## PART I

# THE TRIBE STIPEAE

## 1.1. HISTORY

The tribe Stipeae was described by Nees von Esenbeck (1829, p. 371) based on the genus Stipa L. and including Chaetaria, of which he considered Aristida to be a synonym. In Stipa, Nees included Oryzopsis, Piptatherum and Urachne as synonyms. Four years later Kunth (1833, p. 187) enlarged the tribe by including Streptachne but redivided the comprehensive genus Stipa sensu Nees into five genera: Stipa, Lasiagrostis, Macrochloa, Oryzopsis and Piptatherum. Trinius & Ruprecht (1842, pp. 1 & 97) still further enlarged the concept of the tribe by including Dichelachne and Anisopogon. They divided Stipa into five sections and regarded Urachne and Lasiagrostis as distinct genera, each with two sections; in addition, Aristella and Orthoraphium were upheld as genera distinct from Stipa. Further additions were made by Bentham (1882) and this tendency culminated in Hackel's treatment of the tribe (1896, p. 100–104). Here twelve genera were included although many genera formerly recognized were relegated to synonymy and thus a very wide concept of Stipa was reintroduced. In conformity with the recent trend of dividing the grasses into smaller, more "natural" tribes, most present-day authors have again severely restricted the number of genera included in the Stipeae. In the introduction to his monograph of Aristida, Henrard (1929, p. 13), summarized his concept of the Stipeae in a key to the genera namely Stipa, Oryzopsis, Nasella, Piptochaetium, Aciachne, Milium, Aristida and Timouria. Hubbard (1934, p. 214) treated the tribe essentially in the same manner, but did not mention *Timouria* (apparently including it in *Stipa*).

Avdulov (1931, p. 406) in his classic work on the karyosystematics of the Gramineae pointed out that the genera *Stipa* and *Oryzopsis* are more closely allied to genera such as *Phaenosperma*, *Oryza* and *Ehrharta* than to the genera of the tribe *Agrosteae* in which they are placed by some authors. He came to this conclusion mainly, not only on the basis of karyological similarity, viz. small chromosomes with basic number 12, but also on the basis of the presence of certain primitive features exhibited by the florets, e.g. 3 lodicules in *Oryza* and *Stipa*, and 6 stamens in *Phaenosperma*, *Oryza* and *Ehrharta*. Anatomically the leaf-blades of these genera also show a great deal of similarity. Avdulov pointed out, however, that the genera probably evolved independently and thus represent distinct evolutionary groups.

The fact that Aristida occupied an anomalous position in the Stipeae was realized by Hubbard (Hubbard & Vaughan, 1940, p. 23) who removed this genus from the Stipeae to accommodate it in his new tribe, the Aristideae. (Latin diagnosis published by Hubbard in Bor, 1960, p. 685). Eight years later Hubbard (1948, p. 325) transferred Milium from the Stipeae to the Agrosteae, but did not list the genera to be retained in the Stipeae since only British grasses were dealt with in the relevant work.

An important, though lesser known, work on the *Stipeae*, is that of Elias (1942). His work is unique in the *Gramineae* in that he made a comparative study of the fossil and living forms of the *Stipeae* and by this method was able to indicate certain evolutionary trends of the tribe. In order to enable him to compare fossil remains with living species of *Stipa*, *Oryzopsis*, *Piptochaetium* and *Nasella*, Elias made a thorough study of the morphological characteristics of the "hulls" of these grasses. Where possible he subdivided the genera into sections, each section being composed of a group of closely related species. In addition to the four genera mentioned above, Elias devoted several pages to a discussion of the relationship of *Stipa* to *Aristida* both from a morphological and an anatomical point of view. He arrived at the conclusion that *Aristida* represents a type more advanced than that found in any of the

other genera under consideration. He stated that Aristida probably evolved from Stipidium (a fossil genus) through Stipa, summing up his views as follows: "The comprehensive modern genera Stipa and Aristida of Stipeae, which between themselves differ primarily in the division of the single strong awn of Stipa into three slender awns in Aristida, are apparently descendants of a single fossil genus Stipidium with a non-indurated awn". The reasons why the present author cannot support Elias's views will be elaborated under the discussion of the relationship of Aristida to Stipa, as seen in the light of recent advances in the knowledge of their anatomy, karyology and embryology.

