast are short-lived, and the forms of the var. *neesii* are progressively longer-lived as they occur further inland in areas with a higher rainfall. This transition is reflected in the degree of development of the stereome strands and number of first order vascular bundles as seen in cross sections of the leaf-blade.

The second adaptation takes the form of a severe reduction in the size of the leaf-blades which soon disarticulate leaving the partly bare stems to perform the photosinthetic activity. The leaves of these plants are usually expanded, the stereome poorly developed, so that they resemble the leaves of the annual species to some extent. Examples of this adaptation are found in *S. fastigiata, S. geminifolia* and *S. brevifolia*.

The vast majority of the species rely on simple thickening of the epidernial cell walls and reduction in leaf-surface, to conserve moisture. Practically all these species have very narrow leaves, curved like a horseshoe in cross section, or circular with a deep longitudinal median groove adaxially. The abaxial epidermis is strongly thickened while the adaxial epidermis is relatively thin-walled and usually partly consists of a dense cover of long hairs, which may help to retain a damp atmosphere in the groove. Except in the few species where the stereome forms a continuous band below the abaxial epidermis, stomata occur on both surfaces. In several species they are situated in deep grooves, even on the abaxial surface, and in a few species these grooves are completely filled with long, woolly, longitudinally arranged hairs which protect the stomata.

A number of species are psammophytes, for example S. lanipes occurs at the foot of or between shifting dunes near the coast of South West Africa. If covered by wind-blown sand, it grows out again and may form hummocks held by the extensive system of rhizomes. Only the apical few centimetres of the plants appear above the sand. Herbarium specimens give an entirely erroneous impression, since usually only the flowering tops are represented. S. amabilis and S. sabulicola are found typically on the crest of dunes. Both these species are tall and reed-like and play an important part in stabilizing the dunes. S. sabulicola is found only in areas of the Namib desert with an average rainfall of 75 mm or less. S. amabilis, however, is a typical constituent of the dune-crest vegetation of the Kalahari further inland. Most of the other species are less exacting in their ecological requirements and will grow in a great variety of habitats and soils.

Fruit dispersal in the genus is highly specialized and effective. The relatively light fruits are enclosed in the lemmas, which are furnished with 1-3 plumose awns, and can be transported easily by wind over great distances. The awns are often twisted into a column articulated to the lemma. The lemma is furnished with a very sharp callus, which rarely is bifid; the latter bears a ting of antrorse stiff hairs above its naked, indurate base. These fruits become attached to animals and are probably dispersed often in this way. The lemma, awns and callus form a very efficient mechanism for burying the fruits in the soil. In most of these arid areas heavy dews are experienced at night. The untwisting of the hygroscopic awns, followed by a retwisting under drier conditions during the day, drives the sharp callus into the soil. Observations along the roads in South West Africa have proved that dense masses of awns blown into hollows are only the ends of the awns appearing above the soil surface while the fruits are buried deep in the soil. The awns eventually disarticulate leaving the grains buried at a suitable depth for germination. This enhances the chances of survival of the young seedlings. The soils of most of these desert areas are sandy or gravelly, and obviously ideal for the effective operation of this mechanism. Nevertheless similar adaptations are found in many grasses not subjected to such rigorous conditions.

2.8.3. KARYOLOGY (see Fig. 7).

Previous to this study, only two species of *Stipagrostis* had been investigated karyologically; namely *S. obtusa* (as *Aristida obtusa*) and *A. gracilior* var. *intermedia*, here regarded as a putative hybrid of *S. hirtigluma* var. *pearsonii* and *S. uniplumis* var. *uniplumis*.

The table below summarizes the information available on the chromosome numbers of *Stipagrostis*. The localities and collector's numbers of specimens prepared from the plants investigated by the author are indicated and these specimens are preserved in the National Herbarium, Pretoria. For the other species the authority and year of publication is cited.

		2 <i>n</i>	Locality .	Authority or (Collect	or's No	F
S.	uniplumis var. intermedia (as A. gracilior var. intermedia)	36	South West Africa	de Wet (1956).	and	Anders	son
S.	uniplumis var. uniplumis	44	South West Africa	de Winter	No. 7	119.	
S.	uniplumis var. neesii	44	South Africa	de Winter	No. 7	93.	
S.	uniplumis (as Aristida uniplumis)	44	South Africa	de Wet (19	960a).		
S.	hochstetteriana	44	South West Africa	de Winter No. 7115	No. 5.	7118 a	Ind
S.	namaquensis	44	South West Africa	de Winter	No. 6	715.	
S.	obtusa	44	South West Africa	de Winter	No. 6	712.	
S.	obtusa (as Aristida obtusa)	22	North Africa	Reese (195	7).		
S.	pungens (as Aristida pungens)	44	North Africa	Reese (195	7).		

The basic chromosome number in *Stipagrostis*, like that of *Aristida* sensu stricto, is 11. Most of the species investigated are tetraploid, only one record of a diploid having been found (Reese 1957, p. 604) in North African material of *S. obtusa*. The South West African specimens investigated by the author proved to be tetraploid with 2n = 44. De Wet and Anderson (1956, p. 7) reported 2n = 36 for *Stipagrostis uniplumis* var. *intermedia* (*Aristida gracilior* var. *intermedia*). The high incidence of tetraploids in species of *Stipagrostis*, which occur mainly in areas of extreme aridity, conforms with the findings of those workers who have remarked on the high incidence of polyploidy found in plants from areas with very extreme climatological and edaphic conditions. Reese (1957, p. 631), who made a thorough survey of the occurrence of polyploids in north Saharan plants could, however, find no evidence to support this theory.

As in the case of *Aristida* sensu stricto, the chromosomes are very small and morphological studies of the individual chromosomes were not undertaken. The chromosome numbers are so uniform that, as in *Aristida*, there appeared to be no evidence for the delimitation of sections within the genus. The nucleus in *stipagrostis* frequently persists to the mitotic metaphase (see also remarks on p. 234 under *Aristida*).

2.8.4.

STIPAGROSTIS Nees

Stipagrostis Nees in Linnaea 7: 290 (1832); Kunth, Enum. Plant. 175 (1833); Nees, Fl. Afr. Austr. 171 (1841). Aristida sect. Stipagrostis, Trin. & Rupr., Gram. Stip. 163 (1842); Bentham & Hooker, Gen. plant. 3, 2: 1141 (1883); Hackel, True Grasses, 101 (1896); Henrard, Mon. Gen. Aristida 1: 45 (1929); Schweickerdt in Bothalia 4, 1: 95 (1941); Chippindall in Grasses & Pastures S. Afr. 291–306 (1955); Pilger in Nat. Pflanzenfam. 14d, 11: 123 (1956). Schistachne Fig. & De Not in Mem. Acad. Sci. Tor. 2, 12: 252 (1851). Aristida sect. Schistachne (Fig. & De Not.) Henrard, Gen. Aristida 1: 35 (1929); Schweickerdt, l.c. p. 93; Chippindall, l.c. p. 291; Pilger, l.c. p. 124.

Spikelets solitary, pedicelled, borne in terminal, contracted or open panicles. *Rhachilla* disarticulating above the glumes, not produced beyond the base of the floret. *Floret* 1, hermaphrodite, equalling or shorter than the glumes, the awns usually long exserted, body narrowly oblong, cultrate or linear in outline. Glumes persistent, narrow, acuminate to obtuse, occasionally emarginate, 1-5-nerved (7-9- or 11-nerved in a few species) mostly both 3-nerved; nerves anastomosing or evanescent. Lemma cylindrical, or margins involute and lemma grooved ventrally, indurated at maturity, glabrous or scabrid, 3-nerved, nerves converging towards the apex but not fusing and each produced into an awn, or upper part of lemma narrowed into a canaliculate. 3-nerved, usually twisted, long or short column, each of the nerves of the column excurrent into an awn at the apex of the column, lemma articulated at or above the middle, or articulation situated between the base of the column and body of the lemma: awns all plumose or only central awn plumose, if awns single and not plumose, then with a pencil of hairs from the column; callus well developed, pungent or minutely bifid, usually oblique, bearded or practically glabrous. Palea usually much less than half the length of the lemma, indurated, 2-nerved, not keeled, the margins incurved. glabrous. Lodicules usually 2, occasionally absent, fleshy at the base, membranous upwards, with several nerves, obtuse. Stamens 3, anthers elongated. Ovary glabrous: styles free; stigmas plumose, laterally exserted. Caryopsis terete, tightly enclosed by the lemma but free, frequently shallowly grooved ventrally; hilum linear, slightly shorter than the grain; embryo 1-4 the length of the grain; starch grains compound, composed of numerous granules.

ANATOMY

Shoots long attenuated or abbreviated; in cross section circular or somewhat flattened and the leaf-blades conduplicate in the bud. The sheaths which taper towards the free margins tightly enrol the young leaves, and have groups of large thin-walled cells between the bundles (Fig. 10, A, B, C, p. 237).

Leaf-blades in transverse section sub-circular with a deep narrow groove adaxially, horse-shoe-, crescent-, V-shaped or expanded and flat. A marked tendency towards a circular to V-shaped outline is evident (Fig. 160). Silicified cells circular, depressed circular, rounded rectangular or dumb-bell-shaped in *S. subacaulis* and *S. hermannii*; occasionally dumb-bell-shaped in immature leaves of many other species. The silicified cells which have thickened walls are usually accompanied by thin-walled suberized cells, which they may resemble, but the latter are usually more or less square with somewhat undulated walls. Two types of hair occur. One-celled broad-based, usually retrorse, hairs vary from long attenuate and needle-pointed to very short retrorse barbs and are found mainly adjacent to, or flanking the stereome strands. In the species with abaxial grooves long woolly hairs are occasionally present in the grooves. The second type of hair is two-celled and tubular in shape, the terminal cell being very thin-walled and deciduous. The 2-celled hairs are found in the stomatal area between the narrow ends of the long ripple-walled cells and in strongly xerophytic leaves are often difficult to detect. They occupy positions homologous to the short elements. *Chlorenchyma* consisting of a single row of rectangular cells radially arranged around the bundles and separated adaxially by the motor cells, abaxially by one to two layers of circular or irregularly shaped very thin-walled cells containing a few chloroplasts.

Awns: column of the awns deeply grooved in most species, more rarely shallowly grooved or almost solid, furnished with three vascular bundles; central vascular bundle large, surrounded by colourless, usually strongly lignified cells; lateral bundles somewhat smaller, with a well developed single layer of radially arranged chlorenchyma cells often interrupted by lignified cells ab- and/or adaxially. Setae with a single central bundle surrounded by a single layer of radially arranged chlorenchyma. The bundles in both the setae and column lie embedded in a matrix of cells usually with strongly asymmetrically thickened walls. At the branching point of the awns and in the basal part of the setae, the lateral vascular bundles are devoid of a chlorenchyma sheath, as is the case with the central bundle throughout the column. Above the lower third of the setae all the bundles have a chlorophyll-bearing sheath which is frequently complete (Fig. 8, E and F).

Embryo in longitudinal section showing the absence of an epiblast, but with a free lower part of the scutellum, which is separated from the coleorrhiza by a deep oblique cleft; vascular tissue distinctly elongated between the point divergence of the scutellum bundle and the base of the coleoptile (Fig. 9, C, D, E, F, G). The margins of the first embryonic leaf (sheathed by the coleoptile) meeting but not overlapping and with 5 vascular bundles; the coleoptile sheath with two lateral vascular bundles and the scutellum with one median bundle.

Densely tufted perennials, delicate annuals or suffrutices with a strongly developed knotty rhizomatous base. *Culms* erect, simple or branched, hollow or solid. *Leaf-blades* long and narrow, subterete or folded, rarely more or less expanded, occasionally poorly developed and soon deciuous, only sheaths and the chlorophyll-bearing culms persistent. *Ligule* a dense fringe of hairs. *Panicles* narrow and spike-like, or effuse and open.

Type species: Stipagrostis obtusa (Del.) Nees (=S. capensis Nees).

Name from "stupe" meaning tow, and "agrostis" meaning grass, an allusion to the plumose awns of the type species.

A genus consisting of about 50 species. Confined to the desert or semi-desert areas of the Old World mainly in the western part of South Africa, in Somaliland, North Africa, the Middle East and extending to Western Tibet. One species occurs in the southern desert areas of Russia.

2.8.5. Enumeration of the Sections

Stipagrostis is divided into three sections one of which, viz. Anomala, is mono-typic.

1. § Schistachne

Stipagrostis sect. Schistachne (Fig. & De Not.) de Winter in Bothalia 8:173 (1964) Schistachne Fig. & De Not. in Mem. Acad. Sci. Tor. 2, 12: 252 (1851). Aristida sect. Schistachne (Fig. & De Not.) Henrard, Mon. Gen. Aristida 1: 35 (1929). Type species: S. ciliata Desf.

2. § Stipagrostis

Stipagrostis Nees in Linnaea 7: 290 (1832). Aristida sect. Stipagrostis (Nees) Trin. & Rupr., Gram. Stip. 163 (1842). Type species: S. obtusa (Del.) Nees.

3. § Anomala

Stipagrostis sect. Anomala de Winter in Kirkia 3: 133 (1963). Type species: S. anomala de Winter in Kirkia 3: 133 (1963). (=Stipa namaquensis Pilger).

2.8.6. Key to the Sections

1. Awns three, all or only the central awn plumose:

- 2. Body of the lemma with an articulation situated at or just above its middle; at maturity the awns and column break off with the conical, hollow upper part of the lemma attached 1. Schistachne
 - 2a. Articulation present or rarely absent, if present then situated at or slightly below the point of insertion of the awns or column; column, together with the awns, disarticulating on maturity without, or with only a very short, apical hollow part of the lemma attached 2. Stipagrostis

2.8.6.1. Key to the South African Species Based on Organographic Characters

1. § Schistachne

1. Only the central awn of the lemma plumose:

- 2. Glumes membranous to fairly firm or chartaceous, narrow, acute or acuminate with a fine delicate apex; nodes glabrous, sheaths never woolly:
 - 3. Tufted plants with mostly unbranched culms up to 90 cm high; central awns 4–10 cm long, lateral awns usually less than half as long as the central:
 - 4. Panicle dense and spike-like or branched, if branched the branches strongly contracted and with many spikelets; glumes glabrous or only the lower glume long hairy 1. S. hochstetteriana & vars.
- 2a. Glumes of a very firm texture (cartilaginous), glabrous or rigidly ciliate, subequal, rather broad, obtuse or emarginate with slightly ciliate tips; nodes bearded, or if glabrous, the basal sheaths woolly:
 - 5. Nodes conspicuously bearded with a ring of spreading white hairs, very rarely glabrous; lower sheaths glabrous or villous; plume of awns silvery white...... 2. S. ciliata
- 1a. All the awns plumose, usually equally strongly so, or the lateral awns not as densely plumose as the central awn:

6a. Internodes woolly or pubescent just below the nodes; panicle branches woolly-pubescent 5. S. proxima

2. § Stipagrostis

All the awns plumose with long, spreading hairs, the lateral at times very scantily plumose:
 Culms much branched; branches often fascicled at the nodes; plants suffrutescent, tufted or reedlike; leaves mostly borne on the culms:

- 3. Inflorescence exserted beyond the leaves, effuse and open; leaves usually rather short and pungent; subwoody suffrutex..... 11. S. lutescens
- 3a. Inflorescence overtopped by the leaves, spiciform or narrow and lax; leaves long, setaceous or filiform; plants reedlike or small and tufted:

 - 4a. Plants densely tufted and fine-leaved usually not exceeding 40 cm in height; inflorescences usually less than 10 cm long and with few spikelets (6-20)..... 10. S. ramulosa
- 2a. Culms not or rarely branched and then only from near the base; leaves borne mainly on basal innovation shoots:

 - 5a. Inflorescence effuse and open or somewhat contracted but not interrupted, if narrow then glumes pilose; plume of awns acute and excurrent into a naked tip or obtuse:

 - 6a. Lateral awns always conspicuously plumose, excurrent into a naked tip; plumes acute in outline; inflorescence open or narrow; glumes glabrous or pilose 17. S. zeyheri & subspp.
- 1a. Only the central awn plumose with long spreading hairs, the lateral awns quite naked, or rarely very scantily, appressedly ciliate pubescent:
 - 7. Suffruticose perennials with pubescent or woolly nodes; spikelets grouped together in spiciform clusters and glumes hairy, or spikelets not conspicuously clustered and glumes glabrous, but then vegetative parts densely covered with glandular tubercles:
 - 8. Glumes glabrous; nodes woolly; vegetative parts with glandular tubercles 12. S. brevifolia
 - 8a. Glumes hairy, nodes pubescent to woolly; vegetative parts without glandular tubercles:

 - 9a. Peduncle of mature panicle and upper internodes about equal in length; panicle often sheathed at the base or at least not well exserted; leaf-blades very weakly developed

14. S. geminifolia

- 7a. Caespitose perennials or annuals, if suffruticose, then nodes quite glabrous and glumes glabrous and smooth over the whole surface (occasionally with a few marginal or apical hairs):
 - 10. Glumes glabrous or finely scaberulous:
 - 11. Branching point of the awns glabrous or hairy, never with a distinct pencil of long fine hairs:
 - 12. Lower glume shorter than the upper or subequal, quite glabrous and smooth, or very sparsely scaberulous on the nerves or near the apex only (never all over); perennials with culms much branched downwards, or not branched and panicles effuse:
 - 13. Lateral awns minutely appressedly ciliate near the apices:
 - 14. Caespitose plants, occasionally shortly branched at the very base, leaves mainly basal; glumes brownish purple; apex of central plumose awn obtuse in outline 16. S. dregeana
 - 12a. Lower glume exceeding the upper in length, if subequal then the lower densely, minutely scaberulous over its whole surface; dwarf annuals or perennials with very fine basal leaves and narrow, somewhat contracted panicles:
 - 15. Lower glume very finely scaberulous all over; perennials with a dense basal tuft of fine leaves:

16. Lower leaf-sheaths woolly all over or on the margins only..... 19. S. lanipes 16a. Lower leaf-sheaths occasionally villous but never woolly:

- 15a. Lower glume glabrous and smooth or sparsely scaberulous, but then dwarf annuals not exceeding 10 cm in height:
 - 18. Plants campactly caespitose, culms poorly developed and very short; inflorescence almost hidden amongst the leaf-blades; column glabrous...... 25. S. subacaulis

18a. Plants spreading with the culms geniculately ascending and well developed; inflorescence sheathed at the base but well exserted from the tufts; columns hairy at least at the branching points of the awns:

- 19a. Glumes chartaceous lanceolate, tapering somewhat abruptly into an acute or emarginate apex, awns 1 · 4-2 · 5 cm long, column hairy all over 24. S. namibensis

11a. Branching point of the awns with a distinct pencil of long fine hairs; glumes glabrous 21. S. uniplumis

- 10a. Glumes hirsute or pilose over most of their surface, sometimes glabrous at the tips and on the sides; perennials or annuals:

 - 20a. Inflorescences usually effuse and divaricate or occasionally somewhat contracted, but then the branches not spiciform:
 - 21. Branching point of the awns with a distinct pencil of long fine hairs; callus bristles gradually increasing in length upwards, not interrupted; apex of lemma with obtuse lobes passing abruptly into the awn (best observed when anthers are enlarged but not yet exserted); central awn up to 3 cm long..... 21. S. uniplumis var
 - 21a. Branching point of the awns without a distinct pencil of hairs; the central awn (and column) variously hairy, 4.5-7 cm long; callus bristles arranged in two tufts; apex of the lemma gradually narrowing into the awn...... 22. S. hirtigluma & vars.

3. § Anomala

2.8.6.2. Key Based on Anatomical and Vegetative Characters

- 1. Suffruticose or caespitose perennials; culms firm, usually not compressible; silicified cells of epidermis subcircular, more or less square or transversely oblong never dumb-bell-shaped in outline:
 - 2. Adaxial stereome of the first order bundles consisting of large relatively thin-walled cells with large cell cavities, or of a layer of typical thick-walled fibres below the epidermis which towards the bundles gradually merge into larger, relatively thin-walled cells with large cell cavities:
 - 3. Tall, tufted plants with a branched system of rhizomes; culms reed-like, bearing the branchlets in fascicles at the nodes; abaxial surface of leaves smooth (not deeply and narrowly grooved), or with shallow depressions between the ribs, glabrous:

 - 4a. Adaxial stereome strands consisting exclusively of large cells with large cell cavities and relatively thin walls; bundle units less than twice as deep as wide:

5a. Leaves horseshoe-shaped in cross section, stereome well developed... 7. S. namaguensis

3a. Smaller plants with unbranched culms; the abaxial surface of the leaves distinctly grooved, or if not grooved the plants much branched but the culms not reed-like, the whole plant forming a bushy suffrutex or much branched fine-leaved low tuft:

6. Abaxial surface of the leaves not grooved or with only slight depressions between the ribs, glabrous or scabrid in the grooves:

7. First order bundles 5, bushy suffrutex..... 11. S. lutescens

- 7a. First order bundles 3, fine-leaved, soft and densely tufted...... 10. S. ramulosa 6a. Abaxial surface of the leaves deeply grooved, glabrous, scabrid or hairy in the grooves:
- 8. Abaxial grooves furnished with long hairs; culms woolly or pubescent below the nodes 5. S. proxima
- - 9. Suffrutices with culms much branched at least at the base:

 - 10a. Bundle units of first order not strongly projecting adaxially, only slightly more than bundles of lower order; stereome strands rather weakly developed usually not interrupting the bundle sheaths, or by a very narrow intrusion of fibres:
 - 11. Vegetative parts of plants covered with fine glandular tubercles..... 12. S. brevifolia
 - 11a. Vegetative parts of plants smooth or scabrid, not distinctly gladular-tuberculate:
 - 9a. Caespitose perennials never suffruticose with unbranched or somewhat branched culms; leaves long and well developed:
 - 13. Leaf-blades sub-circular in cross section with only three first order vascular bundles; motor cells in groups flanking or "capping" the midrib, absent elsewhere:
 - 14. Leaves very scabrid with fine, short, broad-based, hyaline spines...... 4. S. dinteri 18. S. gonatostachys
 - 14a. Leaves glabrous, smooth, woolly or villous:

 - 15a. Leaves distinctly and narrowly grooved abaxially:
 - 16. Leaves with long soft appressed hairs in the longitudinal abaxial grooves 19. S. lanipes
 - 13a. Leaf-blades sub-circular, horseshoe- or crescent-shaped, usually with 5 first order vascular bundles (or very rarely with 3 in weak specimens); motor cells present alternating with most bundles or at least not only flanking the midrib, or if only flanking the midrib, consisting of one or two large circular cells supported by a few much smaller cells:
 - 17. Nodes of the culms with a ring of spreading white hairs...... 2. S. ciliata
 - 17a. Nodes glabrous or scabrid:

 - 18a. Abaxial surface of the blade not distinctly grooved but often with shallow wide depressions between the ribs:

 - 19a. Abaxial stereome strands consisting mainly of separate strands or occasionally
 2 adjacent strands united:
 20 Culms somewhat branched from the upper podes
 21. S. uniplumic

21.5. unplums	noues	upper	from the	orancheu	somewhat	20. Cuillis	
17. S. zeyheri		s	the node	nched from	s never bra	20a. Culm	
16. S. dregeana							
b. hochstetteriana	1.5						

1a. Annuals a few cm to over 60 cm high, culms soft and easily compressible; silicified cells of epidermis dumb-bell-shaped or sub-circular in outline:

- 21a. Leaf-blade not moniliform in cross section: the bundle units projecting mainly adaxially; no distinct keel present:

2.8.7. Description of the South African Species

1. S. hochstetteriana (Beck. ex Hack.) de Winter in Kirkia 3: 134 (1963)

Perennial forming dense erect tufts up to 90 cm high. Culms 2-4-noded, scaberulous or glabrous; internodes glabrous. Leaf-sheaths glabrous or sparsely pilose. Leafblades convolute or setaceous, scabrous on the upper surface, glabrous or sparsely pilose below. Panicle dense, spike-like, up to 9 cm long and 1 cm broad, or branched with the branches dense and contracted. Spikelets congested on short branches. Glumes narrowly lanceolate or linear, acuminate, 3-nerved, glabrous or softly hairy. Lemma spindle-shaped, articulated just above the middle; column well developed; central awn plumose in the upper part, lateral awns glabrous, fine; callus acute, densely hairy. Caryopsis very narrowly oblong-elliptic about 3.5 mm long; hilum the length of the grain.