Parodi & Freier (1945), who studied the *Stipeae* both anatomically and taxonomically, include *Aristida*, as a distinct natural genus, in the *Stipeae*. Furthermore they regard the genera *Stipa*, *Nasella* and *Oryzopsis* to be so closely related that the possibility of accommodating them together as taxa of infrageneric rank cannot be precluded. *Aciachne* is regarded not to be a close relative of the foregoing and the view is expressed that it probably represents a distinct subtribe of the *Stipeae* whereas the taxonomic position of *Milium* and *Relchella* in relation to the above is not yet clear.

In a recent account of the *Stipeae*, Roshevitz (1951) divided the tribe into three subtribes and included *Streptachne* and *Amphipogon*, as well as resuscitating several genera such as *Lasiagrostis*, *Macrochloa*, *Orthoraphium*, *Timouria* and *Ptilagrostis* which are placed in synonymy under *Stipa* by most present-day workers. On account of the existence of a large number of species somewhat intermediate in character most of these genera are doubtfully distinct from *Stipa*. In addition *Amphipogon* and *Streptachne* could be placed more satisfactorily in other tribes. Their taxonomic position will be discussed in the course of this paper.

The most recent account of the tribe is that of Pilger (1954, p. 330-332) who again included *Dichelachne*, *Milium* and *Aciachne*, recently removed from the tribe by other authors. His reason for doing so was probably motivated by a distrust of the present-day tendency to over-emphasize the taxonomic value of anatomical features of the vegetative organs thus to some extent under-estimating the importance of the morphology and internal structure of the reproductive organs. Pilger's classification consequently is more artificial than one would have expected, i.e. if all data available had been evaluated in determining relationships. Finally a new genus of the *Stipeae*, *Trikeraia*, based on *Stipa hookeri* Stapf, was described by Bor (1954, p. 555).

### **1.2.** DELIMITATION

From the foregoing outline of the historical evolution of the Stipeae it is evident that, with the exception of Pilger, modern authorities have tended to support a rather narrow delimitation of this tribe. It is the present author's view that the tribe should be limited to the genera Stipa, Oryzopsis, Piptochaetium and Nasella. Trikeraia Bor, a segregate from Stipa obviously also belongs to the Stipeae. These genera agree closely in anatomical, karyological and embryological characters as well as in the general morphology of the spikelet. These characters are: the diffusely arranged cells of the chlorenchyma which is continuous between the bundles (Prat, 1936); the lack of bicellular hairs of the epidermis (Prat, 1936); medium-sized chromosomes with basic numbers 6, 11, 12 (Brown, 1951; Stebbins & Löve, 1941; Darlington & Wylie, 1935); the presence of an epiblast; the characteristic course of the vascular strands in the embryo; the absence of a cleft between the coleorrhiza and base of the scutellum; the first leaf (sheathed by the coleoptile) with the margins not overlapping (Reeder, 1951); the one-flowered spikelet with a usually 5-7 (rarely 3)-nerved, single-awned (rarely with a long central awn and two smaller lateral awns), indurate or rarely hyaline, lemma clasping the caryopsis; the large membranous lodicules, usually 3 (rarely 2) in number; the linear hilum, the usually small embryo and the membranous ligule.

The following genera were, at some time or other, included in the *Stipeae*; they all, however, possess certain characters which do not conform to those of the typical representatives of the tribe and have therefore been excluded.

*Milium.*—(Henrard, 1929; Bentham, 1882; Darlington & Wylie, 1955; Hubbard, 1959; Hackel, 1896). Lemmas awnless, chromosomes in multiples of 4, 9 or 14 and much larger than in the *Stipeae*. Probably—as done by Hubbard (1948)—best placed in the *Agrosteae* on account of the large chromosomes.