FIG. 82.—S. hochstetteriana var. secalina: cross section of the leaf-blade (de Winter 3408).



FIG. 83.-S. hochstetteriana var. secalina: abaxial epidermis of the leaf-blade.



FIG.84.—Distribution of S. hochstetteriana; Ovar. hochstetteteriana; Ovar. secalina; **IS**. proxima.

ANATOMY (Fig. 82, 83 and 160: 1 and 1a)

Leaf-blade crescent-shaped in transverse section, abaxial surface slightly undulate; adaxial surface deeply grooved; numerous long, one-celled hairs on the abaxial surface, keel absent; margins obtuse to sub-acute. Abaxial epidermis: stomatal zones with two rows of stomata and 5-8 rows of ripple-walled cells with strongly undulate walls, interspersed with paired or single, short elements, 2-celled hairs, and indistinct one-celled sharp-pointed hairs; silicified cell zones with 3-4 files of silicified cells adjacent to the third order bundles and 5-6 files adjacent to the first order bundles, long elements in this zone with finely but strongly undulate walls, silicified cells sub-circular, usually accompanied by a rectangular, or broadly oblong, thin-walled suberized cell with undulate walls. Vascular bundle units 5, very broadly oblong in outline gradually reduced in size towards the margin; third order bundle units and rectangular in outline; midrib similar to the other first order units. Bundle sheaths interrupted ad- and abaxially in first order bundles and usually abaxially only in third order bundles. Chlorenchyma a single layer of tabular cells radially arranged around the bundles; a few irregular chlorenchyma and adaxially below the stereome in the third order bundles. Stereome strands well developed and consisting of fibres; abaxially present opposite all bundles, adaxially in anchor-shaped strands opposite the first order bundles, composed of Y-shaped opposite third order bundles. Motor cells present alternating with all bundles, composed of Y-shaped groups of 6-9 cells, occupying $\frac{3}{4}$ of the thickness of the leaf. [See also Theron (1936; p. 12)].

var. hochstetteriana.

Aristida hochstetteriana Beck. ex Hack in Verh. Bot. Ver. Prov. Brandenb. 30 : 144 (1888).

SOUTH WEST AFRICA.—Keetmanshoop: Leistner 1791; de Winter 3254. Gibeon: Schweickerdt 2268. Okahandja: de Winter & Giess 7118. Karibib: de Winter 2660; de Winter 6041.

var. secalina (Henrard) de Winter in Kirkia 3: 134 (1963).

Aristida secalina Henrard, Crit. Rev. Aristida 3: 552 (1928).

CAPE.—Roberts 1057.

SOUTH WEST AFRICA.—Keetmanshoop: de Winter 3408. Windhoek: de Winter 2644. Omaruru: Liebenberg 5035. Outjo: de Winter 3048. Kaokoveld: de Winter & Leistner 5708.

DISTRIBUTION.—(See Fig. 84.)

Typical specimens of this species are distinguished from all other species of the genus by the dense spike-like inflorescences combined with usually erect, unbranched culms, and a caespitose habit.

Organographically the two varieties differ only in the hairy or glabrous lower glume, the habit of the plants and characteristics of the spikelet being identical. Anatomically the varieties do not differ, neither do they occupy different ecological regions. To retain *A. secalina* and *A. hochstetteriana* as separate species on basis of the slender character of the indumentum of the glumes unsupported by any structural differences, seems quite unjustifiable, and for this reason *A. secalina* has been reduced to the status of a variety under *S. hochstetteriana*.

The robust specimens with rather branched inflorescences cited below were at first regarded as putative hybrids between *S. hochstetteriana* and *S. ciliata* since they seemed intermediate in inflorescence characteristics, and were found growing together with the suspected parents. Later observations showed these plants to be widespread in marginal desert areas always in association with *S. hochstetteriana*. Since they are mainly found on loose sand in watercourses they are now regarded as representing very robust specimens of *S. hochstetteriana*.

The following are examples of this form:— SOUTH WEST AFRICA.—Windhoek: Louw spec. B. Swakopmund: Volk 24. Kaokoveld: de Winter & Leistner 5745; 5702; 5746.

2. S. ciliata (Desf.) de Winter var. capensis (Trin. & Rupr.) de Winter in Kirkia 3: 133 (1963)

Aristida ciliata Desf. in Schrad. Neues Journ. Bot. 3: 225 (1809). A. ciliata var. capensis Trin. & Rupr., Gram. Stip. 164 (1842). A. ciliata var. villosa Hack. in Bull. Herb. Boiss 4, 3: 18 (1896). A. ciliata var. pectinata Henrard, Crit. Rev. 1: 95 (1926). A. ciliata var. tricholaena Hack. in Bull. Herb. Boiss 4, 3: 18 (1896).

Perennial, forming dense to rather lax tufts up to 85 cm high. Culms 2–3-noded, glabrous, branched only at the base from short rootstocks; nodes bearded with long spreading hairs. Leaf-sheaths glabrous, somewhat woolly on the margins or densely pilose. Leaf-blades scabrous on the upper surface, glabrous or sparsely pilose below, convolute sub-setaceous, short or long. Panicle up to 30 cm long, narrow but often open and loose, the branches well developed and usually appressed. Glumes sub-equal, 3-nerved, glabrous or covered with hyaline spines, obtuse or subacute, sub-coriaceous, often purplish at the base, $8 \cdot 5$ –12 mm long. Lemma smooth, articulated near the middle; column well developed; central awn plumose; lateral awns glabrous fine; callus long-hairy, acute. Caryopsis very narrowly oblong, about $3 \cdot 5$ mm long; hilum the length of the grain.

ANATOMY (Fig. 85, 86 and 160: 2 and 2a)

Leaf-blade horseshoe-shaped in transverse section with the arms often somewhat elongated; abaxial surface slightly undulate, with slight depressions between the bundles; adaxial surface deeply grooved between the bundles, densely covered with long sharp-pointed unicellular hairs; keel absent; margins subacute. Abaxial epidermis: stomatal zones with 2-3 rows of stomata and 4-6 rows of long, strongly ripple-walled cells; slicified cell zones with 7-9 files of slicified cells adjacent to first order bundles and 4-5 files adjacent to the third order bundles; ripple-walled cells shorter than those of stomatal zone, with finely but strongly undulate walls; silicified cells sub-circular, single or accompanied by slightly larger, more or less square suberized cells with somewhat undulate walls; papilla-like unicellular retrorse hairs present flanking the zones. Vascular bundle units: first order units 5 or rarely 3, oblong in outline; third order units triangular, much smaller than the first order units, two on each side of the midrib otherwise alternating with other first order bundles; unice sheath of large thin-walled cells, the inner of much smaller thick-walled cells; outer and inner sheaths of first order bundles interrupted ab- and adaxially by the stereome strands except for the midrib where the inner sheath is intact adaxially; in the third order bundles the outer sheaths are interrupted abaxially and the outer adaxially. Chlorenchyma a single layer of tabular cells arranged radially around the bundles. Stereome strands well developed, present opposite all bundles. Motor cells in triangular groups of cells alternating with all except the marginal bundles, occupying $\frac{1}{2}$, the width of the leaf-blade.

CAPE.—Prince Albert: Bolus 12432. Clanwilliam: Smith 2600. Kenhardt: Codd 1184. Gordonia: Acocks 18820. Mafeking: Pole Evans 2404. Namaqualand: Marloth 12414.

SOUTH WEST AFRICA.—Keetmanshoop: Oertendahl 120; de Winter 3407. Luderitz: Dinter 3922; Kinges 2248. Swakopmund: de Winter 3209.

DISTRIBUTION.—(See Fig. 87.)

This species is readily distinguished from all others by the conspicuous spreading hairs on the nodes, the obtuse subcoriaceous glumes and the erect mostly unbranched culms. In very old specimens the nodes may appear glabrous but in such cases the bulbous bases of the hairs can still be observed. In a number of specimens collected between Aus and Luederitzbucht in South West Africa, the upper nodes are sometimes glabrous and the spikelets much smaller than in the majority of specimens. Nevertheless these specimens can be referred only to this species. Examples of such specimens are: *Kinges* 2727; 2293; *Giess & van Vuuren* 739; 700a.



FIG. 85.-S. ciliata var. capensis: cross section of the leaf-blade (de Winter 3407).



FIG. 86.-S. ciliata var. capensis: abaxial apidermis of the leaf-blade.

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FIG. 87.—Distribution of S. ciliata var. capensis.

The characters on which the varieties listed as synonyms have been distinguished show practically no correlation with habit or other characteristics, and vary considerably in the degree of development in different plants. For this reason all these have been included in a rather variable "complex variety" which represents the South African material of the species. The typical variety is North African.

This species was investigated anatomically by Guenzel (1921, p. 17). Guenzel's description of the anatomy of the leaf-blade agrees in essentials with the observations presented here but the diagramatic drawing of the cross section shows a stronger development of the stereome than found in most of the specimens studied by the present author. In Guenzel's drawing the third order bundles adjacent to the midrib are adaxially supported by stereome strands, a feature often not present in less strongly sclerized leaves [see also Theron (1936, p. 11)]. Jelenc (1950) investigated the anatomy of this species using north African material. His description agrees in essentials with that given here.

3. S. schaeferi (Mez) de Winter in Kirkia 3: 136 (1963) Aristida schaeferi Mez in Fedde Rep. 17: 152 (1921). A. schaeferi var. biseriata Henrard, Monograph Aristida 1: 41 (1929).

Perennial forming dense tufts up to 70 cm high, with the leaf-blades usually rather short, rootstock somewhat branched and robust. Culms 2–3-noded, nodes quite

glabrous. Leaf-sheaths woolly when young, glabrescent, and even glossy, when older Leaf-blades mostly basal, short, firm, subulate, recurved, villous-pubescent on the upper surface; those borne on the culms considerably longer (all leaves longer and softer in very wet seasons). Panicle up to 26 cm long, contracted but loose. Spikelets usually purplish near the base. Glumes 3-nerved, glabrous or rigidly ciliate, sub-coriaceous 8.0-12.5 mm long. Lemma smooth, articulated near the middle; column well developed; central awn plumose, 4-4.5 cm long, the plumose part often yellowish; lateral awns naked, fine; callus hairy, acuminate. Caryopsis very narrowly oblong-elliptic, about 4 mm long; hilum linear as long as the grain.

ANATOMY (Fig. 88, 89 and 160: 3)

Leaf-blade horseshoe-shaped in transverse sections; abaxial surface grooved between the bundles, the grooves gutter-shaped; adaxial surface deeply grooved between the bundles, furnished with numerous long, sharp-pointed, unicellular hairs; keel absent; margins subacute to acute. Abaxial epidermis: stomatal zones with 2-3 rows of stomata and 4-6 rows of strongly ripple-walled long cells with retrorse unicellular hairs scattered amongst them; silicified cell zones with 7-8 files of silicified cells, alternating with long ripple-walled cells adjacent to the first order bundles, and 3-4 files adjacent to the third order bundles; silicified cells sub-circular, single or usually accompanied by elongate-rectangular or square (sometimes broader than long) thin-walled suberized cells with undulate walls. Vascular bundle units: first order units 5, oblong in outline; third order units oval, 2 on each side of the midrib and alternating with the first order bundles; midrib slightly smaller but otherwise similar to the other first order bundles. Bundle Sheaths: outer consisting of large, regular, thin-walled cells, abaxially interrupted by the stereome strands in all bundles except occasionally the marginal bundle; only adaxially interrupted in the first order bundles. Stereome strands. Chlorenchyma a single layer of tabular cells radially arranged around the bundles. Motor cells present and well developed opposite all bundles abaxially in the third order bundles. Motor cells present in triangular groups alternating with all the bundles except the two marginal bundles, absent or represented by a few fibres adaxially in the third order bundles. Motor cells present in triangular groups alternating with all the bundles except the two marginal bundles and occupying half or more of the width of the leaf-blade [see also Theron (1936; p. 11)].



FIG. 88.—S. schaeferi: cross section of the leaf-blade (Volk 26).



FIG. 89.-S. schaeferi: abaxial epidermis of the leaf-blade.

SOUTH WEST AFRICA.—Luderitz: Giess & van Vuuren 662; 737; Giess 2351; Kinges 2586; 2701. Swakopmund: Volk 19; 26; Giess 3044; 3056.

DISTRIBUTION.—(See Fig. 149.)

A species closely allied to *S. ciliata* but usually easily distinguished by the lanate basal sheaths and the absence of spreading hairs on the nodes. In *S. ciliata* the basal sheaths may be densely villous but are never woolly. The leaf-blades of *S. schaeferi* are harder and thicker than those of *S. ciliata* and usually rather blunt and crescent-shaped but may be longer (in very wet seasons) and then strongly resemble those of *S. ciliata*.

The awns have a tendency to be yellowish in contrast to the silvery awns of S. ciliata.

The presence or absence of bristles on the glumes has proved to be a variable characteristic, and is regarded as unreliable for varietal distinction. The variety *biseriata* is therefore not upheld and regarded as a form.

Anatomically S. schaeferi can be distinguished from S. ciliata by the deep rather narrow grooves between the bundles on the abaxial surface of the leaves.

4. S. dinteri (Hack.) de Winter in Kirkia 3: 134 (1963) Aristida dinteri Hack. in Bull. Herb. Boiss 2, 1: 767 (1901). A. coma-ardeae Mez in Fedde Rep. 17: 152 (1921).

Perennial, forming dense tufts up to 40 cm high. Culms simple, 2–4-noded, nodes glabrous, internodes smooth or scaberulous. Leaf-sheaths glabrous, scabrid. Leafblades convolute, setaceous, very scabrous on both surfaces and with long fine hairs on the upper surface. Panicle narrow, elongate but lax and interrupted, up to 20 cm long; branches solitary or binate, up to 10 cm long, each with 1–3 spikelets. Spikelets erect, pale. Glumes linear-lanceolate, chartaceous, subequal or slightly unequal, 12–16 mm long, 3–5-nerved, sparsely hairy with soft spreading hairs. Lemma glabrous, body including the column 16–18 mm long, articulated 5–5.5 mm from the base of the callus; central awn plumose in upper part; lateral awn fine, glabrous. Caryopsis narrowly oblong-elliptic, the apex subtruncate, about 3.5 mm long; hilum equalling the grain.



FIG. 90.—S. dinteri: cross section of the leaf-blade (de Winter and Hardy 8209).



FIG. 91.-S. dinteri: abaxial epidermis of the leaf-blade (de Winter and Hardy 8209).

ANATOMY (Fig. 90, 91 and 160: 4)

Leaf-blade horseshoe-shaped in cross-section, grooved between the bundles on both surfaces with shortish very sharp unicellular hairs on both surfaces; keel protruding slightly more than the other bundles; margins obtuse. Abaxial epidermis cells rather thin-walled; stomatal zones usually with 2-3 rows of stomata and 4-8 rows of strongly ripple-walled cells; silicified cell zones with 3-4 files of silicified cells opposite the first order bundles and fewer opposite the third order bundles; silicified cells with files of silicified cells broadly oblong or more rarely dumb-bell-shaped but short; ripple-walled cells with fine but distinct undulations; numerous retrorse barbs present; bicellular hairs present flanking the zones;

multicellular somewhat sunken glands present in this zone. Vascular bundle units: first order units 3, subcircular in outline; third order units alternating with those of the first order or sometimes in pairs flanking the midrib. Bundle sheaths: outer consisting of large regular thin-walled cells; inner about half the size of the outer and with somewhat thickened walls; only the outer sheath containing chloroplasts. Chlorenchyma a single radially arranged layer of tabular cells round the bundle. Stereome rather poorly developed, present on both surfaces opposite all bundles except adaxially opposite the third order bundles flanking the midrib; fibres typically thick-walled abaxially, with very large lumen adaxially. Motor cells only present opposite the third order bundles flanking the midrib.

SOUTH WEST AFRICA.—Omaruru: de Winter and Hardy 8209. Outjo: Galpin and Pearson 7416.

This species is poorly represented in herbaria. It is related to S. obtusa and its allies, a fact only fully realized when similarities in the anatomical structure of the leaf-blade are observed. S. dinteri agrees with S. obtusa, S. lanipes and S. gonatostachys in the following organographical characteristics: only the central awn plumose and with a naked base; inflorescence narrow, elongate but laxly branched and often interrupted; leaf-blades setaceous. It is distinguished from these species by the articulation which is situated in the body of the lemma, and not at the base of the column.

Theron (1936, p. 8) places this species next to S. obtusa on basis of its anatomy which is in full agreement with the present author's view. S. dinteri is, technically, a member of the section Schistachne while S. obtusa belongs to the section Stipagrostis. There is no doubt, however, that they are closely allied in spite of the different positions of the articulation on the lemmas of the two species. The prescence of multicellular glands on the culms and nerves (Fig. 91, p. 321) combined with the caespitose habit distinguish the vegetative parts of this species from all others. The only other species known to possess glands is S. brevifolia which is, however, suffruticose in habit.

5. S. proxima (Steud.) de Winter in Kirkia 3: 135 (1963) Aristida proxima Steud., Syn. Plant. Glum. 145 (1855).

Perennial forming erect tufts and furnished with rhizomes; up to 35 cm high. Culms 2-6-noded, densely woolly at and just below the nodes, otherwise pubescent. Leaf-sheaths adpressedly pubescent, the base with a ring or tuft of long white hairs. Leaf-blades convolute, filiform, rigid and sub-pungent, appressedly pilose between the nerves below and scabrid on the upper surface. Panicle narrow but rather lax up to 15 cm long, branches and peduncle pubescent to woolly, especially in the axils, 2-5spiculate upwards. Spikelets yellowish. Glumes unequal, narrow to lanceolate, glabrous, 3-nerved, with the lateral nerves anastomosing with the central nerve; the lower $6 \cdot 5-10$ mm, the upper 8-11 $\cdot 5$ mm long, scaberulous on the keel above. Lemma glabrous, body including the callus $5 \cdot 5-7$ mm long; articulation $3 \cdot 5-5$ mm from the base of the callus; awns plumose, subequal or the central longer; callus acute, hairy. Caryopsis not seen.

ANATOMY (Fig. 92, 93 and 160: 5)

Leaf-blade horseshoe-shaped in transverse section, deeply grooved both abaxially and adaxially; keel absent; margins acute. Abaxial epidermis: stomatal zones usually completely obscured by long wavy one-celled hairs lying longitudinally in the grooves between the bundles; where visible with 2-3 rows of stomata and about 4 rows of rather short, ripple-walled cells with very strongly undulate walls; silicified cell zones with 7-9 files of silicified cells adjacent to the first order bundles and 5-6 files adjacent to the third order bundles; ripple-walled cells short with strongly undulate walls; silicified cells sub-circular, usually accompanied by short smooth-walled suberized cells, which are broader than long; numerous papilla-like retrorse hairs present, those flanking the zones especially well developed. Vascular bundle units: first order units 3, oblong in outline, third order units alternating in groups of 2 with first order units, ovate, much smaller than those of first order; midrib like other first order bundles, and adaxially only in the first order bundles. Chlorenchyma a single layer of radially arranged tabular cells; irregular cells present on the perimeter of the chlorenchyma adaxially. Stereome strands wel developed and present opposite all bundles, consisting of fibres abaxially, and of large, somewhat thickened, parenchyma cells adaxially. Motor cells in Y-shaped groups of 9-17 cells occupying 1 of the leaf thickness [see also Theron (1936; p. 14)].



FIG. 92.-S. proxima. cross section of the leaf-blade (Flanagan 1657).



Fig. 93.--S. proxima: abaxial epidermis of the leaf-blade.

CAPE.—Aliwal North: Sister Stephanie 212; Flanagan 1657.

DISTRIBUTION.—(See Fig. 84.)

A very distinct species distinguished from the related *S. namaquensis* and its allies by the culms which are woolly just below the nodes, the woolly-pubescent panicle branches, and the simple culms not branched at the nodes.

Apparently a rare species which so far has been collected only in the Lady Grey and Aliwal North districts of the Cape Province. Its basal parts are not completely known but there are indications that, like the other suffrutescent species, it has a well developed system of rhizomes.

Anatomically it may be distinguished from *S. namaquensis*, *S. sabulicola* and *S. amabilis* by the deeply grooved abaxial surface of the leaf-blades, and from *S. damarensis*, which likewise has the leaf-blades deeply grooved abaxially, by the long, woolly, longitudinally appressed hairs present in the grooves.



FIG. 94.—Distribution of **I**S. amabilis; S. lutescens; Ovar. lutescens; **•**var. marlothii.

6. S. amabilis (Schweick.) de Winter in Kirkia 3: 133 (1963) Aristida amabilis Schweick. in Bot. Jahrb. 76, 2: 217 (1954).

Similar to S. namaquensis, but only the central awn plumose and the leaves much longer, usually drooping and not as pungent. For other characteristics see description of S. namaquensis.

ANATOMY (Fig. 160: 6)

Leaf-blade sub-circular in outline with a deep groove adaxially; bundles flanking the sides of the groove densely congested; motor cells small, with their walls fairly strongly thickened; cells surrounding the phloem abaxially, very small and strongly thickened, staining much deeper than the fibres of the stereome strands. Otherwise agreeing in all respects with S. namaquensis.

CAPE.—Gordonia: Schweickerdt 2279; Leistner 1365. Namaqualand: Leistner 2510. SOUTH WEST AFRICA.—Keetmanshoop: de Winter 3398. Gibeon: Keet 1641 (Type); Leistner 1820; Codd 5870; Keet 1658.

DISTRIBUTION.—(See Fig. 94.)

As stated by Schweickerdt this species is almost exclusively found on the crest of sand-dunes in the Kalahari, where it acts as a sand-binder. The closely allied *S. namaquensis* on the other hand is found mainly in dry river courses and gullies. According to Mr. O. A. Leistner, who has made an intensive study of the flora of the Kalahari, *S. namaquensis* rarely occurs on the slopes and even the top of sand-dunes but on the whole the two species occupy distinct ecological niches.

7. S. namaquensis (Nees) de Winter in Kirkia 3: 135 (1963). Arthratherum namaquense Nees, Fl. Afr. Austr. 1: 185 (1841). Aristida namaquensis (Nees) Trin. & Rupr., Gram. Stip. 174 (1842). A. namaquensis var. vagans (Nees) Walp. in Ann. Bot. 3: 750 (1852).



FIG. 95.—S. namaquensis: cross section of the leaf-blade (Pearson 3883).



0.1 mm

FIG. 96.—S. namaquensis: abaxial epidermis of the leaf-blade.



FIG. 97.-Distribution of S. namaquensis.

Suffrutescent perennial with a long creeping rhizome forming lax, sprawling to dense, erect tufts up to 2 m high but often very much smaller. Culms fascicled, ascending, prostrate or erect, usually with fascicles of branches from the lower and middle nodes, or rarely practically simple, glabrous. Leaf-sheaths scale-like below, well developed upwards, glabrous or rarely sparsely hairy. Leaf-blades setaceous or subulate, convolute, the lower rigid and very pungent, usually glabrous below and very scabrid on the upper surface. Panicle more or less exserted, narrow, often contracted but loose, up to 30 cm long but usually much shorter; rhachis and branches nearly smooth or scabrid. Spikelets yellowish or pallid. Glumes chartaceous, unequel, lanceolate to linear-lanceolate, acuminate with bluntish tips, 3-nerved, glabrous; the lower 8–13, the upper $9 \cdot 5-15$ mm long. Lemma smooth, ending in a short twisted beak, articulated $2 \cdot 5-5$ mm below the branching point of the awns, lemma and beak (column) together 8–11 mm long, awns all plumose; somewhat unequal and variable

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in length, the central 11-25 mm long and usually more strongly plumose than the lateral. *Caryopsis* very narrowly oblong, about 5 mm long.



FIG. 98.—S. brevifolia \times S. namaquensis: cross section of the leaf-blade (de Winter 3266).

ANATOMY (Fig. 95, 96 and 160: 7)

Leaf-blade crescent-shaped in transverse section with a slightly undulating abaxial and a deeply grooved adaxial surface; upper surface covered with long unicellular sharp-pointed hairs; keel absent; margin obtuse to subacute. Abaxial epidermis cells with strongly thickened walls: stomatal zones with 2 rows of stomata and 6-8 rows of strongly ripple-walled cells, with or without a single, or double, file of silicified cells between the rows of stomata adjacent to the stereome strands subtending the motor cells: *silicified cell zones* with 6-7 files of silicified and suberized cells adjacent to first order bundles and 3-4 files adjacent to the third order bundles; silicified cells broadly oblong, single or accompanied by square or oblong suberized cells with slightly undulate walls, or suberized cells wider than long and smooth-walled; ripple-walled cells with fine but distinct undulations; papillae but no long hairs present; 2-celled hairs few. Vascular bundle units: first order units 5, very broadly oblong in outline; third order units triangular, two on each side of the midrib and alternating with the other bundles, much smaller than the first order bundles; midrib similar to the other first order units but slightly smaller. Bundle sheaths: outer consisting of large regular cells with slightly thickened walls, inner of smaller cells with walls of about equal thickness to those of the outer; inner and outer interrupted by the stereome strands ab- and adaxially in first order bundles or much reduced in size opposite the stereome strands, not interrupted adaxially in the third order bundles. Chlorenchyma a single radially arranged row of tabular cells around the bundles adaxially with a row of irregular cells on the periphery. Stereome strands well developed; adaxially in groups of large relatively thin-walled cells opposite all bundles, often with "enclaves" of thick-walled fibres between the bundle and the larger cells below the epidermis especially in older more strongly sclerized leaves; abaxially in groups of thick-walled fibres opposite all bundles with additional small groups opposite most motor cell groups. Motor cells present alternating with all bundles (except the two marginal ones), forming triangular groups 2 cells wide, or tapering to one cell in width at the apex, occupying more than half the width of the leaf-blade.

CAPE.—Namaqualand: Taylor 1083. Prieska: Bryant 650. Hopetown: Leistner 1306. Kimberley: Leistner 1186.

SOUTH WEST AFRICA.—Waimbad: Keet 1640. Luderitz: van Vuuren 855. Gibeon: Liebenberg 5155. Keetmanshoop: de Winter 3255.

DISTRIBUTION.—(See Fig. 97.)

Distinguished from the related S. amabilis by the plumose lateral awns and the pungent leaves, and from S. damarensis and S. sabulicola by the articulation situated near the middle of the body of the lemma.

For anatomical differences compare Fig. 160: 6, 8, 9 for these species.

An easily recognized species, very constant in floral characteristics but variable in size. Known to hybridize with *S. brevifolia* producing plants usually somewhat closer to *S. brevifolia* in floral characteristics but intermediate vegetatively. Examples of such specimens are: *de Winter* 3266 and *Liebenberg* 5197 from the Keetmanshoop district in South West Africa and *Acocks* 15324 and 15299 from Laingsburg in the Cape.

The anatomy of *de Winter* No. 3266 was investigated and also found to be intermediate (cf. Fig. 98 and 160: 11a).



FIG. 99.-S. damarensis: cross section of the leaf-blade (Moss 17837).



FIG. 100.-S. damarensis: abaxial epidermis of the leaf-blade.

Guenzel's (1913, p. 21) description of the leaf-anatomy of S. namaquensis agrees in all important characteristics with the authot's observations. The essential difference between the latter two species is the large-celled adaxial stereome in S. namaquensis [see also Theron (1936, p. 13)].

8. S. damarensis (Mez) de Winter in Kirkia 3: 134 (1963) Aristida damarensis Mez in Fedde Rep. 17: 152 (1921).

Perennial forming usually rather lax tufts, up to 1.2 m high, branched from near the base and furnished with well developed rhizomes. Culms simple, 3-4-noded, glabrous; nodes glabrous. Leaf-sheaths loose, glabrous except for the occasionally hairy margins. Leaf-blades firm, convolute, grooved abaxially between the nerves, scabrid or scaberulous in the grooves as well as adaxially. Panicle usually sheathed at the base, up to 45 cm long, narrow, contracted but rather lax (not spike-like); rhachis and branches smooth or scaberulous, branches solitary to 3-nate, 10-12flowered. Spikelets erect, pallid or yellow. Glumes unequal, the lower usually longer than the upper, almost glabrous, scabrous, or minutely pilose on the margin and apex, narrowly lanceolate; the lower 3-5-nerved, and 12-17 mm long; the upper 3-nerved and 12-14 mm long. Lemma glabrous including the callus 5-6.5 mm long; column 5-7 mm long; awns plumose, the central 15-22 mm long, the lateral 9-15 mm long. Caryopsis not seen.

ANATOMY (Fig. 99, 100 and 160: 8)

Leaf-blade sub-circular in transverse section with a deep median longitudinal groove and deep, narrow grooves between all the bundles adaxially; furnished with numerous rather short unicellular bristle-like patent or appressed hairs; abaxial surface with narrow grooves between all the bundles; bristle-like sharp-pointed unicellular hairs originating from the sides of the grooves; margins subacute to obtuse. Abaxial epidermis with much thickened walls; stomatal zones: due to deep grooves in which the stomatal zones are situated only narrow parallel strips of the silicified cell zones remain in scrapes; these zones are bordered by numerous, bristle-like, sharp unicellular hairs lying more or less longi-tudinally in the grooves; *silicified cell zones* with 5-6 files of silicified cells alternating with files of deeply ripple-walled long elements adjacent to the third order bundles, and 8-9 files of silicified cells alternating with files of ripple-walled cells adjacent to first order bundles; silicified cells sub-circular, highly refractive, solitary or accompanied by rectangular, broader than long, suberized cells with smooth or slightly undulate walls (occasionally suberized cells situated between two silicified cells); because of the hidden position of the stomatal zones in the grooves two-celled hairs were not observed, although they are probably present. Vascular bundles: first order bundle units oblong; third order units much smaller than those of first order, ovate, two on each side of the midrib and alternating with the other bundles; midrib similar to the other first order bundles. Bundle sheaths: outer of large rectangular, or rounded, thin-walled cells, interrupted ad- and abaxially by the stereome strands in all first order bundles, and abaxially only, in third order bundles; inner sheath of smaller somewhat thick-walled cells irregular in size and shape. Chlorenchyma a single row of tabular cells radially arranged around the bundles. Stereome strands abaxially well developed opposite all bundles, consisting of small thick-walled fibres; adaxially well developed opposite the first order bundles as relatively small, thick-walled parenchyma with distinct cell cavities near the epidermis, increasing in size towards the bundles; those near the bundles being large with only slightly thickened walls; opposite the third order bundles consisting of a few cells only; in the two bundles flanking the midrib and in the marginal bundles forming a small cap of thick-walled parenchyma. Motor cells poorly developed but present alternating with all bundles in triangular or oblong groups two cells wide at the base and 3–5 cells deep, occupying half or more of the leaf thickness [see also Theron (1936; p. 14)].

SOUTH WEST AFRICA.—Omaruru: Liebenberg s.n.; de Winter & Hardy 8131. Karibib: de Winter & Hardy 8067; 8095. Outjo: de Winter & Hardy 8177. Kaokoveld: de Winter & Leistner 5717.

A species strongly resembling the widespread *S. namaquensis* in organographical characteristics and, due to this resemblance, probably often overlooked. Distinguished from *S. namaquensis* by the articulation, which is situated near the apex of the body of the kmma, by the well developed column of the awns and by the culms which are branched at the base, but are simple upwards.

Rather rarely collected but a fairly common species in the upper Namib and coastal Kaokoveld in South West Africa.

Anatomically characterized by the narrow grooves between the nerves on the abaxial surface of the leaf-blade, and thus distinguishable from its close allies such as *S. narnaquensis*, *S. sabulicola* and *S. amabilis*.



FIG. 101.-S. sabulicola: cross section of the leaf-blade (Keet 1612).



FIG. 102. -S. sabulicola: abaxial epidermis of the leaf-blade.

9. S. sabulicola (Pilger) de Winter in Kirkia 3: 135 (1963) Aristida sabulicola Pilger in Engl., Bot. Jahrb. 40: 81 (1908).

Robust *perennial*, stiffly erect, up to 2 m high, laxly to densely caespitose, with a much-branched vigorous system of rhizomes. *Culms* reed-like, erect, glabrous, fasciculately branched from the nodes. *Leaf-sheaths* scale-like at the base of the culms, longer upwards, tight, glabrous. *Leaf-blades* very rigid, 25-60 cm long, more or less convolute and sub-terete, smooth on the lower surface, scabrid on the upper, many-netved. *Panicle* usually overtopped by the blades, usually sheathed at the base, narrow, densely spiciform, 10-30 cm long and 1-2 cm broad. *Spikelets* densely congested. *Glumes* glabrous, smooth, slightly unequal, acute or sub-obtuse; lower 3-nerved, 8-11 mm long; upper 1-nerved, 9-12 mm long. *Lemma* punctulate to smooth, including the callus $4 \cdot 75$ -6 mm long; column 1-1 $\cdot 5$ mm long; awns densely plumose, subequal, $5 \cdot 5$ -10 mm long; branching point of awns with two thin, hairy appendages; callus acute, curved, densely bearded. *Caryopsis* obovate, 3-3 $\cdot 5$ mm long; embryo about half the length of the grain; hilum as long as the grain.

ANATOMY (Fig. 101, 102 and 160: 9)

Leafs-blade horseshoe-shaped in transverse section; abaxial surface smooth or only slighy undulating, glabrous; adaxial surface deeply grooved due to the strongly projecting ribs, densely covered with bristle-like unicellular hairs, except opposite the motor cells; keel absent, margins obliquely subacute. Abaxial epidermis: stomatal zones consisting of one or occasionally 2 rows of stomatal, and 3-5 rows of short ripple-walled cells interspersed with groups of short elements; silicified cell zone of 2-5 files of short elements alternating with 1-2 files of longer ripple-walled cells, adjacent to the third order bundles, and 6-8 files adjacent to the first order bundles; silicified cells sub-circular in ou line, accompanied by 2-4 suberized cells, one on each side, or a pair on each side of the silified cells; suberized cells wider than long, rather angular, the narrow ends subacute, in groups of 2-4t together, groups alternating with silicified cells and very broadly oblong cells with papilla-like apices; oblong-rectangular, alternating with the third order units; third order units much smaller than the first order units; triangular in shape; midrib smaller than the other first order bundles, ovate-oblong in outline (occasionally consisting of a second order bundle). Bundle sheaths: outer of large, round or more or less square, thin-walled cells densely filled with chloroplasts; inner of large rather irregular cells containing no chloroplasts, but with thickened walls. Chlorenchyma a single row of tabular cells radially arranged round the bundles, supported by one or two layers of thin-walled irregular parenchyma cells containing chloroplasts, situated on the periphery of the true chlorenchyma. Stereome strands well developed ad- and abaxially opposite the first order bundles; adaxially consisting of small fibres forming a thick strand, partially enveloping the phloem; abaxially forming a cap of small fibres supported by large thick-walled parenchyma cells stretching down to the xylem; small strands of sclerenchyma also present below the epidermis flanking the vascular buncles usually in a single layer; well developed strands present abaxially opposite the third order bundles and consisting of small fibres; adaxially in small strands consisting of small fibres; large thick-walled parenchyma cells absent, or present as a few cells only. *Motor cells* in elongate very distinct, narrowly-oblong groups, 1–2 cells wide and up to 9 cells deep, usually occupying ½ or more of the thickness of the leaf [see also Theron (1936; p. 17)].

SOUTH WEST AFRICA.—Luderitz: de Winter & Giess 6181; Kinges 3480. Swakopmund: Strey 2443; 2120; Giess 3024; Keet 1705; 1612.

DISTRIBUTION.—(See Fig. 109.)

An easily recognized reed-like species inhabiting dune-tops and sandy gullies in the drier parts of the Namib, where it occupies an ecological niche similar to that occupied by *S. amabilis* and *S. namaquensis* in the more inland, less dry, areas. Distinguished from *S. amabilis* by the awns which are all plumose, and from both *S. amabilis* and *S. namaquensis* by the short awns which spread almost at right angles and do not exceed the glumes, as well as by the spiciform very dense inflorescence and by the very strongly developed stiff rachis which is overtopped by the leaf-blades.

Anatomically it is quite distinct from all the other species of the genus on account of the unique structure of the adaxial stereome of the first order bundles which consists of small fibres below the epidermis grading into large thick-walled parenchyma cells towards the bundles; as well as the shape of the first order bundles which are narrowly oblong in outline.



FIG. 103.-S. ramulosa: cross section of the leaf-blade (de Winter and Hardy 8187).



FIG. 104.-S. ramulosa: abaxial epidermis of the leaf-blade (de Winter and Haray 8197).

10. S. ramulosa de Winter in Bothalia 8:173 (1964)

Perennial, very densely tufted, fine-leaved, much branched, up to 30 cm high and often forming extensive tufts up to 1 m in diameter. Culms very slender and fascicled from the nodes, often rather wiry, many-noded, glabrous. Leaf-sheaths smooth or scaberulous on the back, rather loose. Ligule woolly. Leaf-blades firm, filiform, ribbed, scabrid especially on the ribs, up to 10 cm long. *Panicle* lax, elongate, with relatively few spikelets, sparsely branched, up to 15 cm long (usually shorter), often hidden by the leaves or only shortly exserted beyond the leaves; rhachis and branches densely scabrid, pedicels somewhat swollen towards the tips and furnished with small bristles just below the spikelet. Spikelets erect, pallid. Glumes subequal or the upper slightly longer than the lower, lanceolate, acuminate, scaberulous on the keels and apex, 3-nerved, the lateral nerves situated near to the midnerve and reaching up to half the length of the glumes; the lower 8–9 mm long; the upper 7–8 mm long. *Lemma* firmly chartaceous, tubular, 3-nerved, glabrous, body of the lemma up to the articulation and excluding the callus about 2.5 mm long, articulation situated near the apex of the lemma about 1 mm below the junction of the awns and included in the glumes; column formed by the conical upper part of the lemma, about 1 mm long; awns 3, spreading, all plumose for their whole length, plumes acute to acuminate in outline, awns with a naked excurrent tip; the central $1 \cdot 2 - 1 \cdot 5$ cm long; the lateral 1.0-1.3 cm long; callus very acute, densely hairy. Caryopsis 2-2.5 mm long, narrowly elliptic in outline; embryo $\frac{3}{5}$ the length of the grain; hilum as long as the grain, very shallowly grooved and dark brown.

ANATOMY (Fig. 103, 104 and 160: 25)

Leaf-blade subcircular to horseshoe-shaped in cross section; adaxial surface with a deep median channel shallowly grooved on the sides, furnished with retrorse barbs as well as unicellular sharp hairs; abaxial surface more or less smooth; margins obtuse to almost truncate. Abaxial epidermis: cells fairly thickwalled; stomatal zones with 1–3 rows of stomata and 2–6 rows of long ripple-walled elements, undulations deep and closely spaded; silicified cell zones consisting of files of silicified cells alternating with files of long ripple-walled cells with walls distinctly undulate but less deeply than those of the stomatal zones. Vascular bundle units: first order units 3, very broadly oblong in outline; third order units suborbicular to ovate in outline, alternating with or occasionally in pairs between the first order bundles; midrib similar to other first order bundles. Burdle sheaths: outer of large cells with somewhat thickened walls and containing chloroplasts; inner of smaller cells with thicker walls and devoid of chloroplasts. Chlorenchyma a single layer of tubular cells radially arranged round the bundles. Stereome well developed opposite all bundles abaxially and opposite the first order bundles flanking the midrib or occasionally as a single unit capping these third order bundles.

SOUTH WEST AFRICA.—Outjo: de Winter & Hardy 8197

A very distinct species which cannot be confused with any others. Easily recognised by the extremely short column, the subequal awns which are all plumose, the narrow inflorescences which are overtopped by the leaves, and the finely filiform leaf-blades. In spikelet characteristics it strongly resembles *S. sabulicola* which is regarded as its closest affinity. From the latter it differs mainly in the shorter glumes, longer awns, hairlike leaf-blades and low tufted habit. Anatomically it shows certain similarities with the suffrutescent species (adaxial stereome of large cells with large lumen) on the one hand, and the *S. obtusa* group (subterete leaves with three first order bundles) on the other.

11. S. lutescens (Nees) de Winter in Kirkia 3: 135 (1963)

Perennial, suffrutescent in habit, up to 1 m high, much branched and fascicled in the lower parts and with a strong, branched system of rhizomes. Culms many-noded, glabrous; nodes glabrous or bearded with long white hairs. Leaf-sheaths glabrous, the lower densely covering the culms. Leaf-blades subterete, rigid, short, curved and pungent or long and stiff, glabrous below, scabrid on the upper surface. Panicle effuse, pyramidal, up to 25 cm long, branches 2–5-nate or solitary, axils of branches glabrous or with a pencil of hairs. Spikelets yellowish. Glumes lanceolate, acuminate, shortly awned or narrowed into an obtuse to truncate apex, 3-nerved; the lower 9–11 mm, the upper 11.5–14 mm long. Lemma glabrous; column 0.5–5 mm long, usually twisted; central awn plumose, sparsely hairy in lower part, densely hairy upwards, up to 2.7 cm long; lateral awns scantily plumose or apparently glabrous but then scantily and appressedly ciliate. Caryopsis not seen.

ANATOMY (Fig. 105, 106 and 160: 10)

Leaf-blade horseshoe-shaped in transverse section; abaxial surface undulate, glabrous; adaxial surface deeply grooved due to the projecting bundle units, densely covered with bristle-like unicellular hairs adjacent to the stereome, glabrous elsewhere; keel absent; margins subacute to obtuse. Abaxial epidermis: stomatal zones with one or two rows of stomata and 3–5 rows of rather short ripple-walled cells with very strongly and compactly undulate walls; suberized cells broader than long, oblong to very narrowly oblong in outline; silicified cell zones often without silicified cells, only the suberized cells being developed; 3–4 files of suberized cells, alternating with files of ripple-walled elements with finely but densely undulate walls adjacent to third order bundles, and 5–7 files of suberized cells interspersed with a few silicified cell sopposite the first order bundles; silicified cells sub-circular, solitary or accompanied by a transversely elongated suberized cell; suberized cells from almost square; to narrowly oblong in a transverse direction, solitary or in pairs, wider than those in stomatal zone; no 2-celled hairs, or long unicellular hairs, observed, but a few large cells with papilla-like apex present. Vascular bundle units: first order bundle inits 5, broadly oblong to obovate in outline; third order bundles and with 2–3 first or second order bundles on each margin; midrib similar to the other first order bundles. Bundle sheaths: outer of thin-walled large-cells containing chloroplasts; inner sheath

consisting of cells irregular in size and shape, with thickened walls and without chloroplasts. *Chloren-chyma* a single layer of tabular cells arranged radially around the bundles. *Stereome strands* present abaxially opposite all bundles, as well as opposite the motor cells and composed of small fibres; adaxially present opposite all bundles but less developed in third order bundles and there composed of large thin-walled or slightly thickened parenchyma cells. *Motor cells* grading into the parenchyma opposite the sterzome strands, forming continuous bands across the leaf [see also Theron (1936, p. 18–19) including *A. marlothii*].









var. lutescens.