Aciachne.—(Henrard, 1929; Bentham, 1882; Hubbard, 1959; Hackel, 1896). On morphological and anatomical grounds regarded as probably representing a subtribe of the *Stipeae* (Parodi & Freier, 1945). This genus is in need of further investigation.

Muehlenbergia, Lycurus, Perieilema.—(Hackel, 1896); spikelets 1- or 2-flowered; glumes persistent, shorter than the lemmas; lemmas 3-nerved, practically awnless; hilum punctiform and basal in Muehlenbergia and Perieilema and probably likewise in Lycurus (no fruiting material seen); embryo as in the Paniceae except for the embryonic leaf (i.e. sheathed by the coleoptile) which has the margins overlapping (Reeder, 1957); chlorenchyma of the leaf-blade radially arranged round the bundles (Avdulov, 1931; Schwabe, 1949); two-celled epidermal hairs recorded for Muehlenbergia and Lycurus (Tateoka, 1959); chromosomes small, in multiples of 8, 10 or 14 (Darlington & Wylie, 1955). Darlington & Wylie (1955) place Muehlenbergia and Lycurus in the Sporoboleae, while Reeder (1957) places them in the Chloridoid-Eragrostoid group (which includes Sporobolus), mainly on the characters of the embryo. Pilger (1954) places all three genera in the tribe Eragrosteae; Perieilema and Lycurus in the subtribe Lycurinae, and Muehlenbergia in the subtribe Muehlenbergiae. Schwabe (1949) likewise suggests that Lycurus and Muehlenbergia should be placed in the Eragrosteae. On the available evidence this seems an excellent way of expressing their affinities.

*Brachyelytrum.*—(Bentham, 1882; Hackel, 1896). Rhachilla produced beyond the base of the floret; grains flattened and grooved ventrally; embryo "festucoid" except for the cleft present between the base of the scutellum and the coleorrhiza; chromosomes always in multiples of 11. Placed by Pilger in the *Festuceae*. Reeder (1957) however, doubted whether it belongs to this tribe and suggested possible affinities with *Oryza* and *Stipa*.

Dichelachne.—(Trin. & Rupr. 1842; Pilger 1954, 1956). Very little information regarding this genus is available. The awn, however, originates from the back of the lemma as in the Aveneae and Agrosteae and, for this reason, the genus should not be included in the Stipeae. Hubbard (1959) and Gardner (1952) place Dichelachne in the Agrosteae.

Aristida and Amphipogon.-For discussion see page 221.

Streptachne.—(Henrard, 1929; Kunth, 1833; Trin. & Rupr., 1842; Roshevitz, 1951). Transferred by Henrard (1929) to Aristida as the section Streptachne which accommodates the single-awned species.

### **1.3. PHYLOGENETIC POSITION**

At the end of the sub-family *Festucoideae*, Pilger (1954) lists several tribes, which he apparently regarded as having no clear affinities. Here he placed the *Stipeae* between the *Pappophoreae* and the *Nardeae*. Studies of the anatomy and embryo of the *Pappophoreae* have shown that the latter probably is closely related to the *Eragrosteae*, and cannot, therefore, be regarded as allied to the *Stipeae*. It is possible that the *Nardeae* is correctly placed in the *Festucoideae*, but the *Stipeae* is probably misplaced in this sub-family. In his scheme of relationships of the tribes of the *Gramineae*, which is based largely on leaf anatomy, Brown (1958, p. 173) placed the *Danthonieae* and *Stipeae* adjacent to each other, and indicated that the affinities of these tribes are still uncertain. Stebbins (1956, p. 894), in a diagram showing the evolutionary interrelationships of the principal sub-families and tribes, places the *Stipeae* as an isolated group and regards it as probably an offshoot of the *Danthonioid-Arundinoid* complex. The *Stipeae* differs mainly from the members of the *Danthonioid-Arundinoid* complex in having strictly one-flowered spikelets, an indurate lemma tightly enclosing the grain, a terete not flattened awn, a linear hilum and in the internal structure of the embryo. The *Stipeae* differs from the *Festuceae* in the one-flowered spikelet, indurate lemma tightly clasping the grain and the small chromosomes usually in multiples of 6, 11 or 12; and from the awn which originates from the apex and not from the back of the lemma.