Arthratherum lutescens. Nees, Fl. Afr. Austr. 1: 179 (1841).

Aristida lutescens (Nees) Trin. & Rupr., Gram. Stip. 173 (1842); A. corythroides J. Karl in Mitt Bot. Staatssamml. Muenchen 1, 3:87 (1951).

SOUTH WEST AFRICA.—Luderitz: Kinges 2547; Dinter 3944; de Winter & Giess 6104; Giess & van Vuuren 734; Merxmueller & Giess 2332; Acocks 15653.

var. marlothii (Hack.) de Winter in Kirkia 3: 135 (1963).

Aristida marlothii Hack. in Engl. Bot. Jahrb. 11: 400 (1889). A. lutescens var. marlothii (Hack.) Stapf in F.C. 7: 567 (1889).

SOUTH WEST AFRICA.—Luderitz: Kinges 2348; de Winter & Giess 6098; 6134. Swakopmund: Giess 3070; Strey 2445.

DISTRIBUTION.—(See Fig. 94.)

The two varieties mentioned above were previously regarded as specifically distinct but differ so little, and are anatomically so similar, that if their identical distributional ranges are taken into consideration one must conclude that at most they represent varieties of a single species.

S. lutescens is related to S. dregeana and S. garubensis but the relationship is not a very close one. It may be distinguished from all the other species by the effuse inflorescence, the stiff rigid leaf-blades, combined with stout culms and a suffrutescent habit.

Anatomically it fits in well with the other suffrutescent species possessing branched rhizomes.



FIG. 107.-S. brevifolia: cross section of the leaf-blade (Adamson 1538).



FIG. 108.-S. brevifolia: abaxial epidermis of the leaf-blade (Adamson 1538).



FIG. 109.—Distribution of $\bigcirc S$. brevifolia; $\equiv S$. sabulicola.

12. S. brevifolia (Nees) de Winter in Kirkia 3: 133 (1963) Arthratherum brevifolium Nees, Fl. Afr. Austr. 1: 183 (1841). Aristida brevifolia (Nees) Steud., Nom. Bot. 2: 130 (1841).

Perennial, bushy suffrutex up to 1 m high with a much branched woody rootstock. Culms many-noded, rough and covered with numerous glands; nodes with an evanescent flake of wool. Leaf-sheaths gland-dotted, covered with evanescent wool at the mouth and along the margins, upper sheath less woolly than the lower; auricles with a flake of wool. Leaf-blades convolute or flat, 3 mm wide, up to 12 cm long, but usually much shorter, asperulous below, scabrid on the upper surface. Panicle exserted, contracted, linear and spike-like but loose and interrupted, up to 20 cm long, usually shorter. Spikelets yellowish often tinged with purple. Glumes lanceolate, acuminate, unequal, glabrous, glandular, puberulous or ciliate near the margins the lower 8–15 mm, the upper 11.5-17 mm long, 3–5-nerved. Lemma smooth, including the callus 5.5-7 mm long; column twisted, 4–9 mm long; central awn densely plumose upwards, 2.3-4 cm long; lateral awns naked, fine, 1–2 cm long. Caryopsis not seen.

ANATOMY (Fig. 107, 108 and 160: 11)

Leaf-blade crescent-shaped in transverse section; abaxial surface strongly undulate with very slender, retrorse unicellular hairs in the grooves; adaxial surface deeply grooved between the projecting bundle units, with many, rather long, unicellular hairs opposite the stereome strands; multicellular gland-like protruberances, similar to those on the culms, present, margins subacute to obtuse. Abaxial epidermis: stomatal zones with one to four rows of stomata and 3-5 rows of long, strongly ripple-walled cells; many slender, unicellular, broad-based sharp hairs present, as well as linear two-celled hairs; silicified cell zones with about 6 files containing silicified cells, alternating with long, finely ripple-walled cells, adjacent to first order bundles; 3-5 files containing silicified cells alternating with files of ripple-walled cells adjacent to the third order bundles; silicified cells sub-circular, usually accompanied by transversely-oblong to oblong thin-walled suberized cells, which have undulate walls; broad-based but rather slender retrorse barbs flanking the zones. Vascular bundle units: first order units 5; broadly oblong in outline; third order units ovate to oblong, 2-3 units flanking the midrib on each side: 1-3 between the lateral first order bundles and 2-3 on the margins; midrib similar to the other first order bundles. Bundle sheaths: outer sheaths of large rather thin-walled cells containing chloroplasts, usually not interrupted by the stereome, the cells opposite the abaxial stereome often rather small; inner sheaths of somewhat smaller cells with slightly thickened walls in the first order bundles, and of cells much smaller than those of outer sheath in the third order bundles. Chlorenchyma a single row of tabular cells arranged radially around the bundles. Stereome strands rather weakly developed in all bundles of fairly well-developed both ad- and abaxially opposite the first order bundles; poorly developed opposite the third order bundles, the latter having relatively small groups of fibres; all strands consisting of typical small-celled fibres. *Motor cells* in triangular groups of thin-walled colourless cells occupying more than half the thickness of the leaf and alternating with all the bundles [see also Theron (1936; p. 12)].

CAPE.—Vanrhynsdorp: Liebenberg 5605. Kenhardt: Acocks 18835. Namaqualand: Zeyher 1813; Pearson 3405

SOUTH WEST AFRICA.—Keetmanshoop: Dinter 4970; Oertendahl 575.

DISTRIBUTION.—(See Fig. 109.)

A very characteristic species due to its dense, bushy suffrutescent habit, very short leaves and glandular protruberances on the culms and sheaths. It occasionally hybridizes with *S. namaquensis* (see p. 328).

13. S. fastigiata (Hack.) de Winter in Kirkia 3: 134 (1963) Aristida fastigiata Hack. apud Schinz in Bull. Herb. Boiss. 1: 768 (1901); A. walteri Suessenguth in Mitt. Bot. Staatssamml. Muenchen 11: 39 (1954).

Perennial, sub-suffruticose with much branched thick rhizomes. *Culms* arising in fascicles from the rhizomes, 4–5-noded; internodes more or less equal in length, somewhat scaberulous, nodes densely bearded with long spreading white hairs. *Leaf-sheaths* slightly scabrid, with ciliate margins; auricles densely bearded. *Leaf-blades* flat, or convolute upwards, 2–3 mm wide, up to 12 cm long but usually much shorter, scaberulous below, scabrid to pubescent above. *Panicle* usually exserted, more or less obovate, dense, sub-fastigiate, up to 8 cm long; branches scabrid, bearded in the axils; pedicels short, hairy. *Spikelets* clustered, often brownish at the base. *Glumes* unequal, 3-nerved, pubescent, with glabrescent tips, the lower 10–14 mm long, the upper 14–18 mm long. *Lemma* smooth, $5-5\cdot5$ mm long including the callus; central awn plumose, $3-3\cdot5$ cm long; lateral awns naked, fine, 1–2 cm long.



FIG. 110.-S. fasiigiata: cross section of the leaf-blade (de Winter 3573).

and tannamana mmm IC mannin mman - ST mmmmmm ากก VIDA mmmmmm www man í 0.1 mm

FIG. 111.-S. fastigiata: abaxial epidermis of the leaf-blade.

Leaf-blade expanded, flat; abaxial surface undulate with a few short hairs opposite or flanking the bundles; adaxial surface with shallow grooves between the bundles and densely covered with rather short, unicellular hairs; keel absent; margins obtusely rounded. Abaxial epidermis cells fairly thickwalled; stomatal zones with 2-3 rows of stomata, and 4 to 8 rows of ripple-walled cells with strongly undulate walls; many uni-cellular retrorse barbs present; silicified cell zones with 1-3 files of silicified cells, and 3-6 files of ripple-walled cells with distinct but fine undulations; silicified cells sub-circular, solitary or accompanied by oblong-rectangular, square, or transversely oblong, thin-walled subcrized cells; many broadly oblong papilla-like unicellular retrorse barbs present; no two-celled hairs observed. Vascular bundle units all approximately of the same size, sub-circular in outline; first order bundle units 5; 2 second order units near the margin; third order bundle units alternating in pairs with the first order bundles, and singly with the marginal second order bundles; midrib similar to the other first order bundles. Bundle sheaths: outer of large sub-circular, thin-walled cells containing chloroplasts; inner of smaller less regular cells with slightly thickened walls. Chlorenchyma a single layer of tabular cells radially arranged around the bundles. Stereome strands very weakly developed both ab- and adaxially, usually consisting of one or two layers of small fibres not in contact with the bundles. Motor cells present alternating with all the bundles, groups stretching across the whole width of the leaf near the mibrib, and gradually diminishing in size to less than half the width near the margin.

CAPE.—Kenhardt: Leistner 2360.

SOUTH WEST AFRICA.—Warmbad: Acocks 18808; de Winter 3573. Bethanien: Walter 2161. Without locality: Boss s.n. (Tvl. Mus. 36148); Volk s.n. (Natal Herb. 33280).

DISTRIBUTION.—(See Fig. 123.)



Fig. 112.-S. geminifolia cross section of the leaf-blade (Marloth 12415).



FIG. 113.-S. geminifolia: abaxial epidermis of the leaf-blade.

Closely related to S. geminifolia from which it differs in the internodes being more or less uniform in length and by the somewhat smaller spikelets. It is usually a larger plant than S. geminifolia and occurs further inland, where the rainfall is slightly higher. S. geminifolia has the upper two leaf-sheaths subtending the inflorescence approximate, and even more strongly reduced leaf-blades than S. fastigiata. S. fastigiata occurs mainly in the very dry desert near the coast in the Luderitz district of South West Africa and in the Richtersveld of South Africa.

Anatomically the species differ only in minor details. In spite of the fact that Theron (1936; p. 26) placed this species very near to *S. geminifolia*, he compares it with *Aristida spectabilis*, a completely unrelated species and a true *Aristida*.

14. S. geminifolia Nees, Fl. Afr. Austr. 173 (1841) Aristida geminifolia (Nees) Trin. & Rupr. Gram. Stip. 169 (1842).

Perennial, small suffrutex, or sub-suffrutex up to 25 cm high. Culms erect or ascending, glabrous or hairy below the panicle, few-noded; internodes very unequal, the lowermost short, the intermediate nodes much longer and exserted, up to 12 cm long, the upper short to very short, 5-20 mm long; nodes bearded or glabrescent. Leaf-sheaths short, glabrous, with woolly or ciliate margins, the lower tight, the upper laxer, often almost spathe-like; auricles bearded. Leaf-blades very short, often rudimentary, subulate or flat, involute, very rigid, spreading, smooth below, pubescent on upper surface. Panicle erect or nodding, short, ovate to oblong, up to 4 cm long and 2.5 cm wide; rhachis glabrous or hairy; pedicels very short, hairy. Spikelets densely clustered, brownish, often tinged with purple. Glumes unequal, linear-lanceolate, acuminate and awned, hairy at least upwards, the lower 8-12 mm long, 3-nerved, the upper 10-12 mm long, 1-3-nerved. Lemma including the callus 4-6 mm long, smooth; central column 1-2 mm long, slightly twisted; central awn 2-3 cm long plumose; lateral awns fine, glabrous, 1.5 cm long. Caryopsis narrowly elliptic, small, 2 mm long; embryo $\frac{1}{3}$ to $\frac{2}{5}$ the length of the grain, hilum as long as the grain.

ANATOMY (Fig. 112, 113 and 160: 13)

Leaf-blade occasionally horseshoe-shaped but usually expanded in transverse section; keel absent; abaxial and adaxial surfaces undulate giving the section a moniliform appearance; adaxial surface furnished with long unicellular hairs; abaxial surface with a few papilla-like retrorse barbs; margins obtuse. Abaxial epidermis: cells thin-walled; stomatal zones with 2-4 rows of stomata and 4-7 rows of long ripple-walled cells with distinctly undulate walls interspersed with single, or occasionally paired, short elements, which are transversely elliptic to narrowly elliptic in shape; sparsely furnished with papilla-like retrorse hairs; *silicified cell zones* with 1-4 files of silicified cells opposite the first order bundles, and 1-2 files opposite the third and second order bundles; long elements with the walls finely undulate; silicified cells irregularly scattered in the files, solitary or accompanied by thin-walled subcrized cells; subcrized cells similar in shape to those in the stomatal zones, solitary or in pairs; unicellular papilla-like large retrorse barbs, present usually accompanied by 1 or 2 subcrized cells; two-celled hairs present in the stomatal zone. *Vascular bundle units:* first order units 3, the two marginal bundles on each margin usually of the second order; 2 third order bundles on either side of the midrib and alternating with the other bundles; first and third order units subequal, sub-circular in outline; midrib similar to the other first order bundle units. Bundle sheaths: outer of large thin-walled cells containing chloroplasts, inner of more irregular smaller cells with slightly thickened walls; both sheaths in all bundles complete. Chlorenchyma consisting of a single row of tabular cells radially arranged around the bundles. Stereome strands present abaxially opposite all bundles, and usually in contact with these but not interrupting the bundle sheaths; small weakly developed, adaxial groups present; all strands consisting of small-celled fibres. Motor cell groups alternating with all but the three marginal bundles; groups elongate, forming bands stretching across the whole width of the leaf.

CAPE.—Namaqualand: Drege s.n. (Kunkunnuwub); Marloth 12415.

SOUTH WEST AFRICA.—Luderitz: Dinter 3829; 4099; 6365; Schaefer (Marloth Herb. 12987); Kinges 2573; 2699; de Winter & Giess 6107; Giess & van Vuuren 670.

DISTRIBUTION.—(See Fig. 114.)



FIG. 114.—Distribution of S. geminifolia; S. garubensis.

A distinct species unlikely to be confused with any of the others except for the closely allied *S. fastigiata* (see page 341).

Anatomically it forms part of the small group of species which have more or less expanded, flat leaf-blades in contrast to the majority of species of *Stipagrostis* where the blades are terete, grooved, rolled or folded (see Fig. 160).

The blades have very little sclerenchyma, and in this respect resemble those of the annual species. The reduced blades are deciduous and in the dry season only the bare culms remain. The culms contain chloroplasts and when dormant are strawcoloured but become green soon after rain, even before the new leaves have appeared. Although this has been observed in only one other species viz. *S. uniplumis*, it probably applies to all the suffrutescent species as well as some of the remaining species. Theron (1936, p. 26) places this species between Aristida bipartita and A. spectabilis, species not related to S. geminifolia and only very superficially similar in the general shape of the cross-section of the leaf-blade. In error he designated the specific epithet as "geminiflora".

15. S. garubensis (Pilger) de Winter in Kirkia 3: 134 (1963) Aristida garubensis Pilger in Engl. Bot. Jahrb. 118: 343 (1912).



FIG. 115.—S. garubensis: closs section of the leaf-blade (Kinges 2289).

Perennial, bushy suffrutex, the basal part of the culms almost woody, up to 60 cm high. Flowering culms arising from the woody basal part, thin and elegant, glabrous, 2–3-noded; nodes glabrous. Lower leaf-sheaths scale-like, the upper longer, and bearing fully developed blades, glabrous. Leaf-blades sub-terete, setaceous and wiry, up to 12 cm long, glabrous on the latter surface, and finely grooved, hirtellous on the upper surface. Panicle very lax but often contracted and rather narrow, up to 20 cm long; branches solitary or 2–3-nate. Spikelets pallid, purplish at the base. Glumes lanceolate, glabrous; the lower up to 12 mm long, sub-obtuse, slightly bidentate; the upper 12.5–15 mm long, subacute. Lemma smooth, including the callus 5.5 mm long; column 8–10 mm long, twisted; central awn up to 40 mm long, plumose to the base or glabrous in the lower third; lateral awns glabrous, fine, up to 15 mm long.

ANATOMY (Fig. 115, 116 and 160: 14)

Leaf-blade horseshoe-shaped in transverse section; keel not developed; adaxial surface with the bundles strongly projecting and with short sharp unicellular hairs adjacent to the stereome strands; abaxial surface with deep narrow grooves between all the bundles with short retrorse barbs projecting diagonally across the grooves; margins obtuse. *Abaxial epidermis*: cells with extremely thickened tangential walls especially in the grooves, radial walls much less thickened hence epidermis appearing thin-walled in surface view. Stomatal zones with 2 to 3 rows of stomata and 4-6 rows of long ripplewalled cells; walls of long cells very strongly undulate with the proximal ends of the undulations often constricted and showing up as circles in the surface view of the epidermis; a few short elements, occasionally paired, present; unicellular hairs rare; bicellular linear hairs rare but present; *silicified cell zones* with 3-5 files of short elements usually alternating with 1-2 files of long ripple-walled cells adjacent to the stereome strands of the third order bundles, and 5-7 files adjacent to the first order bundles; walls of long elements finely and compactly undulate. Vascular bundle units: first order units 5, broadly oblong to obovate in outline; third order units more or less ovate in outline, 2 on each side of the midrib and alternating with the other bundles; midrib similar to the other first order bundles. Bundle sheaths: outer of large parenchymatous cells filled with chloroplasts, interrupted ad- and abaxially in the first order bundles, and abaxially only in the third order bundles; inner sheath of smaller thick-walled cells. Stereome strands consisting of small fibres throughout, very strongly developed abaxially and projecting into all bundles; adaxially projecting only into the first order bundles, and present as small distinct groups of cells opposite the third order bundles: Motor cells alternating with all except the marginal bundles, forming Y-shaped groups of thin-walled cells occupying about half of the leaf thickness [see also Theron (1936; p. 8)].



0.1 mm



SOUTH WEST AFRICA.—Luderitz: Acocks 15647; Kinges 2289; 2349; Merxmueller & Giess 2369; Giess & van Vuuren 853; Giess 2329.

DISTRIBUTION.—(See Fig. 114.)

S. garubensis is a distinct species without close affinities. It is easily recognized by its suffrutescent habit; the basal part is robust and almost woody whereas the flowering culms are very slender and graceful, the inflorescence is lax and open and the leaves are setaceous and wiry. It has so far been recorded only from the very dry coastal Namib in the vicinity of Luederitzbucht in South West Africa.

16. S. dregeana Nees, Fl. Afr. Austr. 172 (1841) Aristida dregeana (Nees) Trin. & Rupr., Gram. Stip. 169 (1842).

Perennial, up to 30 cm high, laxly to densely caespitose, branched at the base. Culms slender, erect or geniculate, simple, 1–3-noded; nodes and internodes glabrous. Leaf-sheaths scale-like at the base of the culms, well developed upwards, scaberulous. Leaf-blodes setaceous, convolute, up to 13.5 cm long, glabrous beneath, hirtellous on the upper surface. Panicle erect or somewhat nodding; branches mostly bi-nate, branches and branchlets capillary and somewhat flexuous. Spikelets usually suffused with purple. Glumes linear-lanceolate, acute, sub-equal, 3-nerved; the lower 11–13 mm long, minutely scaberulous on the keel, when young often sparsely hairy; the upper 11–13 mm long, obtuse, emarginate to bifid and mucronulate, minutely scaberulous upwards, otherwise glabrous. *Lemma* glabrous, smooth, including the callus about 4 mm long; column 4 mm long, twisted, glabrous; central awn 3–4 cm long, plumose in the upper half; lateral awns naked or almost so, up to 19 mm long; callus acute, densely hairy.



FIG. 117.—S. dregeana: cross section of the leaf-blade (Kinges 2572).





ANATOMY (Fig. 117, 118 and 160: 15)

Leaf-blade horseshoe-shaped in transverse section; keel not developed; adaxial surface with the bundles strongly projecting and covered with rather short, sharp unicellular hairs opposite the stereome strands; abaxial surface undulate, with very few hairs; margins obtuse. *Abaxial epidermis:* cells with strongly thickened walls; *stomatal zones* with 1 to 2 rows of stomata and 3 to 4 rows of very long strongly ripple-walled cells, often alternating with short elements; short elements transversely oblong in shape; undulations of the ripple-walled cells often very strongly developed, the ends of the undulations constricted and forming papilla-like structures which show up as circles in surface view, these structures are especially well developed near the stomata and form four papillae overhanging and almost completely obscuring each stoma; silicified cell zones with 4-8 files of short elements opposite the third order bundles and 9-12 files opposite the first order bundles; silicified cells square to sub-circular in outline, solitary or accompanied by a thin-walled, transversely-oblong, square to oblong suberized cell with soften somewhat undulate walls; long ripple-walled cells finely and compactly undulate; unicellular, sharp, rather short hairs present, flanking some of the silicified zones and projecting inwards over the stomatal zones; no bicellular trichomes observed but probably present. Vascular bundle units well developed; first order units oblong-rounded; third order units much smaller, more or less ovate in outline; midrib similar to the other first order units. Bundle sheaths: outer of large thin-walled cells containing chloroplasts, interrupted abaxially by the stereome strands in all the bundles except occasionally the marginal third order bundles, interrupted adaxially only in the first order bundles; inner sheath of smaller cells with thickened walls, not interrupted. Chlorenchyma a single row of tabular cells arranged radially around the bundles. Stereome strands well developed and projecting into all the bundles abaxially, adaxially well developed opposite the first order bundles and projecting into them, present as small distinct groups opposite most of the third order bundles. Motor cells alternating with all except the marginal bundles, forming Y-shaped groups of thin-walled cells occupying half or more of the leaf thickness.

CAPE.—Namaqualand: Drege s.n. (Mouth of Orange River). SOUTH WEST AFRICA.—Luderitz: Dinter 6344; Giess & van Vuuren 682; Kinges 2572; Marloth 4664.

DISTRIBUTION.—So far collected only in the coastal area of South West Africa from the Orange River to Luderitz.

A species probably best placed near S. zeyheri and S. garubensis. It differs from S. zeyheri in having only the central awn plumose and from S. garubensis in lacking a suffrutescent much-branched base.

For anatomical differences compare the Figures for these species (Fig. 115, 116, 117–122, 160). Theron (1936, p. 20) compares this species with *Aristida burkei* (reduced by Schweickerdt to a var. of *A. diffusa*) from which it, however, differs by the single large-celled chlorophyll-bearing sheath, and the glabrous awns. Theron's description of the anatomy agrees in general with the present author's observations.