From the foregoing it is evident that until more detailed information concerning the characteristics of the different tribes is available, the relationship of the *Stipeae* to other tribes cannot be determined and established with certainty. As indicated by Stebbins (1956) and by Brown (1958), it will probably prove to be an isolated group with no close affinity to any of the other tribes.

In an excellent paper on the tertiary prairie grasses of the High Plains of North America, Elias (1942, p. 68) traced the relationship of some of the "Stipoid" genera by medium of fossils found in Miocene and Pliocene deposits. The genus *Stipa*, it is postulated, has evolved from two different fossil genera namely *Parastipidium* and *Stipidium*, the former having given rise to the 6 crownless sections of *Stipa*, whereas the latter is considered to be ancestral to the 3 sections possessing crowns. The tribe *Stipeae* thus presents one of the rare cases in the Gramineae where the pre-history is known to some extent.

### 1.4. DISTRIBUTION

The *Stipeae* in the concept of the present author is restricted mainly to the temperate and warm temperate regions of both hemispheres, only rarely occurring in the tropics. The majority of the species, are typical dry grassland inhabitants, however, a few are found in forests or moist habitats. In the Northern Hemisphere the centres of greatest concentration of species occur in North America, the Mediterranean area, and the Russian Steppes. In the Southern Hemisphere the most important areas of distribution are South America, Australia and Tasmania.

Among the component genera of the *Stipeae* the genus *Stipa* is the largest and also the most widespread. Many species, particularly those of the Southern Hemisphere, are typical constituents of desert grassland. The Australian representatives, however, form a rather distinct group, differing in a number of minor characters from the species occurring in other parts of the world.

*Oryzopsis* is a small genus confined to the Northern Hemisphere. It is closely related to *Stipa*.

*Nasella*, regarded by Parodi as a section of *Stipa*, occurs in Peru, Chile and the Argentine.

*Piptochaetium*, a genus of about 21 species, is confined to southern South America with the exception of one species found in the United States. This genus was revised recently by Parodi (1944, pp. 244–310) who described six phyto-geographical areas of distribution for South America, ranging from the high mountain grassland of the Andes to the lowland steppes of the Argentine.

### **STIPEAE** Nees

### Agrost. Bras. 371 (1829)

Annual or perennial herbs, frequently with tough, rigid culms. Ligule membranous or membranous and fimbriate, obtuse. Leaf-blade narrow, rolled and wiry, or fairly wide and expanded. Spikelets all similar, bisexual, 1-flowered, arranged in contracted or open panicles. Rhachilla disarticulating above the glumes, not produced beyond the floret [" occasionally present as a wart-like projection at the base of the palea": Flias (1942)]. Glumes persistent, the upper (and often the lower) as long as or longer than the florets. Lemma usually terete, with convolute or involute margins, rarely hyaline and thin, 3–7 (usually 5)-nerved with the nerves anastomosing at the apex, awned from the entire or minutely 2-lobed tip; the awn apical, single, or rarely with two additional, shorter, lateral awns, three of the nerves of the lemma passing into the awn; callus short or long, obtuse or acute, bearded. Lodicules 3 (rarely 2). Caryopsis tightly embraced by the lemma and palea; hilum linear, at least half the length of the grain; embryo  $\frac{1}{4-4}$  the length of the grain (Fig. 2, F and 4, D).

#### **ANATOMY**

Leaf-blade expanded, folded or semicircular. Chlorenchyma continuous between the bundles, not arranged in a definite pattern, cells circular or angular. Bundle sheaths two: inner of small cells with thickened walls; outer or large more or less circular thin-walled cells furnished with chloroplasts, gradually merging into the adaxial stereome or interrupted by the fibres of the stereome both ad- and abaxially. Epidermis of a relatively simple type: long ripple-walled elements generally rather shallowly undulate, alternating with paired short elements; silicified cells variable, often dumb-bell-shaped (many species with elongate, square or sub-circular silicified cells), always accompanied by a suberized cell; unicellular hairs of various types present, two-celled hairs absent; stomata present on the adaxial surface only, or present on both surfaces.

Awn.—Column angular to sub-circular in cross-section, occasionally grooved on one side, containing a large central vascular bundle flanked by 2 groups of chlorenchyma cells, each subtended by a smaller, lateral vascular bundle; central bundle surrounded by small or large much-lignified cells; small vascular bundles in close contact with the chlorenchyma on one side, and supported by usually small muchlignified cells on the other; chlorenchyma groups situated just beneath the lateral epidermis; epidermis opposite the chlorenchyma groups containing stomata; seta agreeing anatomically with the column, but the lateral vascular bundles, as well as the layers of lignified cells surrounding the central bundle disappearing towards the apex, and the groups of chlorenchyma cells converging and finally contacting the central bundle.

*Caryopsis.*—Starch grains compound; embryo usually with a well-developed epiblast (occasionally small but always present); no cleft present between the coleorrhiza and the lower part of the scutellum: vascular strand diverging into the scutellum directly below the coleoptile; first leaf (sheathed by the coleoptile) with the inflexed margins not overlapping (Fig. 2, E and 4, E, F).

References.—Duval-Jouve, 1875; Kennedy, 1899; Holm, 1901; Hughes, 1921; Prat, 1936; Parodi, 1944; Reeder, 1957.

#### KARYOLOGY

The chromosomes are small and occur in multiples of 9, 10, 11, 12, 14, 16 and 17. Stebbins (1941, p. 379) suggests that most of the numbers found in the aneuploid series of chromosome numbers in *Stipa* probably could have been derived from the basic numbers X = 11 and 12. Consequently these two basic numbers probably could also account for the numbers found in the other genera as well, most of them being multiples of 11 and 12.

Brown & Emery (1957) report for *Stipa leucotricha* Trin. & Rupr. that in the mitotic division the nucleolus disappears before metaphase. They found the presence or absence of nucleoli persisting to metaphase to have some bearing on classification in the Gramineae, since the nucleolus disappears before metaphase in the subfamily *Festucoideae* and in a part of the group *Phragmitiformes* Avdulov, whereas it persists to metaphase at least in a large percentage of cases in the subfamily *Panicoideae* as well as in the *Oryzeae*, *Unioleae* and *Bambuseae* of the group *Phragmitiformes*.

#### Genera: Stipa, Trikeraia, Oryzopsis, Nasella, Piptochaetium.

References.—Avdulov, 1931; Hunter, 1934; Stebbins & Löve, 1941; Brown, 1951; Darlington & Wylie, 1955; Brown & Emery, 1957.

### 1.6. DELIMITATION OF THE GENERA

Stipa is the largest of the genera included in the tribe and also the most variable, as testified by the nine sections into which it is divided by Elias. Although Oryzopsis is retained as a distinct genus by practically all authors, it is closely allied to Stipa and some species are intermediate between these two genera [Clements ex Elias (1945, p. 71)]. It is for this reason that, at different times authors have placed one and the same taxon either in Oryzopsis or in Stipa.

*Nasella* a genus with relatively few species is regarded as distinct by Hitchcock (1950, p. 443) and others, but as a section of *Stipa* by Parodi. Parodi & Freier (1945) studied the genera anatomically as well as organographically and at present their key to the genera appears to be the best available. Parodi & Freier found that *Nasella*, *Oryzopsis* and *Stipa* could not be separated solely on anatomical grounds, whereas *Piptochaetium* is a genus both organographically and anatomically distinct.

*Trikeraia* Bor (1954, p. 555) differs from *Stipa* in the hyaline, not indurated lemma, furnished with two short lateral bristles, formed by the elongation of the lateral nerves of the lemma, in addition to the stout median awn typical of the *Stipeae*. Most likely *Trikeraia* is correctly placed in the *Stipeae*. Metcalfe (1960, p. 504) described the anatomical features of the genus.