17. S. zeyheri (Nees) de Winter in Kirkia 3: 136 (1963)

Perennial, compactly caespitose. Culms simple or rarely branched from the base, up to 75 cm high, wiry, glabrous. Leaf-sheaths glabrous or with a few scattered hairs; auricles glabrous or bearded. Leaf-blades filiform, folded, subterete, up to 40 cm long; the lower surface smooth, the upper scaberulous to hispid. Panicle erect or nodding, narrow, contracted or open to divaricate. Spikelets pale brown to purplish. Glumes glabrous or hairy, unequal to sub-equal, 3-nerved; the lower 10–19 mm long; the upper 11–20 mm long. Lemma including the callus 5-8.5 mm long, smooth or finely pustulate; column 1–14 mm long, glabrous to hairy; the central awn 16–40 mm long, plumose; the lateral plumose, 13–35 mm long; callus 2.5 mm long, acuminate densely hairy. Caryopsis very narrowly elliptic, about 5 mm long; hilum as long as the grain.

ANATOMY (Fig. 119, 120, 121, 122 and 160: 16a-d)

Leaf-blade V-shaped or sub-circular with a deep adaxial median groove; abaxial surface slightly undulate to almost smooth; adaxial surface on either side of the median groove undulate with a cleft on each side of the midrib; or deeply grooved between the bundle units, densely covered with short papilla-like unicellular hairs; margins subacute or obtuse. Abaxial epidermis: stomatal zones with 1-2 rows of stomata and 3-4 rows of long, strongly ripple-walled cells with scattered, intermixed paired short elements; or stomata very few and whole epidermis of short elements alternating with long ripple-walled cells; silicified cell zones consisting of files of silicified cells alternating with finely but densely undulate walls. Vascular bundle units: first order units 5, broadly oblong in outline; third order units ovate in outline, flanked by motor cell groups or situated more or less below them, alternating with first order units or with two bundles flanking the midrib, sometimes absent between the 2 marginal first order bundles; indirib similar to the other first order bundles. Bundle sheaths: outer of large rather regular cells, only interrupted adaxially by the stereome strands in all but occasionally some of the third order bundles. Stereome well developed opposite all bundles including the margin, or forming a continuous abaxial layer; adaxial stereome poorly developed and consisting of large cells with only slightly thickened walls, or if well developed, consisting of typical fibres. Motor cells present on either side of the midrib, absent elsewhere, or alternating with all bundles.

Glumes glabrous:

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Glumes usually purplish, leaves usually not overtopping the inflorescence; winter rainfall areas of the Cape
Glumes usually straw-coloured; leaves usually overtopping the inflorescence, east coast of the Cape subsp. barbata
Column glabrous subsp. macropus
Glumes hairy subsp. sericans

(a) subsp. zeyheri.

Arthratherum zeyheri Nees, Fl. Afr. Austr. 177 (1841). Aristida zeyheri (Nees) Steud., Nom. Bot. 2: 132 (1841). A. capensis var. canescens Trin. & Rupr., Gram. Stip. 178 (1842). A. capensis var. zeyheri (Nees) Walp. in Ann. Bot. 3: 751 (1852).

Perennial, forming an erect tuft from a short knotty rhizome. *Panicle* lax and open, usually exceeding the leaves. *Spikelets* often purplish. *Column* of the awns hairy, $2 \cdot 5-12$ mm long; plumes of the awns greyish to silvery.

ANATOMY (Fig. 160: 16)

Leaf-blade subterete with a deep adaxial groove. *Stereome strands* usually fused to form a continuous abaxial sheath of fibres. Deep grooves present between the bundle units on the adaxial surface. *Motor cell groups* present alternating with all the bundles.

CAPE.—Cape Peninsula: Hitchcock 24086 & 24083; Adamson 3103; Ecklon & Zeyher s.n.; Wolly Dod 1969. Paarl: Schlechter 9105. Caledon: Schlechter 9843; Parker 4471. Worcester: van Breda 3. Tulbagh: Ecklon & Zeyher s.n.; Malmesbury: Acocks 14103; Barenbrug 6. Stellenbosch: Smuts s.n.; Sandwith 153. Clanwilliam: Pillans 8740.

DISTRIBUTION.—(See Fig. 123.)

This subsp. is not well differentiated from subsp. *barbata*, which in its typical form however, looks entirely different. The lax spreading inflorescences, longer column of the awns and usually purplish spikelets characterize the subspecies *zeyheri* which is limited to the winter rainfall area of the Cape. Anatomically the leaf-blades of subsp. *zeyheri* and subsp. *barbata* are practically identical.

(b) subsp. barbata (Stapf) de Winter in Kirkia 3: 136 (1963). Aristida capensis var. barbata Stapf in F.C. 7: 565 (1899).

Perennial, forming large erect densely leafy tufts. *Panicle* usually rather dense and contracted, overtopped by the setaceous, often curling, leaves. *Spikelets* usually pallid. *Column* of the awns hairy, 2–4 mm long; plumes of the awns greyish or tawny.

ANATOMY as for subsp. zeyheri (Fig. 160: 16a)

CAPE.—Uitenhage: Zeyher 4501; Ecklon & Zeyher 502. Alexandria: Burtt-Davy 14196; Archibald 5506. Bathurst: Hutton 2631; Tyson BH. 14877. East London: Codd 9240. Kentani: Flanagan 1782; Pegler 265; Theron 1188; Acocks 13588. NATAL.—Mtunzini: Guy & Ward 63. Lower Tugela: Edwards 1723.

This subspecies has a well-defined geographic distribution along the coastal areas of the eastern Cape and northern Natal (see Fig. 123). Recognized by the very well developed often curling, setaceous leaf-blades which usually overtop the rather narrow straw-coloured inflorescences. It usually inhabits coastal dunes and forms very robust leafy tufts.

(c) subsp. macropus (Nees) de Winter in Kirkia 3: 136 (1963).

A. capensis Thunb., Prodr. 19 (1794) non Stipagrostis capensis Nees. Aristida capensis var. macropus Nees, Fl. Afr. Austr. 176 (1841). A. capensis var. fulviberbis Tiin. & Rupr., Gram. Stip. 179 (1842). A. capensis var. genuina Henrard, Crit. Rev. Aristida 1: 77 (1926).

Chaetaria capensis (Thunb.) Beauv., Agrost. 30 (1812)







FIG. 120.-S. zeyheri subsp. macropus: abaxial epidermis of the leaf-blade.

Perennial, forming erect tufts from a short knotty rhizome. *Leaves* not very dense, usually not exceeding the inflorescence; blades setaceous. *Panicle* lax and effuse, the branches occasionally somewhat contracted. *Spikelets* brown to purplish. *Glumes* glabrous. *Lemma* articulated; column of the awns glabrous, variable in length, 6-12 mm long, shorter than or exceeding the glumes; plumes of the awns dirty white to distinctly yellow.

ANATOMY (Fig. 119, 120 and 160: 16b)

Leaf-blade sub-terete with a deep adaxial groove. Stereome strands well developed but not fused into a continuous layer. No deep grooves present between the bundle units. Motor cell groups well developed only adjacent to the midrib.

CAPE.—Malmesbury: van Rensburg 144. Worcester: Fairall 333. Piquetberg: Hafstrom & Acocks 2. Clanwilliam: Liebenberg 4302; Schlechter 8213. Vanrhynsdorp: Rood 789; Acocks 14747; 19503. Namaqualand: Drege s.n. (Ebenezer); Esterhuyzen 1329 & 1406; Acocks 16467.

DISTRIBUTION.—(See Fig. 123.)

This subspecies occurs mainly in the dry western Cape. It is distinguished from the other subspecies by the long glabrous column and the usually yellowish plumes of the awns. Its distribution partially overlaps with subspecies *zeyheri*. Insufficient information is available to decide whether it is ecologically separated from subspecies *zeyheri* in these areas, but this seems probable. Anatomically it differs rather strikingly from subspecies *zeyheri* by the interrupted stereome, and from the subspecies *barbata* by the absence of deep grooves between the bundle units adaxially, as well as in the presence of only two well developed motor cell groups flanking the midrib (cf. Fig. 160: 16, 16a and 16b).

(d) subsp. sericans (Hack. apud Schinz) de Winter in Kirkia 3: 136 (1963). Aristida sericans Hack. apud Schinz in Bull. Herb. Boiss 3: 381 (1895). A. capensis var. dieterleniana Schweick. in Kew Bull. 1939: 613 (1939). *Perennial*, forming erect tufts, densely leafy at the base. *Leaves* shorter than the exserted inflorescence; blades filiform, erect. *Panicle* erect stiff spike-like, or narrow and interrupted. *Spikelets* pallid to purple. *Glumes* densely to sparsely villous. *Lemma* distinctly articulated, or articulation poorly developed or even absent; column of the awns 2–7 mm long, hairy; plumes of the awns dirty white to pinkish.

ANATOMY (Fig. 121, 122 and 160: 16c and d)

Leaf-blade sub-terete to V-shaped in cross-section. Stereome strands separate, or more or less united to form a continuous layer abaxially. Deep grooves present between the bundle units adaxially. Third order bundle units two on either side of the midrib and alternating with the first order bundles, or absent between the marginal pairs of first order bundles. Motor cell groups present between all bundles except the marginal first and third order bundles.



FIG. 121.-S. zeyheri subsp. sericans: cross section of the leaf-blade (Story N.H. 24574).



FIG. 122.-S. zeyheri subsp. sericans: abaxial epidermis of the leaf-blade.

CAPE.—Steynsburg: Acocks 8670. Aliwal North: Acocks 18853. Lady Grey: Acocks 13825. Mount Currie: Acocks 13282.

BASUTOLAND.—Maluti Mtn.: Staples 146. Quthing: Dieterlen 1205. Mamathes: Guillarmod 914.

ORANGE FREE STATE.—Tabanchu: Celliers 11. Ficksburg: Dyer 4742. Bethlehem: Story 1947; Acocks 12341. Harrismith: Acocks 11206; Acocks 13559. TRANSVAAL.—Vereeniging: Forster s.n. (N.H. 24575); Story (N.H. 24574); Story 1022.

TRANSVAAL.—Vereeniging: Forster s.n. (N.H. 24575); Story (N.H. 24574); Story 1022. Krugeisdorp: Mogg 23270. Pretoria: Pole Evans 388. Carolina: Codd 1718; Acocks 12925.



DISTRIBUTION.—(See Fig. 123.)

FIG. 123.—Distribution of S. zeyheri: ●subsp. zeyheri; ○subsp. macropus; ⊗ subsp. barbata; ●subsp. sericans; ■S. fastigiata.

This sub-species may be distinguished from all the others by the hairy glumes and the elongate contracted or spike-like panicle. It is the only representative of the genus in the highveld grasslands of the Cape, the Orange Free State and the Transvaal.

In the past this subspecies has been referred to the section *Chaetaria (Aristida)* since an articulation is lacking. The presence of plumose awns, as well as the anatomical structure of the leaf-blade offers, however, conclusive evidence that it occupied an anomalous position in the section of true *Aristida*. It should be accommodated in *Stipagrostis*, in spite of the absence of an articulation. The specimens cited are not quite homogeneous and a gradual transition from the non-articulated *A. sericans* to the articulated *A. capensis* var. *dieterleniana* can be traced. No other differences could be detected and since in addition the distribution of these taxa co-incides there seems to be little doubt that they belong to one subspecies.

The taxa designated by Henrard and Schweickerdt as varieties of *Aristida capensis* have been reclassified in an attempt to create more natural units. This has been made possible by the larger range of specimens now available. Since more or less distinct distributional ranges could be established for the taxa now recognized it was decided to establish subspecies rather than varieties.

As reported by Henrard and by Schweickerdt, *A. ciliata* occasionally hybridizes with *S. zeyheri* var. *macropus* (*A. capensis* var. *macropus*). This hybrid was assigned the name *A. schlechteri* by Henrard. (The present author has, however, not adopted this name as many other hybrids have since come to notice, and to assign specific names to all these would cause confusion). Only one additional record of this hybrid has come to the author's notice since Schlechter's original gathering, namely *Acocks* 14817. Thus the hybrid may be regarded as being one of relatively little importance.

The anatomy of the leaf-blade supports Henrard's view that his Aristida schlechteri is of hybrid origin, the general features being intermediate between those of S. zeyheri and S. ciliata.



FIG. 124.-S. gonatostachys: cross section of the leaf-blade (Dinter 1022).



FIG. 125.-S. gonatostachys: abaxial epidermis of the leaf-blade.

18. S. gonatostachys (Pilger) de Winter in Kirkia 3: 134 (1963) Aristida gonatostachys Pilger in Engl. Bot. Jahrb. 48: 343 (1912).

Perennial densely caespitose dwarf plants, 2–10 cm high; *Culms* exserted beyond the small tussocks, naked, geniculate, 1-noded, thickened towards the node, hairy just below the upper node or glabrescent. *Leaf-sheaths* reduced to scales near the base, long upwards, glabrous or scantily villous on the margin, the upper sheath leafless or with a short blade. *Leaf-blades* up to 4 cm long, involute, obtuse, deeply grooved beneath, densely covered with long crisped hairs arising in the grooves, scaberulous on the upper surface. *Panicle* shortly peduncled, partially enveloped by the uppermost sheath, contracted, narrow, bearing 3–6 spikelets; rhachis pubescent. *Glumes* subequal, or the lower slightly exceeding the upper; the lower 9–10 mm long, minutely scaberulous; the upper almost glabrous. *Lemma* glabrous, purplish or pallid, including the callus about 4 mm long; column twisted, glabrous, up to 4 mm long; central awn up to 16 cm long, densely plumose in the upper part; lateral awns naked, up to 9 mm long.

ANATOMY (Fig. 124, 125 and 160: 17)

Leaf-blade narrowly horseshoe-shaped in transverse section; abaxial surface deeply grooved between the bundles; adaxial surface undulate, covered with long, sharp unicellular hairs; margins acute, often terminated by papilla-like hairs. Abaxial epidermis: cells with extremely thickened walls; stomatal zones often completely hidden by very long, wavy unicellular hairs lying longitudinally appressed in the grooves; silicified cell zones of 3-5 files containing silicified cells, alternating with narrower ripple-walled cells; silicified cells square or sub-circular, usually accompanied by thin-walled suberized cells, the latter square, broadly oblong or transversely-oblong in shape; many papilla-like broad-based retrorse barbs present, especially along the margins of the zones; two-celled hairs not observed but probably present. Vascular bundle units: first order units 3, broadly ovate-oblong; third order units alternating with those of the first order, broadly oblong to oblong-circular; midrib similar to the other first order bundles. Bundle sheaths: outer of large thin-walled parenchyma cells containing chloroplasts, interrupted only in the first order bundles by the stereome strands; inner sheaths of much smaller thick-walled cells lacking chloroplasts; complete in all bundles. Chlorenchyma a single row of tabular cells arranged radially around the bundles. Stereome well developed abaxially opposite all bundles but in contact only with the first order bundles; adaxially poorly developed, present in small groups opposite all the first order bundles and the marginal third order bundles; consisting of small-celled fibres throughout. Motor cells present only opposite the third order bundles flanking the mibrib, consisting of large groups of thin-walled parenchyma cells.

SOUTH WEST AFRICA.—Luderitz: Range 1177; Giess 2334; Kinges 2731; de Winter & Hardy 7907; 7888. Swakopmund: de Winter & Hardy 8098.

DISTRIBUTION.—So far only recorded from the Luderitz and Swakopmund districts in the dry central Namib Desert. It occurs on wind-blown sand between rocks on mountainsides, as well as in depressions on the gravelly desert flats where water collects during showers.

This species is closely allied to S. obtusa with which it may be confused. Distinguishing features are the very scabrid leaf-sheaths and blades; the bristles on the swollen part of the upper internode; the culm which is geniculate at the upper internode so that the inflorescence and sheath form an angle with the rest of the culm; the, on the whole, shorter central awn (± 1.5 cm); a longer callus and the narrower more contracted, subsecund inflorescence which is usually not fully exserted from the rather broad uppermost sheath. S. gonatostachys forms a connecting link between S. obtusa and S. hermannii, species which on a superficial examination would not appear to be related. The latter two species both occur in the Namib in South West Africa S. hermannii is mainly found in the very dry central and coastal parts of the desert while S. obtusa has a wide distribution but also inhabits marginal desert areas, penetrating deeper into the desert in wetter seasons. In this way the two species occasionally come into contact. A careful examination of the material of S. gonatostachys has led the author to consider the possibility that this species originated as a result of hybridization between S. obtusa and S. hermannii. S. hermannii has very scabrid sheaths and leaf-blades, culms which are geniculate at the uppermost node, spicate inflorescences sheathed at the base, and a well developed callus. It can

therefore be seen that most of the characters by which *S. gonatostachys* is distinguished from *S. obtusa* are possessed by *S. hermannii*. *S. gonatostachys* can however be regarded as having become a well stabilized reasonably distinct species.



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FIG. 127.-S. lanipes: abaxial epidermis of the leaf-blade.

The Swakopmund specimens (de Winter & Hardy 8098) have very hairy glumes but do not differ in other respects from the Luderitz specimens, and probably only represent a hairy form.

19. S. lanipes (*Mez*) de Winter in Kirkia 3: 135 (1963) Aristida lanipes Mez in Fedde Rep. 17: 153 (1921).

Practically the only difference between this species and S. obtusa is the woolly leaf-sheaths of the former. Only two collections of S. lanipes are known, viz. the type gathering, Range 1822, apparently a rather depauperate specimen and de Winter & Giess 6133 both from the Luderitz district in South West Africa. The latter specimen has inflorescences up to 21 cm long, strongly resembling those of S. obtusa, but more depauperate inflorescences on the same plants reach a length of only 4 cm and bear 5-7 spikelets, thus greatly resembling the type. In de Winter & Giess 6133 the lower glume exceeds the upper in length whereas in the type the lower glume is subequal to or shorter than the upper. This character, however, is known to vary in other species and, therefore, may be of secondary importance.

Anatomically S. lanipes agrees very closely with S. obtusa (see Fig. 126, 128 and 160: 18 and 19).

From the above it is evident that the status of S. lanipes as a species distinct from S. obtusa is somewhat doubtful. Until a fuller range of specimens becomes available a final decision must be withheld.

20. S. obtusa (Del.) Nees in Linnaea 7: 293 (1832) Aristida obtusa Del., Fl. Aegypt 31 (1813); A. bifida J. Karl in Mitt. Bot. Staatssamml. Muenchen 3: 86 (1951). Arthratherum obtusum (Del.) Nees, Fl. Afr. Austr. 179 (1841).

Stipagrostis capensis Nees in Linnaea 7: 291 (1832).

Perennial, compactly caespitose due to the numerous innovations bearing dense tufts of leaves. Culms from a few cm up to 60 cm high, slender, 1-noded, internodes and nodes glabrous. Leaf-sheaths glabrous or rarely villous, the basal occasionally woolly on the margin; auricles bearded. Leaf-blades variable in length, 1.5-25 cm long, setaceous, convolute, subterete, occasionally sparsely villous or scaberulous, hirtellous on the upper surface, apex obtuse. *Panicle* very narrow, erect, contracted, but rather loose and interrupted at the base, 2.5-20 cm long, branches solitary, axils Spikelets pallid or flushed with purple at the base. Glumes subequal, glabrous. dorsally scaberulous with the very fine spines in numerous, more or less parallel longitudinal rows; the lower obtuse, 3-nerved, usually exceeding the upper in length, 8.5-12 mm long; the upper subacute, 1-3-nerved, 8-11 mm long. Lemma smooth, about 3 mm long including the callus; column variable in length 4-10 mm long, straight or twisted; central awn scaberulous in the lower half, plumose upwards, $2-3\cdot 2$ cm long; lateral awns naked, very fine $0\cdot 75-1\cdot 75$ cm long; callus acute or occasionally minutely or obliquely bifid. Caryopsis narrowly elliptic-oblong, about 2 mm long; embryo about $\frac{2}{3}$ the length of the grain; hilum as long as the grain.

ANATOMY (Fig. 128 and 160: 19)

Leaf-blade sub-circular in transverse section with a smooth-sided deep adaxial median groove and long, thin unicellular hairs on the epidermis opposite the stereome strands in the adaxial groove; abaxial surface with deep narrow grooves between all the bundles; margins obliquely obtuse. Abaxial epidermis, when scraped, breaking up into narrow strips due to the deep grooves, in which the stomatal zones are situated. The scrapes show only the silicified cell zones which consist of up to 8 files containing only silicified cells, alternating with files of long ripple-walled cells; silicified cells sub-circular, solitary or accompanied by thin-walled suberized cells which vary in shape from transversely narrowly-oblong to oblong with somewhat undulate walls; broad-based papilla-like retrorse barbs are present in these zones. Vascular bundle units: first order units 3, square or oblong in outline; third order units similar to those of the first order but smaller, two on either side of the mibrib and one in each margin; midrib

similar to the other first order bundles. *Bundle sheaths:* the outer of large thin-walled cells, interrupted by the stereome strands ab- and adaxially in the first order bundles, and abaxially in the third order bundles flanking the midrib, intact in all the other bundles; inner sheath of smaller cells with thickened walls interrupted abaxially only in the first order bundles, otherwise intact. *Stereome strands* well developed abaxially opposite all bundles forming narrow bands of approximately constant width; present adaxially opposite first order bundles, and in very small groups opposite the marginal third order bundles. *Motor cells* present only in two very large many-celled groups flanking the midrib.

CAPE.—Prince Albert: *Marloth* 3055. Kimberley: *Leistner* 944. Kenhardt: *Leistner* 2466. Kuruman: *Pole Evans* 2089. Hay: *Esterhuyzen* 2317. Gordonia: *Story* 5512. Namaqualand: *Zeyher* 1815.



FIG. 128.-S. obtusa: cross section of the leaf-blade (Krapohl PRE 21862).



FIG. 129 .- Distribution of S. obtusa.

ORANGE FREE STATE.—Fauresmith: Pole Evans 1572.

SOUTH WEST AFRICA.—Luderitz: Giess 2040. Keetmanshoop: Dinter 4952. Gibeon: Codd 5878. Rehoboth: Strey 2103. Windhoek: de Winter & Giess 7139. Omaruru: Liebenberg 5031. Swakopmund: de Winter 3204.

DISTRIBUTION.---(See Fig. 129.)