Though it seems fairly certain that a greater degree of uniformity has been obtained by the exclusion of anomalous genera from the *Stipeae*, it is, nevertheless evident that in the classification of the genera retained in the tribe progress is improbable unless a monograph of the group as a whole is undertaken. There are indications that anatomical studies, particularly of the awn, will be of considerable value in arriving at a classification more natural than the one existing at present. In future work this aspect should be taken into account.

# 1.7. THE GENUS STIPA

## 1.7.1. DELIMITATION

It was decided that for the purpose of this study it would be more satisfactory to follow Elias in retaining *Stipa* as a comprehensive genus subdivided into sections, than to accept the large number of ill-defined genera upheld by Roshevitz and, to some extent by Pilger. The South African representatives are therefore retained in *Stipa* and provisionally placed in the appropriate sections as defined by Elias (1942). It is realized that a re-assessment of Elias' treatment of the sections may necessitate nomenclatural changes, but such a study does not fall within the scope of the present paper.

It may be pointed out here that Roshevitz (1951), in spite of dividing the *Stipeae* sensu stricto (i.e. with the exclusion of *Amphipogon* and *Streptachne*) into eleven "genera", did not achieve a natural grouping in all respects. For instance, he included the African *Oryzopsis keniensis* Pilg., a taxon indistinguishable from the South African *Stipa dregeana* Steud. var. *elongata* (Nees) Stapf, in the genus *Piptatherum*. Undoubtedly this plant is more closely related to some Asian and North American species of *Stipa* placed by Roshevitz in the subtribe *Stipiinae*, than to *Piptatherum coerulescens* (Desf.) Beauv., the type of the genus *Piptatherum*, which belongs to the subtribe *Timouriinae*.

Only two sections, *Ptilagrostis* and *Tortilia*, both possessing crownless lemmas, occur in South Africa. *Ptilagrostis* consisting of several species is widely distributed in North America, Europe and Asia with one representative, viz. *Stipa dregeana* Steud., in Africa. The monotypic section *Tortilia* is based on *Stipa tortilis* Desf. described from North Africa, but also occurring in South Africa. For reasons of priority *S. capensis* Thunb. supersedes *S. tortilis* so that the latter must be placed in synonymy.

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-	S. capensis	S, dregeana	Stipagrostis anomala de Winter = (S, namaguensis)	Aristida parvula (Nees) de Winter = (S. parvula)
Ligule Lemma Lemma Lodicules Embryo embryo embryo	membranous, ciliolate 5-7-nerved 2, large, membranous 4 the length of the grain present, well developed scutellum bundle diverging directly below the base of the coleoptile	membranous	a fringe of hairs	a fringe of hairs 3. large, fleshy at the base 4 the length of the grain absent scutellum bundle diverging some distance below and with a distance below and vascular tissue leading up to
Base of the scutellum Anatomy of leaf-blade	not distinct from the coleor- rhiza chlorenchyma continuous be- tween the bundles, not radially arranged	not distinct from the coleor- rhiza chlorenchyma continuous be- tween the bundles, not radially arranged	the base of the coleoptile divided by a deep cleft from the coleorrhiza chlorenchyma cells in a single row, radially arranged rown the vascular bundles, contracted	the base of the coleoptile divided by a deep cleft from the colcorrhiza chlorenchyma cells in a single row, radially arranged row the vasular bundles,
Epidermis	of simple type; bicellular hairs absent; silicified cells dumb-bell-shaped	of simple type; bicellular hairs absent; silicified cells dumb-bell-shaped	of intricate type; bicellular hairs present; silicified cells dumb-bell-shaped	of intricate type; bicellular hairs present; silicified cells sub-circular to square