This widespread and common species is one of a small group of four closely related species, i.e. S. obtusa, S. lanipes, S. gonatostachys and S. dinteri. The relationship of these species is referred to on page 353 in the general discussion of the affinities of the species of Stipagrostis. For specific differences the reader is referred to the discussion under the other species and to the keys.

Aristida bifida J. Karl, described in 1951, is regarded to be synonymous with S. obtusa, as no differences other than the bifid callus could be detected. This character is not constant: the callus being acute in the majority of specimens examined, very obliquely bifid in some specimens, and distinctly bifid in others. Specimens with bifid and acute calli have been collected even in the same population. S. obtusa is the only species of Stipagrostis for which a bifid callus has been recorded.

One record of a putative hybrid between *S. obtusa* and *S. dregeana* was collected near Aus in South West Africa. The vegetative parts of this plant resemble *S. obtusa* but the abaxial grooves on the leaf-blade are shallower and less hairy. Whereas the inflorescence is narrower than in *S. dregeana*, the glumes are brownish and flushed with purple and the plumes of the awns tend to be yellowish, as in typical *S. dregeana*. 5752152-6 The lower glume is finely scaberulous (this roughness is more like that of *S. obtusa* than of *S. dregeana* which is coarser and sparser) and slightly exceeds the upper glume (see *Giess & van Vuuren* 815 in PRE and Windhoek).

The diagrams of the cross-section of the blade of *S. obtusa* given by Guenzel (1921; Fig. 22b) and Theron (1936; t. 26 Fig. 1) agree closely with Figure 128 in this paper. Guenzel's diagram probably depicts a young leaf since the stereome is absent adaxially opposite the midrib and the marginal third order bundles. Guenzel also comments on the variability of the shape of the silicified cells, which further indicates that the



FIG. 130.-S. uniplumis var. uniplumis: cross section of the leaf-blade (de Winter 3410).



FIG. 131 -S. uniplumis var. uniplumis: abaxial epidermis of the leaf-blade.

material he used most probably was young. In this respect juvenile leaves of *Stipa-grostis* species occasionally show variability: the silicified cells vary from dumb-bell-shaped to circular in some young leaves whereas they are almost invariably circular in well developed, mature leaves. See also Jelenc (1950) for an account of *S. obtusa* (*Aristida obtusa*) in North Africa.

21. S. uniplumis (Licht.) de Winter in Kirkia 3: 136 (1963)

Perennial or weak perennial, usually densely caespitose, up to 75 cm or more high. Culms erect, 3-4-noded, simple or branched upwards, scaberulous, or smooth and glabrous; nodes glabrous. Leaf-sheaths glabrous; auricles densely long-bearded. Leaf-blades setaceous, convolute, up to 15 cm high, glabrous on the lower surface, scaberulous on the upper, and with a few long hairs towards the ligule. Panicle exserted, narrow and contracted or effuse. Spikelets palid. Glumes glabrous or with a few hairs on the margins, chartaceous, unequal; the lower 8-9 mm long; the upper 9-11 mm long, flat or grooved on the back and conspicuously veined. Lemma abruptly passing into the awn, including the callus $2 \cdot 5 - 4 \cdot 0$ mm long; callus about 1 mm long, acute, densely bearded; column about 5 mm long with a dense pencil of hairs at the branching point of the awn, otherwise glabrous, central awn up to $2 \cdot 5$ cm long, naked in the lower third or plumose to the base; lateral awns naked, up to 12 mm long, very fine. Caryopsis narrowly elliptic-oblong, $2-2 \cdot 5$ mm long; embryo nearly half the length of the grain; hilum as long as the grain.

ANATOMY (Fig. 130, 131 and 160: 20a-c)

Leaf-blade more or less flat to widely V-shaped in transverse section; keel almost absent; abaxial surface undulate or practically smooth; adaxial surface with first order bundles slightly protruding; margins sub-acute to obtuse. Abaxial epidermis: cells fairly thin-walled to thick-walled: stomatal zones with one to three rows of stomata and 3-6 rows of long strongly ripple-walled cells as well as scattered narrowly-oblong short elements; bicellular hairs present; slicified cell zones with 4-7 files of silicified cells, alternating with files of finely undulate ripple-walled cells; silicified cells sub-circular, in young leaves occasionally kidney-shaped or dumb-bell-shaped, solitary or accompanied by square, oblong or transversely oblong suberized cells with slightly undulate walls; both zones usually flanked by broad-based, retrorse barbs. Vascular bundle units: first order units 3-7, broadly oblong to broadly ovate in outline; marginal bundle units of the second or third order; third order units ovate, 1-2 on either side of the midrib and one between the second and first order marginal units; midrib similar to the other first order bundles. Bundle sheaths: outer sheath of large thin-walled cells containing chloroplasts, abaxially interrupted by the stereome strands in the first order bundles and orcasionally interrupted in some of the third order bundles; inner sheath of smaller thick-walled cells, complete in most bundles. Chlorenchyma a single row of tabular cells arranged radially around the bundles. Stereome strands developed and usually in contact with the first order bundles adaxially, small groups of fibres present exposite the third order bundles adaxially, but absent adaxially. Motor cells forming large triangular groups of large thin-walled cells alternating with all bundles; occupying $\frac{3}{4}$ of the width of leaf-blade.

S. uniplumis sens. lat. is closely allied to S. hirtigluma but may be distinguished by the finer tubercles on the upper part of the lemma which abruptly passes into the awn; by the naked column and distinct pencil of hairs at the branching point of the awns; the shorter central awn with the apex of the plume usually obtuse in outline; the usually glabrous glumes; and the bristles of the callus which gradually increase in length upwards but are not arranged in tufts.

The var. *intermedia* has pilose glumes and occasionaly the plume ends in a naked tip.

Glumes glabrous; perennial or weakly perennial:

Panicle with numerous spikelets, contracted or open; central awn of lemma naked in the lower third, or if plumose to the base, then neither rigid and bristle-like nor dark in colour but diverging at a sharp-angle from the lemma; glumes usually not exceeding 10 mm in length var. uniplumis

(a) var. uniplumis.

Aristida uniplumis Licht. in R. & S., Syst. Veg. 2: 401 (1817). Aristida uniplumis var. pearsonii Henrard, Crit. Rev. Aristida 3: 647 (1928). Arthratherum uniplume (Licht.) Nees, Fl. Afr. Austr. 181 (1841).

Sub-perennial or perennial with simple culms, or culms branched upwards. Glumes usually not exceeding 10 mm in length. Lemma from $2-3 \cdot 5$ mm long excluding the callus; column glabrous or hairy upwards, central awn variable in length, plumose to the base or only in the upper two-thirds, usually pallid (rarely purplish), the plumes silvery.

CAPE.—Herbert: Acocks 1938. Kuruman: Pole Evans 2094. SOUTH WEST AFRICA.—Bethanien: Kinges 2167. Luderitz: Kinges 2402. Otjiwarongo: Volk 1694. Okavango: de Winter & Wiss 4415; Volk 394. Windhoek: Liebenberg 4512; de Winter 2610.

ORANGE FREE STATE.-Boshof: Burtt-Davy 10123.

TRANSVAAL.-Waterberg: Pole Evans 8817. Soutpansberg: Pole Evans 906.

DISTRIBUTION.—(See Fig. 132.)

This variety is rather variable, as may be seen from the description. Specimens from the drier coastal areas (with less than 150–200 mm rainfall) are usually weakly perennial; they possess a rather long central awn with a conspicuous, naked basal part, short lemmas, $2-2\cdot5$ mm long excluding the callus, and usually contracted inflorescences. A gradual increase in stature and the development of a more perennial base seems to be coupled with an increase in rainfall further inland. On the inland plateau of South West Africa some specimens have the central awn plumose to the base but differ in no other respect from the typical specimens. These represent the former var. *pearsonii*.

Hybrids between var. *uniplumis* and *S. hirtigluma* occur fairly frequently. These hybrids have very long awns, a pencil of hairs at the branching point of the awn and very sparsely hairy glumes, thus combining the characteristics of the two species. Examples of such specimens are: *Boss* s.n. (Tvl. Mus. No. 35618); *Boss* s.n. (Tvl. Mus. No. 36205); *Boss* s.n. (Tvl. Mus. No. 36357); *Bradfield* 373; *de Winter* 5710.

(b) var. neesii (Trin. & Rupr.) de Winter in Kirkia 3: 136 (1963). Aristida uniplumis var. neesii Trin. & Rupr., Gram. Stip. 173 (1842).

Perennial, forming dense tufts and usually with a short knotty branched rhizome. Culms simple or branched upwards. Panicle often rather narrow but lax and bearing few spikelets. Glumes usually exceeding 10 mm in length. Lemma 3.5-4 mm long excluding the callus, column hairy or glabrous; central awn usually rather short, plumose to the base, usually dark in colour, stiff and almost bristle-like, diverging at a right angle from the lemma and column.

ANATOMY (Fig. 160: 20b)

Leaf-blade more or less V-shaped in transverse section, much more strongly developed than in var. uniplumis; stereome very well developed abaxially opposite the 5–7 first order bundles and relatively weakly developed opposite some of the third order bundles; adaxially fairly well developed opposite the first, and to a lesser degree opposite the third order bundles; the marginal first and second order bundles with a fused stereome. Vascular bundle units hardly projecting adaxially, abaxial surface smooth.

CAPE.—Vryburg: Stent H. 21515; Sharpe 7473. Mafeking: Pole Evans 2441. Barkly West: Esterhuysen 1044. Piquetberg: Pole Evans 2057. ORANGE FREE STATE.—Hoopstad: Goossens 1248. Boshof: Wolff 12. TRANSVAAL.—Pretoria: de Winter 793. Marico: Story 1210; Codd 1326. Wolmaransstad: Liebenberg 2437.

DISTRIBUTION.—(See Fig. 132.)

This variety grades into var. *uniplumis* and many specimens can only be referred to either variety arbitrarily. In its typical form it is very distinct both organographically as well as anatomically (see Fig. 160: 20, 20a, 20b).

It occurs in the same areas as var. *uniplumis* but often on soil which is less sandy than that frequented by the latter and in this way is to some extent ecologically separated from it. Anatomically it also grades into var. *uniplumis*.

(c) var. intermedia (Schweick.) de Winter in Bothalia 8:173 (1964) A. gracilior var. intermedia Schweickerdt in Bothalia 4, 1: 124 (1941).

Annual with simple culms. Glumes usually not exceeding 8 mm in length (rarely 9 mm long). Lemma from $2 \cdot 5 - 3 \cdot 00$ mm long excluding the callus; column glabrous, central awn pallid or purplish, plume obtuse or with a short excurrent naked tip.

Anatomical features very similar to that of the var. *uniplumis* but the stereome less developed, the hairs on the adaxial surface longer and the blade somewhat V-shaped in cross section.

SOUTH WEST AFRICA.—Swakopmund: de Winter & Hardy 8030. Karibib: Volk 150. Omaruru: Merxmueller & Giess 1680, de Winter & Hardy 8211. Outjo: de Winter 3059; Liebenberg 4962; de Winter & Hardy 8141; 8136; 8160; 8172.

DISTRIBUTION.—(See Fig. 132.)

This variety is mainly confined to the submarginal Namib Desert. Even though rare in normal years, when little rain falls in the desert it is dominant in many areas in the Karibib, Omaruru and Outjo districts in favourable years. This probably explains its poor representation in Herbaria.

As indicated by the varietal epithet this variety is somewhat intermediate in character between *S. uniplumis* and *S. hirtigluma*. This may possibly indicate a hybrid origin especially since it occupies areas where the parent species are usually not present. Stebbins (1950, p. 279) has shown that where species hybridize the hybrid, if able to maintain itself, usually occupies habitats to which the parent species are not well adapted. The var. *intermedia* occurs deeper into the desert, i.e. in areas too dry for the parent species.

Schweickerdt places this variety under (Aristida gracilior) = S. hirtigluma because of the pilose glumes. Except for this character, however, the spikelets indicate a much closer affinity to S. uniplumis: the lemmas pass abruptly into the awn, the branching point of the awns is furnished with a distinct pencil of hairs and the callus bristles are evenly distributed not arranged in two distinct tufts. The presence or absence of hairs on the glumes has proved to be diagnostically unreliable in other species of the genus and not too much weight should be attached to this character.

22. S. hirtigluma (Steud.) de Winter in Kirkia 3: 134 (1963)

Annual or perennial, caespitose, usually erect up to 80 cm high. Culms 2-5-noded; internodes terete, scaberulous or almost glabrous; nodes glabrous. Leaf-sheaths finely scaberulous; auricles densely long-bearded. Leaf-blades 6-20 cm long, setaceous, convolute, shallowly grooved below, or smooth, scaberulous; the upper surface scabrid to hirtellous. *Panicle* loose and much branched, or contracted with short branches, or very open and effuse with the branches spreading, up to 30 cm long and 20 cm wide or much shorter and narrower; pinkish in colour. *Spikelets* pallid to green or purplish. *Glumes* unequal to sub-equal, acute to sub-acute, densely pilose all over or at least on the back, 3-nerved; the lower rounded or obtusely keeled on the back, 6–11 mm long; the upper grooved on the back or at least flattened, never keeled, 10–13 mm long. *Lemma* including the callus about $3 \cdot 5-4$ mm long, conspicuously tuberculate, especially upwards; column 7–10 mm long, hairy or glabrous or scabrid, twisted; central awn plumose from base to apex or only in the upper part with a naked excurrent tip, 5–7 cm long; lateral awns naked, up to $2 \cdot 5$ cm long; callus $0 \cdot 5-0 \cdot 75$ mm long, curved, the acute tip glabrous, for the remainder hairs more or less in two series: a short fringe near the base of the callus and a long fringe at the base of the lemma. *Caryopsis* very narrowly elliptic, about 2 mm long; embryo 1 the length of the grain; hilum as long as the grain.



FIG. 132.—Distribution of S. uniplumis: Ovar. uniplumis; Ovar. necsii; Ivar. intermedia.

ANATOMY

Leaf-blade V-shaped in transverse section; abaxial surface flat or slightly undulating, furnished with large retrorse barbs; keel slightly protruding; margins obtusely rounded. Abaxial epidermis: stomatal zones with one or two rows of stomata and 2–5 rows of long ripple-walled cells with strongly and compactly undulate walls; short elements in these zones usually produced into retrorse barbs; linear 2-celled hairs present; silicified cell zones with 4–6 files containing silicified cells, and 8–12 files of ripple-walled cells with finely undulate walls adjacent to the first order bundles; 1–2 files containing silicified cells sub-circular, usually single or occasionally accompanied by a thin-walled more or less square
suberized cell with somewhat undulate walls; broad-based retrorse barbs flanking this zone. Vascular bundle units: first order bundles 3, with or without second order bundles accompanying the marginal first order bundles, very broadly oblong and rounded in outline; third order bundles 2–3 on each side of the midrib and one on each margin; midrib similar to the other first order bundles but broadly ovate in outline and adaxial stereome strands much smaller and not in contact with the bundle. Bundle sheaths: outer of large thin-walled cells, interrupted abaxially by the stereome strands in the first and second order bundles; inner sheaths of smaller cells with slightly thickened walls in the abaxial half of the bundle, and strongly thickened walls adjacent to the stereome strands: Chlorenchyma a single layer of tabular cells radially arranged around the bundles. Stereome strands of the marginal first and second order bundles fused but small groups opposite the third order bundles; adaxial strands well developed only opposite the two marginal first order bundles; small groups of cells present opposite all the other bundles including the midrib. Motor cells strongly developed flanking the midrib and occupying $\frac{3}{4}$ or more of the leaf thickness, groups rapidly diminishing the size outwards to absent near the margins.

The characteristics of the spikelets of S. hirtigluma were compared critically with those of A. gracilior and no constant differences could be detected. As stated by Henrard (1928) the only difference between these species is the denser more contracted inflorescence of S. hirtigluma. Although small differences are found in the anatomy of the leaf-blade their general pattern is remarkably similar. Since the species in question both occur in South West Africa, it does not seem justifiable to distinguish them solely on the contraction of the inflorescence. A. hirtigluma was described from Arabia and the disjunct distribution could be advanced as a reason for separating the species if forms identical with A. hirtigluma were not present in South West Africa. Nevertheless this argument would not be a very strong one since many species have a similar disjunct distribution (see p. 304). A. gracilior and its varieties are here, therefore, united with S. hirtigluma.

S. hirtigluma sens. lat. is closely allied to S. uniplumis but may be distinguished by the strongly tuberculate upper part of the lemma which gradually narrows into the awn; by the longer central awn which is excurrent into a naked tip; and by the pilose glumes.

Annuals with very few leaves at the base, the culms not hidden by the leaves; internodes rather soft and easily compressible:

Panicle rather narrow, when fully exserted much longer than wide..... var. hirtigluma Panicle very lax, open and spreading, when fully exserted not much longer than wide var. pearsoni

(a) var. hirtigluma.

Aristida hirtigluma Steud. ex Trin. & Rupr., Gram. Stip. 171 (1842).

Annual, with few basal leaves. Panicle much longer than wide. Spikelets with the column of the awns glabrous or hairy, central awn hairy down to the branching point of the awns.

ANATOMY (Fig. 133, 134 and 160: 21)

As described for the species, but the marginal first order bundle units not accompanied by large second order units as is the case in var. *patula*.

SOUTH WEST AFRICA.—Swakopmund: Giess 3034; Boss (Tvl. Mus. No. 36191). Rehoboth: Fleck 802. Bethanien: van Son (Tvl. Mus. No. 31827); Kinges 2166; 2159; 2218; 2099.

DISTRIBUTION.—(See Fig. 137.)



FIG. 133.-S. hirtigluma var. hirtigluma: cross section of the leaf-blade (Trott s.n.: Arabia).



FIG. 134.-S. hirtigluma var. hirtigluma: abaxial epidermis of the leaf-blade.

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This variety has a fairly wide distribution in the Namib Desert from Bethanien in South West Africa to Loanda in Angola; it also occurs in North Africa and the desert areas of the Middle East. Relatively few specimens from Southern Africa are available for study. The original description is based on *Schimper* 165 collected in Abyssinia.

Variety *hirtigluma* does not seem to be selective as to habitat and is found growing in sandy and gravelly soils as well as in rocky substrata.

(b) var. pearsonii (Henrard) de Winter in Kirkia 3: 134 (1963). Aristida gracilior var. pearsonii Henrard, Crit. Rev. Aristida 3: 695 (1928).

Differing from var. *hirtigluma* in the effuse, open and spreading panicle which when fully exserted from the sheaths usually is only slightly longer than wide. Some specimens have the central awn of the lemma plumose for its whole length while others are naked towards the base and plumose only upwards.

The anatomy of the leaf-blade of this variety agrees in detail with that of var. hirtigluma.

SOUTH WEST AFRICA.—Keetmanshoop: de Winter 3259; 3411; Oertendahl 140; 158. Gibeon: Schweickerdt 2267; van Vuuren & Giess 1161. Omaruru: de Winter 6035a; 3167; Kinges 3439, 3213; Schweickerdt 2261; 2257; Boss s.n. (Tvl. Mus. No. 36379; 36371; 363746). Outjo: Liebenberg 4937; de Winter 3124; Volk 2874. Kaokoveld: de Winter & Leistner 5693; 5621; 5307; 5377.

This variety occurs in desert and semi-desert areas from the Warmbad district in the South to the Kaokoveld in the North of South West Africa (see Fig. 137) as well as in Angola. The type specimen was collected in the Mossamedes area of Angola (*Pearson 2249*).

The character on which the annual var. *pearsonii* was distinguished in the past from the perennial var. *patula* (*Aristida gracilior*) i.e. the bare lower part of the central awn, is unreliable. Both plumose awns as well as awns with a naked base occur in var. *pearsonii*. The annual habit and absence of a dense basal tuft of leaves seems to be a more reliable character for distinguishing var. *pearsonii* from var. *patula*, since the latter is a perennial and possesses a dense basal tuft of leaves.

A. gracilior var. intermedia Schweickerdt agrees with S. hirtigluma sens. lat., only in the pilose glumes and annual habit. In the characters of the lemma and awns it matches S. uniplumis var. uniplumis in detail. For this reason it has been transferred to S. uniplumis.

(c) var. patula (Hack.) de Winter in Kirkia 3: 134 (1963).

Aristida hirtigluma var. patula Hack. in Denkschr. Kais. Akad. Naturw. 78: 401 (1906). Aristida gracilior Pilger in Engl. Bot. Jahrb. 40: 80 (1907).

Densely tufted, strictly erect *perennial*, with a dense basal tuft of tough setaceous leaves. *Panicle* effuse and spreading with the branches well developed, when fully exserted from the sheaths not much longer than wide. *Lemma* with the central awn plumose for its entire length; the column glabrous or hairy.

Anatomical structure of the leaf-blade is as described for the species but the marginal first order bundle and the stereome of these bundles fused to form a single unit (Fig. 135, 136 and 160: 21a).

CAPE.—Vryburg: Brueckner 1180. Kimberley: Leistner 1634.

SOUTH WEST AFRICA.—Windhoek: de Winter & Giess 7135; de Winter 3527; Schweickerdt 2264; Liebenberg 4511. Otjiwarongo: Liebenberg 4903. Karibib: de Winter 2680. Grootfontein: Merxmueller & Giess 1340; Schweickerdt 2168; 2294; de Winter 2833; de Winter & Giess 6801; Story 5229. Estosha Game Reserve: Volk 2411; Breyer s.n. (Tvl. Mus. No. 20614). BECHUANALAND.—Mabua Sehoba Pan, de Winter 7464. TRANSVAAL.—Soutpansberg: Codd 4088; de Winter & Codd 310. Leydsdorp: Soekmekaar: Hafstrom & Acocks 3.



FIG. 135.—S. hirtigluma var. patula: cross section of the leaf-blade (de Winter 3527).



FIG. 136.-S. hirtigluma var. patula: abaxial epidermis of the leaf-blade.

DISTRIBUTION.--(See Fig. 137.)

This variety which occurs in less dry areas than the previous varieties shows a marked preference for calcareous soils and is common on limestone outcrops on the

inland plateau of South West Africa from Windhoek northwards. It is seen occasionally in sandy areas usually with limestone outcrops occurring in the vicinity.

As in the case of *S. uniplumis* the habit of the varieties of *A. hirtigluma* is strongly correlated with the annual rainfall; those occurring in the drier coastal areas being annuals whereas var. *patula*, the inland variety, is a perennial.