## 1.7.2. THE SOUTH AFRICAN REPRESENTATIVES

Stipa is the only genus of the Stipeae represented in South Africa. In the most recent account of the South African Gramineae by Chippindall (1955) four species are mentioned. A careful study of the organography and anatomy of these species has, however, revealed that only two of them should be retained in the tribe Stipeae. The use of the single awn as a generic criterion has proved to be quite unnatural. As early as 1898 Stapf pointed out that Stipa parvula Nees probably represented a reduced Aristida, in which the lateral awns have disappeared. Henrard (1929), however, overlooked this and omitted the species from his monograph. Elias (1942) investigated Stipa parvula organographically and concurred with Stapf's view, but did not transfer the species to the genus Aristida. Chippindall (1955) and de Wet (1960) likewise remarked on the presence of misplaced species of Aristida in the genus Stipa (on information supplied by the present author).

In Fig. 1 the four species under consideration are contrasted: *S. parvula* and *S. namaquensis* exhibit all the characters regarded as typical of the *Aristideae* except for the single awn, whereas *S. dregeana* and *S. capensis* are typical representatives of the *Stipeae. Stipa parvula* and *Stipa namaquensis* have therefore been transferred to the genera *Aristida* and *Stipagrostis* (a section of *Aristida* now given generic rank) respectively (pp. 242 and 375). *Stipa namaquensis* is the sole representative of a new section viz. *Anomala* of the genus *Stipagrostis* whereas *Stipa parvula* is placed in the monotypic section *Schizachne* transferred from the genus *Stipa* to *Aristida* (p. 236).

## 1.7.3.

## STIPA L.

## Sp. Pl. 78 (1753)

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, usually shorter than the glumes, linear in outline. Glumes persistent, narrow, acute, acuminate or tipped by a bristle (rarely obtuse), 1-3 (rarely 5)nerved, equal or unequal. Lemma convolute, or with margins not overlapping at the base, cylindrical or slightly dorsally compressed, indurated at maturity, glabrous or hairy, 3-7-(usually 5)-nerved, nerves anastomosing at the apex, apex acute or minutely 2-lobed; awn persistent, single, straight, flexuous or once to twice-geniculate, column twisted, glabrous or hairy, bristle glabrous, pubescent or distinctly plumose; callus pungent or obtuse, short, or long bearded. Palea as long as or shorter than the lemma, completely enclosed by, or visible between, the margins of the lemma near the base, membranous or somewhat indurated, 2-nerved. Lodicules 2-3, equal and large, or posterior reduced, usually rounded at the apex, glabrous, indistinctly nerved. Stamens 2-3, anthers elongated, sometimes penicillate at the apex. Ovary glabrous; styles free; stigmas plumose, apically exserted. Caryopsis tightly enclosed by the lemma and palea, free; hilum linear, slightly shorter than the grain; embryo  $\frac{1}{4}$  (seldom  $\frac{1}{4}$ ) the length of the grain.

Densely tufted perennials or rarely annuals. *Culms* usually erect, branched or simple; internodes hollow or solid. *Leaf-blades* usually long and narrow, often convolute, more rarely flat and fairly wide. *Ligule* membranous, lacerated, or a membranous ciliate rim. *Panicle* narrow and contracted, to effuse and open.

Anatomy.—As described for the tribe. Karyology.—As described for the tribe.

Type Species: Stipa pennata L.

Name from the Greek "stupe" meaning "tow" alluding to the plumose awns of the type species.

A very large genus widely distributed in temperate and warm-temperate regions of the world.

1.7.4. Key to the South African Species based on Organographic Characters

Annual; callus of the floret elongated, tapering to an acute point; awn at least eight times as long as the floret, *twice geniculate*; palea much shorter than the lemma, glabrous 2. S. capensis

1.7.5. Key Based on Anatomical Characters

Midrib of leaf-blade much enlarged and protruding abaxially, furnished with colourless parenchyma surrounding the bundle; first order bundle units wider than deep, hardly protruding adaxially 1. S. dregeana

Midrib of the same size as the other first order bundle units, without additional colourless parenchyma; first order bundle units broadly ovate in outline and protruding adaxially 2. S. capensis

1.7.6. Description of the South African Species

1. S. dregeana Steud., Syn. Pl. Glum. 1: 132 (1855). Type: Albany, Hills near Grahamstown, Drége s.n. (B<sup>+</sup>; PRE, fragment of holo.!).