In the Waterberg and Grootfontein areas of South West Africa very robust specimens, possessing pilose glumes, occur. Because of the hairy glumes these have previously been referred to the var. *patula* (A. gracilior) but differ from typical plants in the taller harder culms, the often shorter awns and the less conspicuously tuberculate lemmas. These specimens are very variable in floral characters: the glumes being almost glabrous to densely pilose whereas the habit is strongly reminiscent of S. uniplumis. Volk who collected extensively in the Waterberg area remarked on the resemblance in habit of some of these specimens to S. uniplumis, occurring in the same area. There seems to be little doubt that the following specimens represent hybrids between S. hirtigluma var. patula and S. uniplumis var. neesii: Volk 1080; 1020; 376; 1531; 2338; de Winter 2778; Giess 2223; Boss (Tvl. Mus. Nos. 36456; 36205). Esterhuysen 1026; le Roux 1043. The anatomy of the leaf-blade of these specimens approaches that of S. uniplumis var. neesii much more closely than that of S. hirtigluma var. patula (see Fig. 138, 139 and 160: 20c).



FIG. 137.—Distribution of S. hirtigluma: Ovar. hirtigluma; Ovar. patula; Ovar. pearsonii.



FIG. 138.—S. uniplumis var. neesii \times S. hirtigluma var. patula: cross section of the leaf-blade (de Winter 2778).



FIG. 139.-S. uniplumis var. neesii × S. hirtigluma var. patula: abaxial epidermis of the leaf-blade.

23. S. hermannii (Mez) de Winter in Kirkia 3: 134 (1963)

Aristida hermannii Mez in Fedde Rep. 17: 153 (1921).

Annual, laxly caespitose, up to 15 cm high. Culms geniculately ascending, 2-4noded, shortly hairy below the uppermost node; internodes densely but minutely pubescent. Leaf-sheaths loose, chartaceous densely scabrid especially on the ribs, margins ciliolate; auricles bearded. Leaf-blades much reduced, folded or convolute, densely scabrid on both surfaces, 1-2 cm long and about 1 mm wide. Panicle partly enclosed by the uppermost sheath, ovate-oblong, dense, up to 8 cm long; rhachis and branches scabrid; axils pubescent. Spikelets silvery. Glumes narrowly lanceolate, acute, shortly awned, 3-nerved, the lower usually exceeding the upper, 9-11.5 cm long, densely but minutely scaberulous; the upper 8-10 cm long, scaberulous towards the apex. Lemma punctuate-scaberulous, including the callus 3.5-4 mm long; callus very acute, densely bearded, 1-1.25 mm long; column very scabrous, twisted, hairy below and at the branching point, very variable in length, 1-10.5 mm long; central awn scabrid in lower third, plumose upwards, 2-4 cm long; lateral awns naked, very fine, 1-1.5 cm long. Caryopsis very narrowly oblong-elliptic; embryo about 1 the length of the grain; hilum as long as the grain.



FIG. 140.-S. hermannii: cross section of the leaf-blade (Kinges 2634).

ANATOMY (Fig. 140, 141 and 160: 22)

Leaf-blade V-shaped in transverse section, both surfaces strongly undulate giving the section a moniliform appearance; hairs present both ad- and abaxially, the abaxial longer and thinner; keel well developed; margins obtuse. Abaxial epidermis thin-walled: stomatal zones with 3-5 rows of stomata and 4-7 rows of long ripple-walled elements interspersed with long retrorse barbs; bi-cellular linear hairs present in these zones. Silicified cell zones with 3-4 files of short elements alternating with usually single files of long ripple-walled cells (undulations less marked than in the stomatal zones) adjacent to the first order bundles; 2-3 files of short elements present adjacent to third order bundles; silicified cells variable in shape, but usually dumb-bell-shaped and alternating with oblong to almost square, slightly, to distinctly, ripple-walled suberized cells, or large broad-based retrorse hairs; bicellular hairs found mainly in the transitional area between the stomatal and silicified cell zones. Vascular bundle wits: first order units 3, circular in outline; third order units 3 on either side of the midrib and two on each margin, almost as large as the first order units; midrib better developed than the

other first order bundles. *Bundle sheaths:* outer sheath of large thin-walled cells; inner of smaller irregular cells with thickened walls, interrupted only abaxially by the stereome in the first order bundles and in the midrib, but complete in all the third order bundles. *Chorenchyma* a single row of tabular cells radially arranged around the bundles. *Stereome strands* well developed only opposite the first order bundles adaxially, but present as small groups of fibres, often only one cell layer thick, both ab- and adaxially in all the other bundles. *Motor cell* groups present, alternating with all except the two marginal bundles on either side; 4–6 cells in each group, occupying about half the leaf thickness.



FIG. 141.-S. hermannii: abaxial epidermis of the leaf-blade.

SOUTH WEST AFRICA.—Luderitz: Dinter 6396; Kinges 2021; 2634; Giess & van Vuuren 729. Swakopmund: Boss s.n. (Tvl. Mus. Nos. 36395; 36439).

DISTRIBUTION.—(See Fig. 142.)

Closely allied to S. subacaulis from which it may be distinguished by the better developed culms which are somewhat exserted from the tuft of leaves, and by the sparsely, bristly hairs below, and at the branching point of the awns. Anatomically these two species are rather distinct, differing from all the other species in the moniliform appearance of the leaf in cross-section and the pronounced keel projecting abaxially. It is difficult to distinguish *S. hermannii* from *S. subacaulis* anatomically. To some extent *S. hermannii* is also related to *S. uniplumis* particularly the sub-perennial desert forms of the latter species.

S. hermannii is confined to the drier coastal areas of South West Africa.

24. S. namibensis de Winter in Bothalia 8:173 (1964)

Annual forming sprawling lax tufts, up to 20 cm high, but usually smaller. Culms simple, 2-3 (4)-noded, internodes densely scabrid to sub-pubescent, geniculately ascending, nodes glabrous. Leaf-sheaths loose, scabrid. Leaf-blades rather thin, ribbed abaxially and adaxially and scabrid on the ribs. Ligule a fringe of hairs. Panicle somewhat contracted but much branched and not very dense, rhachis and branches densely scabrid, branches usually 2-nate, alternate. Spikelets erect, pallid, usually purplish at the very base. Glumes unequal, inverse, glabrous, rather firm, chartaceous, lanceolate; lower usually distinctly exceeding the upper in length, 8-9 mm long, sub-obtuse emarginate and with a few short hairs at the hyaline apex 3- (4-5)-nerved, rounded on the back; upper 3-nerved acute, 6-7 mm long and flattened on the back. Lemma 3-nerved, tubular with the margins strongly overlapping, glabrous, smooth, including the callus 3.5-5 mm long, articulation situated between the apex of the lemma and foot of the column; column very variable in length 2.5-5 mm long, hairy; awns 3, with only the central plumose in the upper $1-\frac{2}{3}$, shortly hairy downwards (plumes acute to sub-obtuse) 4-2.5 cm long; lateral awns fine half or usually less than half the length of the upper, very finely scabrid, strongly diverging from the central; callus very acute, often somewhat twisted, densely bristly, the bristles at the base of the lemma longer. Caryopsis narrowly elliptic in outline, 2-2.5 mm long; embryo about $\frac{2}{3}$ the length of the grain; hilum as long as the grain, dark brown.



FIG. 142.—Distribution of S. hermannii; S. subacaulis.

ANATOMY (Fig. 143, 144 and 160: 22a)

Leaf-blade horseshoe-shaped in transverse section or somewhat expanded; ad- and abaxial surfaces somewhat undulated, furnished with retrorse barbs on the abaxial surface; adaxially mainly with fairly long unicellular hairs; keel mainly projecting abaxially; margins obtuse. Abaxial epidermis: cells thin-walled; stomatal zones with 2-4 rows of stomata and 4-8 rows of long ripple-walled cells, undulations moderately deep and close together; silicified cell zones 4-6 files of short elements alternating with 5-7 files of long ripple-walled elements adjacent to the first order bundles; 1-3 files of short elements present opposite the third order bundles; silicified cells dumb-bell-shaped; bicellular hairs present but few. Vascular bundles: first order bundle units 3, subcircular; third order bundles subcircular, 2-3 on each side of the midrib and one on either margin; midrib forming a fairly distinct keel. Bundle sheaths: outer of large regular thin-walled cells filled with chloroplasts; inner smaller and lacking chloroplasts. Chlorenchyma of a single layer of tabular cells radially arranged around the bundles. Stereome strands well developed only abaxially opposite the first order bundles, present as small groups opposite the third order bundles, very weakly developed or absent adaxially. Motor cells fairly well developed between all bundles except the marginal two.



FIG. 143.-S. namibensis: cross section of the leaf-blade (Keet 1698).



FIG. 144.-S. namibensis: abaxial epidermis of the leaf-blade.

SOUTH WEST AFRICA.—Swakopmund: de Winter & Hardy 8025. Omaruru: de Winter & Hardy 8199. Namib Desert (no precise locality), Keet 1698.

S. namibensis is allied to S. hermannii and S. subacaulis. From S. subacaulis it can be distinghuished easily by the well developed culms. Its closest affinity is with S. hermannii which on the whole has longer awns (2-4 cm) and membranous narrow glumes which taper to a very fine apex. In S. namibensis the awns are usually shorter

 $(1 \cdot 4 - 2 \cdot 5 \text{ cm})$ and the glumes broadly lanceolate with acute to sub-obtuse and emarginate apices. It is not uncommon in the desert near the coast in the Swakopmund and Omaruru districts, at least in good years. It occurs in the same habitat as the other two related species, often together with them.

25. S. subacaulis (Nees) de Winter in Kirkia 3: 136 (1963) Arthratherum subacaulis Nees, Fl. Afr. Austr. 1: 180 (1841). Aristida subacaulis (Nees) Steud., Nomencl. Bot. 2, 1: 132 (1842).

Annual forming small compact tufts up to 10 cm high, but usually much smaller. Culms minutely hairy; internodes finely hairy; nodes more or less glabrous. Leafsheaths loose, chartaceous, scabrid, above; auricles bearded. Leaf-blades short, folded or convolute, up to 3 cm long and about 1 mm wide, strongly striate, densely scabrid below, hispid on the upper surface. Panicle contracted, usually hidden by the leaves, enclosed at the base by the upper sheath; rhachis and branches scabrid. Spikelets silvery. Glumes linear-lanceolate, acuminate, 3-nerved, membranous; the lower 10–13 mm long; the upper 8–10 mm long. Lemma smooth, glabrous, including the callus 3–4 mm long; column very variable, 1–13 mm long, twisted; central awn scaberulous to shortly hairy in the lower part, plumose above the middle, up to 4.3cm long; lateral awns fine, glabrous, up to 1.8 cm long. Caryopsis very narrowly oblong-elliptic; embryo about half the length of the grain; hilum as long as the grain.

ANATOMY (Fig. 145, 146 and 160: 23)

Leaf-blade V-shaped in transverse section; upper and lower surface strongly undulate, furnished abaxially with papilla-like cells and retrorse barbs; adaxially mainly with long, thin unicellular hairs; keel strongly developed and projecting both ad- and abaxially but more strongly so abaxially; margins truncate to obtuse. Abaxial epidermis: cells thin-walled: stomatal zones with 2-4 rows of stomata and 4-6 rows of long ripple-walled cells, undulations deep and well-spaced; silicified cell zones with 5-7 files of short elements alternating with 1-2 files of long ripple-walled cells (undulations much less distinct than in stomatal zones) adjacent to the first order bundles; 2-3 files of short elements present, adjacent to third order bundles; silicified cell sumb-bell-shaped alternating with narrowly oblong to almost square, slightly to distinctly undulate, suberized cells and large broad-based retrorse hairs; bicellular hairs present, flanking the stomatal zones. Vascular bundles: first order bundles units 3, broadly ovate to oblong-circular; third order units subcircular, 2 or 3 on either side of the midrib and one on either margin; midrib larger and with a larger stereome strand than the other first order bundles, forming a conspicuous keel. Bundle sheaths: outer of large, regular, thin-walled cells filled with chloroplasts; inner of smaller very slightly thickened more irregular cells, lacking chloroplasts; outer sheat interrupted only abaxially opposite the first order bundles, small few-celled groups present adaxially opposite adaxially arranged around the bundles. Stereome strands well developed only abaxially opposite the first order bundles, small few-celled groups present adaxially opposite second and third order bundles. Motor cells consisting of two large groups of cells flanking the midrib; smaller groups alternating with the other bundles except the marginal two.

CAPE.—Namaqualand.—Drege s.n. (Verleptpram; isotype); Hardy 551; Marloth 12394.

SOUTH WEST AFRICA.—Luderitz: Giess & van Vuuren 740; 705; Giess 2348; Dinter 4104; Kinges 2633. Swakopmund: Boss s.n. (Tvl. Mus. 36316); Schweickerdt 2222; 2232; 2241.

DISTRIBUTION.—(See Fig. 142.)

For affinities see notes under *S. hermannii* (p. 370). The distributional range of this species is approximately identical to that of *S. hermannii* and the two species often occur together.

Theron (1936) compares S. lanipes with S. subacaulis. The more or less V-shaped leaves of S. subacaulis, in which the motor cell groups alternate with most of the bundles, differ markedly from those of S. lanipes where the subterete leaves possess very prominent motor cell groups only flanking the midrib. The affinity of S. subacaulis no doubt lies with S. hermannii, a fact that Theron (1936, p. 31) also mentions but only under

S. hermannii. S. hermannii and S. subacaulis are, however, not placed next to each other in Theron's enumeration. Theron's Fig. 31 depicting a cross-section of the leafblade of S. subacaulis, agrees reasonably well with Fig. 160: 23 of this paper with the exception that no stereome strands are indicated abaxially opposite the third order bundles.



FIG. 145.—S. subacaulis: cross section of the leaf-blade (Kinges 2633).



FIG. 146.—S. subacaulis: abaxial epidermis of the leaf-blade.

26. S. anomala de Winter in Kirkia 3: 133 (1963) Stipa namaquensis Pilger in Bot. Jahrb. 51; 12: 412 (1914) non Stipagrostis namaquensis, (Nees) de Winter. Type: Namaqualand, Dinter 2602 (leg. Koppel) (B, holo[†]; fragment PRE).

Perennial, or weak perennial, forming erect dense to lax tufts 10-60 cm high, densely to sparsely leafy at the base. *Culms* erect or somewhat geniculate near the base, 1-2-noded; nodes glabrous: internodes glabrous, finely striate. *Leaf-sheaths* lax, chartaceous shallowly grooved upwards, upper sheaths often firmer and tightly clasping the culms, glabrous. *Leaf-blades* setaceous, the basal often short (1 cm) and curved, or up to 20 cm long and curling at maturity; subterete, deeply grooved and scabrid on the upper surface, more or less smooth or slightly grooved and minutely scaberulous below. *Panicle* erect, stiff, very narrow and elongate, much interrupted, or more dense when very short, 3-17 cm long; rhachis and branches scabrid and narrowly grooved. *Spikelets* densely congested on short branches or in fascicles on the rhachis. *Glumes* chartaceous, subequal or unequal, the lower shorter than the upper, lanceolate, pallid or purplish, 3-nerved, apices erose-truncate or acute; the lower



FIG. 147.-S. anomala: cross section of the leaf-blade (Scott s.n.).

rounded on the back to slightly keeled, scabrid to scaberulous on the outer surface, 7-10 mm long; the upper flat to slightly furrowed between the lateral nerves dorsally, scaberulous to scabrid, 9-12 mm long. Lemma glabrous, finely punctate with scattered white tubercles upwards, about 4 mm long including the callus; column of the awn with a pencil of long stiff hairs at the base, glabrous upwards, twisted, grooved, 4-7 mm long; awn solitary, rarely with the rudiments of the lateral awns visible as small protuberances, glabrous and densely scabrous, when mature diverging at almost a right angle from the column, pallid or purple; callus acute, densely bristly. Palea very short, scale-like, about 1 mm long, 2-nerved, glabrous. Lodicules 2, lanceolate, membranous, many-nerved, 1-1.5 mm long. Ovary glabrous, styles distinct, stigmas linear, plumose. Caryopsis narrowly spindle-shaped; embryo about $\frac{1}{3}$ the length of the grain; hilum linear, situated in a narrow shallow groove.

ANATOMY (Fig. 147, 148 and 160: 24)

Leaf-blade subterete or horseshoe-shaped in transverse section; abaxial and adaxial surfaces almost smooth or very shallowly grooved; keel absent; margins sub-obtuse. Abaxial epidermis: stomatal zones with 1-3 rows of stomata and 3-5 rows of elongate-rectangular, long ripple-walled cells with strongly undulate walls, bicellular hairs present; retrorse unicellular barbs few; silicified cell zones with 6-9 files of silicified cells alternating with 5-8 files of narrow, elongate long elements with finely undulate walls; silicified cells sub-circular or weakly dumb-bell-shaped, usually accompanied by square to oblong suberized cells with undulate walls. Vascular bundle units: first order units 3, shape not well defined; the third order units flanking the midrib, paired, the marginal units single or paired, much smaller than the first order units; midrib similar to the other first order bundles. Bundle sheaths: outer sheath cells much exceeding the slightly thickened inner sheath cells in size, only the outer interrupted abaxially by stereome, all others complete. Chlorenchyma consisting of a single layer of tabular cells radially arranged around the bundles. Stereome strands exceedingly well developed abaxially opposite the first order bundles, present only as small strands adaxially opposite the third order cells forming a single large fused group opposite the midrib and the pairs of flanking third order bundles; otherwise absent.



FIG. 148.-S. anomala: abaxial epidermis of the leaf-blade.

CAPE.—Swellendam: Esterhuysen 1865. Beaufort West: Acocks 14329; Fairall 325. Prieska: Liebenberg 4114; Bryant K 35; Scott s.n. (N.H. 20131). Herbert: Leistner 1316. Hay: Acocks 2357 and 2336. Kenhardt: Minnell s.n. (N.H. 20203); von Broembsen 92; Leistner 2362.

SOUTH WEST AFRICA.—Liebenberg 5165; Schweickerdt 2280; 2272; de Winter 3409; 3258. Luderitz: de Winter & Giess 6135, Kinges 2362; 2638. Bethanien: Kinges 2161; 2165. Mariental: Schweickerdt 2370; 2270.

DISTRIBUTION.—(See Fig. 149.)

This anomalous species was in the first instance described as a *Stipa* because it has a single awn. Investigation of the anatomy of the leaf-blade as well as the organography of the spikelet has shown that it belongs to the genus *Stipagrostis* (see also Fig. 1). It is related to *S. obtusa* which it resembles in the anatomy of the leaf-blade (cf. Fig. 128 and 147) in habit, and in the finely scabrid glumes. It differs from all the other species of the genus on account of its single glabrous awn and for this reason is placed in the new section *Anomala*.



FIG, 149.-Distribution of O.S. anomala; XS. schaeferi.

Although the awn is glabrous the base of the column is furnished with a pencil of long fine hairs resembling the pencil of hairs present at the branching point of the awns in *S. uniplumis*. The large outer chlorophyll-bearing bundle sheath, circular silicified cells and the three-nerved glumes are characters typical of *Stipagrostis* and there is no doubt that *S. anomala* belongs to the latter rather than to *Aristida*. The presence of vestiges of lateral awns in some specimens indicates that *S. anomala* probably originated from a three-awned ancester, and provides an additional reason for including it in a new section of *Stipagrostis*, rather than placing it in a new genus on account of the single awn.

2.8.8. INTERRELATIONSHIP OF THE SOUTH AFRICAN SPECIES AND SECTIONS

The closer affinities of the various species have been discussed under the description and enumeration of the species (2.8.7., p. 313). A summary of these views is given in diagrammatical form in Fig. 150, p. 378. Here very closely related species are connected by double lines, closely related species by single unbroken lines, and more distant affinities by dotted lines.



FIG. 118 INTERRELATIONSHIPS OF SOUTH APPICAN SPECIES OF STIPAGROSTIS

This diagram illustrates that subdivision of the genus *Stipagrostis* into the §*Schistachne* and §*Stipagrostis* on the basis of the position which the articulation occupies in the lemma, results in the recognition of two groups of species which in their delimitation are not entirely natural. For example, *S. namaquensis* (§*Schistachne*) appears to be very closely related to both *S. amabilis* (§*Schistachne*) and *S. damarensis* (§*Stipagrostis*), and, to a lesser degree, to *S. proxima* (§*Stipagrostis*), and furthermore to *S. brevifolia* and *S. sabulicola*, both of the §*Stipagrostis*. *S. damarensis* (§*Stipagrostis*), on the other hand, shows a stronger degree of relationship to *S. namaquensis* (§*Schistachne*) and *S. sabulicola* (§*Schistachne*) and *S. namaquensis* (§*Schistachne*) than to *S. brevifolia* (§*Stipagrostis*). *S. sabulicola* (§*Stipagrostis*) shows affinities both with *S. namaquensis* (§*Schistachne*) and *S. amabilis* (§*Schistachne*), but little affinity with the remaining species of the §*Stipagrostis* except for *S. damarensis*, thus occupying a somewhat isolated position (perhaps unnaturally so) among the members of this section.

Similarly, S. dinteri (§Schistachne) finds its closest relatives in the §Stipagrostis, in particular the species S. obtusa, S. lanipes and S. gonatostachys, although affinity with S. hochstetteriana (§Schistachne) is not lacking. S. ciliata, a member typical of the §Schistachne, shows a very close degree of relationship to S. schaeferi, less so to S. hochstetteriana, both members of §Schistachne, but the sphere of relationship includes S. zeyheri and S. dregeana, both members of the §Stipagrostis.

The vertical dotted line in Fig. 150 divides, on the left hand, an interrelated group of suffrutescent, rhizomatous species from, on the right hand, a separate interrelated group of which the species are *mainly* caespitose (*S. garubensis* and *S. lutescens* have suffrutescent bases). The two groups, individually, are composed of species of both *§Schistachne* and *§Stipagrostis*.

In view of the above, from a taxonomic point of view, the sections *Schistachne* and *Stipagrostis* should be united. However, the position of the articulation in the lemma is so useful and convenient a character in the identification of the species, that for the present the two sections have been retained.

Hybrids occur fairly frequently and of these, at least two are the result of crossing where one parent belongs to \$Stipagrostis and the other to \$Schistachne (S. brevifolia \times S. namaquensis; S. zeyheri \times S. ciliata). No hybrids have been reported involving on one hand, a species from the suffrutescent group and, on the other, from the predominantly ceaspitose group.

No karyological evidence could be found for dividing the genus *Stipagrostis* into sections, all the South African species investigated being tetraploids with 2n = 44.

2.9.

THE GENUS SARTIDIA

2.9.1. AFFINITIES

In the discussion on the generic delimitation of the Aristideae on p. 226, the genus Aristida sensu lato, is divided on basis of organographic as well as anatomical characteristics into three groups (see Table on p. 226). Groups A and B represent the genera Aristida and Stipagrostis respectively, whereas group C, which consists of three species, represents a new genus. Enumeration of the characteristics of the three groups showed that this new genus, Sartidia, may be distinguished from Aristida and Stipagrostis by the size and structure of the embryo, and the anatomy of the leaf-blade and awns. In addition, Sartidia differs from Stipagrostis in the nature of the awns: Sartidia has stiff rigid spirally contorted awns, while Stipagrostis has very slender finely plumose awns. Sartidia and Aristida are, however, very similar in organographic characteristics and thus may easily be confused. Sartidia is characterized by the possession of 3-5-nerved glumes, lemmas which are hardly narrowed towards the apex and are produced into three stout, spirally contorted bristles, a very small embryo and a deeply

ventrally grooved caryopsis, as well as leaves which are rolled in the bud. Although all these characteristics are present in the genus *Aristida*, they are never represented jointly in any of the *Aristida* species. Should an examination of the spikelet be inconclusive in establishing the generic identity of a species, study of the anatomy of the leaf-blade and embryo will show clearly whether the species belongs to *Sartidia* or *Aristida*. (Fig. 152, 154, 156.)

The question now arises whether it would be sound to create a new genus on the basis of such seemingly weak organographic differences, quite apart from the fact that these are supported by distinctive anatomical differences.

For the Gramineae, a family characterized by extreme reduction of the floral parts, many cases could be cited where, in the past, genera were created on apparently insignificant organographic differences. For example, one need only mention *Poa* and *Eragrostis, Eragrostis* and *Diplachne, Monerma* and *Lepturus*, and many others. All of these genera are today accepted as being quite distinct: some of them are even regarded as belonging to different tribes. The present-day tendency in grass taxonomy is to recognize as genera those groups which, to a degree, are uniform in their combined organographic, anatomical as well as cytological characteristics, and this approach undoubtedly has resulted in a greatly improved classification. It is therefore felt that retention of the species of *Sartidia*, which differ from *Aristida* in the anatomical structure of both the embryo and the leaf-blade, in the otherwise homogeneous *Aristida*, would be contrary to the accepted practice.

The two genera Aristida and Stipagrostis together form a relatively homogeneous tribe, although Aristida has double chlorophyll-bearing bundle sheaths, whereas in Stipagrostis only the cells of the outer sheath contain chloroplasts. If Sartidia were to be included in the tribe, the Aristideae would be a tribe heterogeneous in anatomical constitution. In addition, the structure of the embryo of Sartidia differs from that of Aristida and Stipagrostis in the absence of a cleft between the coleorrhiza and the base of the scutellum. For these reasons collectively it was decided to treat Sartidia as a separate entity, and hence its characteristics were excluded from the description of the Aristideae.

On the other hand, a chromosome count of Sartidia jucunda revealed a basic number of n = 11 (2n = 22) and no significant size differences could be detected between the chromosomes of S. jucunda and those of the various species of true Aristida. The possibility should therefore not be ignored that Sartidia may yet prove to be an anomalous genus of the Aristideae.

Of many genera investigated, the Australian genera Amphipogon, Diplopogon, Plectrachne and Triodia show the greatest similarity to Sartidia in the anatomy of the leaf-blade. In these genera the chlorenchyma cells are arranged diffusely while bicellular hairs are present, characters agreeing with those of Sartidia. In Amphipogon and Plectrachne the embryo has a cleft between the coleorrhiza and the base of the scutellum, a character they thus have in common with members of the Danthonieae, and in addition, the anatomy of the leaf-blade agrees in general features with that of Danthonia, so that they probably could be placed in the same tribe. However, the characters of the embryo and hilum, as well as the structural differences of the lemma, prevent Sartidia from being placed near these genera and exclude it from the Danthonieae. Although the embryo of Diplopogon and Triodia have not been examined, othet characters show such similarity to those of Amphipogon and Plectrachne that it is probable that their embryos are similar in structure.

Since the attempts to establish close affinities for *Sartidia* have failed, it is felt that further progress will hardly be possible until a wider knowledge of the anatomical features of various other genera has been acquired. Thus for the time being the genus is placed next to *Aristida*.

SARTIDIA de Winter

In Kirkia 3: 137 (1963)

Spikelets solitary, pedicelled. Rhachilla disarticulating above the glumes, not produced beyond the base of the floret. Floret 1, hermaphrodite, exceeding the glumes (the awns long exserted), linear in outline. Glumes persistent, narrow, acute to acuminate, with or without apical awns, the lower usually 3-nerved, the upper 3-5-nerved. nerves evanescent. Lemma somewhat dorsally compressed, sub-cylindrical, grooved ventrally, with involute margins, thinly to thickly coriaceous when mature, glabrous and smooth or scabrid, 3-nerved, the nerves more or less parallel and not anastomosing, hardly narrowed upwards and without an articulation, passing into three awns, each furnished with a single nerve, with or without a column; column when present slightly twisted, as thick as the body of the lemma; awns glabrous or scabrid only, thick and coarse, spreading, collectively laxly spirally contorted at the base when mature, subequal; callus well-developed, acute, densely but shortly bearded. Palea very small, scale-like, usually coriaceous below with a sub-membranous apex, glabrous, dorsally grooved, 2-nerved, apex obtuse. Lodicules 2, membranous, about as long, or slightly longer than the palea, lanceolate, many-nerved. Stamens 3, anthers broadly linear. Ovary glabrous; styles free, laterally exserted. Caryopsis tightly enclosed by the lemma but free, dorso-ventrally compressed, deeply grooved on the ventral face; *hilum* linear, nearly as long as the grain and situated in the groove; embryo 1-1 the length of the grain; starch grains compound, composed of 3-4 granules; first leaf of the seedling, narrowly linear in outline (Fig. 152F).

Densely caespitose *perennials*, without rhizomes. *Culms* erect, usually simple, solid. *Leaf-blades* linear, often involute towards the base, reddish brown when dry. *Ligule* a dense fringe of long or short hairs. *Panicles* erect, narrow, rather contracted, usually interrupted, with few spikelets, branches solitary or binate.

ANATOMY

Shoot elongated and more or less circular in cross section, leaf-blades rolled in the bud (Fig. 152E).

Leaf-blade flat, widely V-shaped or horse shoe-shaped. Silicified cells of epidermis dumb-bell-shaped, short to very long, usually accompanied by square to elongate-rectangular suberized cells with undulate walls. Two types of hair present: unicellular broad-based retrorse barbs, which may be very short to well developed and long; and linear bicellular hairs. Bundle sheaths: outer sheath of large thin-walled parenchymatous cells containing chloroplasts; inner sheath devoid of chloroplasts, thin-walled adaxially, gradually becoming more thick-walled towards the abaxial surface, the lower cells often indistinguishable from the fibres of the stereome. Chlorenchyma of irregular cells forming a continuous tissue between the bundles.

Awns: Column of the awns, when present, oblong to sub-circular in cross-section, grooved ventrally with the edges overlapping, forming a thick-walled more or less cylindrical structure furnished with three vascular bundles. Vascular bundles each flanked by two oblong groups of diffusely arranged chlorenchyma cells. Chlorenchyma and vascular bundles embedded in a matrix of thick-walled cells. Groove densely clothed with short bristle-like hairs. Stomata flanking the groove, and opposite groups of chlorenchyma cells. Setae with only one vascular bundle, subtended by a single large group of chlorenchyma cells, adjoining the epidermis ventrally. Matrix of setae consisting of small thick-walled cells (Fig. 8, G & H)

Embryo in sagittal section showing the absence of an epiblast; cleft between the coleorrhiza and base of the scutellum absent; a distinct elongation of the vascular tissue forming an internode between the point of divergence of the scutellum bundle and the coleoptile. The cross section of the coleoptile region shows the first embryonic leaf with five vascular bundles and with the margins meeting but not overlapping; the coleoptile with three bundles (one median and two lateral) and the scutellum with a single median bundle only (Fig. 152, H & I).

KARYOLOGY (Fig. 7: 20, p. 232)

Chromosomes (of S. jucunda) of the small type and with a basic number of n = 11 (2n = 22). The karyology of the other two species is unknown.

Type species: Sartidia angolensis (C. E. Hubb.) de Winter.

The generic name *Sartidia* is an anagram of *Aristida*, which *Sartidia* resembles closely in organographic characteristics.

A genus consisting of three African species, so far recorded from the Belgian Congo, Angola, South West Africa and the Transvaal Province of South Africa.

2.9.3. Key to the Species Based on Organographic Characters

Lemma including the awns 8.5-13 cm in length, body of the lemma smooth, thickly coriaceous:

Lemma 1.5-2.3 cm long, column absent; branches of the panicle smooth or nearly smooth; basal leaf-sheaths estriate, smooth or nearly smooth, often somewhat glossy.. S. angolensis

Lemma up to 4 cm long including the well developed loosely twisted column; branches of the panicle scabrid especially on the angles; basal leaf-sheaths dull and distinctly striate

S. vanderijstij

2.9.4. Key Based on Anatomical and Vegetative Characters

barbs, basal leaf-sheaths dull and striate..... S. vanderijstii

2.9.5. Description of the Species



FIG. 151.—Sartidia jucunda: A, lower glume, $\times 3$; B, upper glume, $\times 3$; C, lemma, \times D spirally contorted base of the awns, $\times 3$; E, callus, $\times 8$; F, palea, $\times 8$; G, lodicules, $\times 8$; H, anthers, $\times 8$; I, gynoecium, $\times 8$; J, caryopsis, showing hilum, $\times 7$; K, caryopsis showing embryo, $\times 7$; L, cross section of caryopsis showing the grooved ventral side, $\times 7$



FIG. 152.—Sartidia jucunda: A, cross section of vascular bundles of the leaf-blade; B, diagram of leaf-blade in cross section; C, abaxial epidermis of the leaf-blade; D, chlorenchyma cells in longitudinal section; E, cross section of the shoots; F. seedling showing first leaf; G, caryopsis showing the embryo; H, longitudinal section of the embryo; 1, cross section of the embryo (Codd 8686).

1. S. jucunda (Schweickerdt) de Winter in Kirkia 3: 137 (1963)

Aristida jucunda Schweickerdt in Bot. Jahrb. 76, 2: 221 (1954). Type: Transvaal, Pietersburg distr. Blaauwberg, Schweickerdt 1807 (UPR, holo!, PRE, iso!). (Fig. 152)

Perennial, densely caespitose, up to 1 m high including the inflorescence, with numerous slender intravaginal innovation shoots. Culms erect, usually simple, 2-3noded, finely striate, terete, glabrous; nodes included or exserted, glabrous. Leafsheaths glabrous, striate, lax, the upper pallid or occasionally flushed with purple, the lower usually a deep rusty brown, or rarely pallid, margins membranous free. Ligule a fringe of long cilia; auricles long ciliate or glabrous; collar except for the midrib with a line of very short bristles. Leaf-blade, when dry, a deep rusty brown, linear, up to 45 cm long, narrowed towards the often convolute base, about 3-4 mm wide, tapering to fine apex, scabrous on the upper surface, finely scaberulous below, striate; blades of innovations very fine, convolute. *Panicle* strongly exserted, narrow, laxly contracted, much interrupted, up to 35 cm long with relatively few spikelets, branches erect, solitary or binate, very unequal, bearing 1–6 spikelets upwards. Spikelets deep rusty brown, shortly to long pedicillate, pedicels flattened on one side, margins scabrous. *Glumes* rusty brown, glabrous, membranous, narrowly lanceolate, subequal, up to 23 mm long, awn-tipped, finely scaberulous on the nerves and awn; upper 3-nerved, scaberulous on nerves and awn. Lemma chartaceous, elongate, spindle-shaped, suffused with purple, about 12 mm long, glabrous near the base, finely scaberulous all over in the upper part, ventrally longitudinally furrowed (ripe grains often visible in the open groove), gradually narrowed upwards passing into three long, flattened, scaberulous awns, margins thinly membranous, involute; callus subacute, 1.3 mm long, densely bearded; awns subequal, up to 45 mm long, spreading, when mature collectively laxly spirally contorted. Palea 2-nerved, cuneate, hyaline, apex erose, 2 mm long and 1 mm wide. Lodicules 2, membranous, glabrous, many-nerved, up to 2 mm long. Anthers 3, linear to about 6 mm long. Stigmas densely plumose, pale. Caryopsis linear, somewhat compressed, glabrous, brown, ventrally grooved, about 10 mm long; hilum linear grooved; starch grains compound, consisting of numerous granules. *Embryo* the length of the grain.

ANATOMY (Fig. 152, A–D)

Shoot: Young leaves rolled in the bud (Fig. 152, E).

Leaf-blade: Stereome strands projecting into the first order bundles, partly or completely encircling the phloem and interrupting the outer bundle sheath. *First order bundles* 3–5; adaxial surface with relatively few hairs; abaxial surface with very few hairs. Otherwise as described for the genus.

Awns as described for the genus (Fig. 8 G-H, p. 235).

Embryo as described for the genus (Fig. 152 H-I).

TRANSVAAL.—Pietersburg Blaauwberg above Leipzig Mission Station, Codd 8686; v.d. Schijff 5378; Strey & Schlieben 8502; Blaauwberg, Malaboch's kraal, Schweickerdt 1820; 2019; 1807 (type).

This species has been collected only on the Blaauwberg in the Pietersburg district of the Transvaal. It is possible that it also occurs in the Soutpansberg and other mountains of the northern Transvaal since suitable habitats are undoubtedly present in these ranges. It occurs on stony slopes at a altitude of 1,300–2,000 metres.

Though undoubtedly closely related to the other two species of the genus, S. *jucunda* is distinguished by much smaller spikelets and scabrid lemmas.

2. S. angolensis (C. E. Hubb.) de Winter in Kirkia 3: 137 (1963) Aristida angolensis C. E. Hubbard in Kew Bull. 1949: 359 (1949). Type: Angola: Benguella, Gossweiler 4099a (holo, K). (Fig. 153).



FIG. 153.—Sartidia angolensis: A, lemma $\times \frac{1}{2}$; B, callus $\times 6$; C, contorted basal parts of the awns $\times 2\frac{1}{2}$; D. lower glume $\times 2\frac{1}{2}$; E, upper glume $\times 2\frac{1}{2}$; F, palea $\times 6$; G, lodicules $\times 60$; H, anthers $\times 6$; l, gynoecium $\times 6$.

Perennial, densely caespitose up to 1-2 m high with numerous intravaginal innovations. *Culms* erect about 2 mm in diameter, simple, very firm, solid, terete, glabrous, finely striate; nodes mostly included; ultimate internode long exserted. Leaf-sheaths glabrous, estriate and often with a dull sheen in the lower part, lax, finely puberulous and striate upwards, the basal imbricate and persistent, pallid or pale brown, margins free, firmly membranous. Ligule a dense fringe of short silky cilia; auricles bearded; collar except for midrib with a line of long to short bristles. *Leaf-blade* when dry a deep brown, linear, up to 35 cm long, narrowed and convolute below, 2-4 mm wide, tapering to a fine apex, pilose above the ligule and densely scaberulous on the upper surface, finely scaberulous below. Panicle stiff and erect, narrow, laxly contracted, up to 40 cm long including the awns, and with relatively few spikelets; rhachis striate, compressed, sub-glabrous; bianches solitary or binate, erect simple or little divided, compressed, sub-glabrous or finely scaberulous upwards, bearing 1 to few spikelets in the upper part, the lower most about 10 cm long, shorter upwards; pedicels smooth, the lateral 3–8 mm long, the terminal elongated. Spikelets pale brown to pallid. *Glumes* narrowly linear-lanceolate, firmly chartaceous below, tapering to a membranous acute apex, subequal or slightly unequal; the lower 2.5-3.3 cm long, 5-nerved; the upper about 2.5 cm long, 3-nerved. Lemma linear, coriaceous, 15-23 mm long excluding the callus, glabrous (very finely scaberulous under a strong lens), without a column or articulation, gradually passing into three long bristles, margins membranous and involute in the lower part; callus elongate, acute 3.5-4 mm long, densely and shortly bearded; bristles 3, scaberulous, flattened and shallowly grooved on the inner surface, subequal, 7.5-10 cm long, spreading, when mature collectively laxly spirally contorted at the base. Palea oblong, about 3 mm long, coriaceous below, membranous upwards, ventrally grooved. Lodicules about 3 mm long, lanceolate, membranous, many-nerved. Caryopsis linear, 9 mm long, very dark brown; hilum linear, nearly as long as the grain, forming a narrow shallow groove; starch grains compound, composed of numerous 3-4 granules; embryo $\frac{1}{4}$ the length of the grain.



FIG. 154.—Sartidia angolensis: A, cross section of vascular bundles of the leaf-blade; B, abaxial epidermis of the leaf-blade; C, diagram of leaf-blade in cross section (de Winter 2779).

ANATOMY (Fig. 154, A–C)

Leaf-blade: stereome strands in contact with the bundles but not or only partly interrupting the outer sheath and not projecting into the bundle nor enveloping the phloem; first order bundles usually 5; adaxial surface with very few hairs; abaxial surface usually densely covered with hairs opposite the bundles. Otherwise as for the genus.

Awns as described for the genus.

Embryo as described for the genus.

NORTHERN RHODESIA.—Kafue National Park, Ngoma, *Mitchell* 7/6. SOUTH WEST AFRICA.—Otjiwarongo: top of the Waterberg Plateau, *de Winter* 2779. Grootfontein: 30 m N. of Gautscha Pan, *Story* 6473.

A species found on Kalahari sand in north western South West Africa. It also occurs in N. Rhodesia and Angola.

Henrard in his Monograph included specimens of this species in Aristida vanderijstii de Wild. This error was recognized by Hubbard who pointed out the differences, including the characteristic absence of a column in S. angolensis. The South West African specimens, collected many hundreds of miles from the type locality, agree very well with the type and constantly lack a column. This confirms Hubbard's opinion that Henrard was incorrect in stating that the lack of the column in the Angolan specimens was due to the immaturity of the material. As pointed out by Hubbard, in Aristida species the awns and column develop before the body of the lemma and this probably also holds good for Sartidia species.

S. angolensis is very closely allied to S. vanderijstii. The differences by which the species may be distinguished are fully set out in the key to the species.

3. S. vanderijstii (*De Wild.*) de Winter in Kirkia 3: 137 (1963) Aristida vanderijstii De Wild. in Bull. Jard. Bot. Brux. 6: 40 (1919) (Fig. 155). Types: Congo: Nyungu, Vanderijst 3216; Mukulu, Vanderijst 3182 (syn., BR.).



FIG. 155.—Sartidia vanderijstii: A, lower glume, $\times 2\frac{1}{2}$; B, upper glume, $\times 2\frac{1}{2}$; C, lemma, $\times 2\frac{1}{2}$; D, callus, $\times 6$; E, spirally twisted basal part of the awns, $2\frac{1}{2}$; F, palea, $\times 6$; G, lodicules, $\times 6$; H, anthers, $\times 6$; I, gynoecium, $\times 6$.

Perennial, densely caespitose, up to 80 cm high including the panicle. *Culms* erect, usually simple, 1–3-noded, finely striate, glabrous or slightly scaberulous, terete, solid, nodes included or rarely exserted, glabrous; upper internode long exserted.

Leaf-sheaths striate, rather dull, scaberulous, lax, pallid to pale reddish brown, margins membranous, ciliate, free. *Ligule* a dense fringe of cilia; auricles glabrous or bearded with long cilia; collar usually glabrous. *Leaf-blade* when dry a deep reddish brown,



FIG. 156.—Sartidia vanderijstii: A, cross section of vascular bundles of the leaf-blade; B, diagram of leaf-blade in cross section; C, abaxial epidermis of the leaf-blade (Callens s.n.).

linear, up to 20 cm long, narrowed towards the base, 2-3 mm wide, tapering to a fine apex, scabrous on the upper surface, finely scaberulous below, striate. *Panicle* strongly exserted, erect, narrow, laxly contracted, much interrupted, up to 20 cm long, with relatively few spikelets, rhachis scabrid, branches erect, flattened, solitary or binate. scabrous, bearing 1-6 spikelets in the upper part. Spikelets deep reddish brown, rarely pallid. Glumes linear-lanceolate, firmly chartaceous below, tapering to a submembranous acute apex, subequal or unequal, glabrous (finely scaberulous under a strong lens), not awned; the lower 30-40 mm long, 5-nerved; the upper 25-30 mm long, 3-nerved. Lemma linear, coriaceous convolute, 3-nerved, 40-60 mm long including the slightly twisted column but not the callus, glabrous (very finely scaberulous under a strong lens), margins membranous and involute in the lower part, column loosely twisted, up to 40 mm long, without an articulation; body of the lemma gradually passing into the column which is terminated by 3 thick, coarse bristles: callus elongate, acute, 3-3.5 mm long, densely but shortly bearded; bristles 3, scaberulous, flattened and somewhat grooved on the inner surface, subequal, 8-9.5 cm long, spreading, collectively laxly spirally contorted at the base when mature. Palea oblong, about 2.5 mm long, ventrally furrowed, coriaceous below with a membranous obtuse apex, nerves two, short, evanescent. Lodicules about 2.5 mm long, membranous, lanceolate, many-nerved. Carvopsis linear, 8-9 mm long, dark brown; hilum linear, nearly as long as the grain, grooved; starch grains compound, composed of 3-4 granules; embryo $\frac{1}{2}$ the length of the grain.

ANATOMY (Fig. 156 A-C)

Leaf-blade: stereome strands in contact with the bundles but not interrupting the outer bundle sheaths nor projecting into the bundle; first order bundles 7–9; adaxial surface with a few short rather abruptly acute hairs; abaxial surface with numerous rather short, blunt retrorse barbs. Otherwise as described for the genus.

Awns as described for the genus.

Embryo as described for the genus.

CONGO.—Leopoldville: Gombe ya Tumba, Collins 3411; Katanga: Biano, Risopaulos 358.

S. vanderijstii has so far been recorded only from the Congo Republic where it occurs in grassland and bush-savannah on sandy soils. The differences by which it may be distinguished from the closely allied S. angolensis are fully set out in the key to the species.