FIG. 2.—Stipa dregeana: A, diagram of leaf-blade in cross section; B, cross section of vascular bundles of the leaf-blade; C, abaxial epidermis of the leaf-blade; D, cross section of the young shoot; E, longitudinal section of the embryo; F, caryopsis showing the embryo; G, seedling showing first leaf; H, chlorenchyma cells in longitudinal section (de Winter 7607).

Perennial with a short, knotty, branched system of rhizomes. Culms erect, usually simple, 3-noded, smooth, glabrous, 90-120 cm high; internodes enclosed in, or exserted from the sheaths, terete, hollow, glabrous, striate; nodes conspicuous, often dark in colour, glabrous. Lower leaf-sheaths reduced to elongated bracts tightly enclosing the base of the culms, increasing in size upwards, usually smooth, striate. Ligule membranous, up to 5 mm long, obtuse or lacerated, often with the margins produced into auricle-like outgrowths. Leaf-blades linear, flat, widest near the middle, up to 12 mm wide and 60 cm long, narrowed towards the base and acuminate, glabrous or sparsely villous, firm in texture, smooth below and slightly rough on the nerves above, finely nerved with nerves numerous. Panicle effuse and wide, or contracted and narrow, erect or nodding, when fully developed 15-40 cm long; branches very finely scabrid, single, 2-3 nate or fascicled, short to long and flexuous, up to 15 cm long. filiform and smooth. Pedicels scabrid, shorter or longer than the spikelets. Spikelets pale green, 6-7 mm long, one-flowered, linear-lanceolate. Glumes sub-equal, 3-nerved, lanceolate in outline, the lower broader than the upper, finely acuminate, menbranous and hyaline in the scabridulous upper half. Lemma convolute, narrowly lanceolatecylindric, about 5.5 mm long, appressed hairy all over, 5-nerved, obscurely bi-lobed with a stiff, straight or arcuate awn from the apex; awn persistent, scabrid, slightly twisted below, usually bent about 2-4 mm above the base, 10-15 mm long; callus very short, obtuse, shortly bearded. Palea subequal to the lemma, lanceolate, subobtuse, not keeled, appressed hairy on the back, 2-nerved. Lodicules 3, oblong, obtuse, the two anterior membranous, hyaline, the posterior smaller. Stamens 3, anthers yellow, about 3-3.5 mm long, glabrous. Caryopsis spindle-shaped, brown, 3-4 mm long; hilum linear, black, about  $\frac{3}{4}$  the length of the grain; embryo small, about  $\frac{1}{4}$ the length of the grain, no constriction present beteen the coleorrhiza and the coleoptile (Fig. 2, F.).



FIG. 3.—Distribution of Stipa dregeana: @var. dregeana; Ovar. elongata; Stipa capensis.

ANATOMY (Fig. 2, A, B)

Leaf-blade flat, very thin, wide, tapering gradually towards the margins; abaxial surface flat, with very few hairs; adaxial surface flat except for the very slightly projecting first order bundle units, with short unicellular hairs flanking the motor cell groups. Abaxial epidermis: Stomatal zones with 1-2 rows of stomata along each margin, very wide (12-15 rows of cells), long ripple-walled cells with walls only slightly undulate, elongate and tapering towards the ends, alternating with pairs of short

elements; *silicified zones:* silicified cells dumb-bell-shaped, often with a double constriction and usually accompanied by a short or elongate thin-walled suberized cell with slightly undulate or almost smooth walls, a few unicellular broad-based retrorse barbs present in this zone, bicellular hairs absent. *Vascular bundle units* poorly differentiated, wider than deep, more or less rectangular; first order bundles 9–13 or more, alternating with groups of 2–4 second order bundles; bundle sheaths variously interrupted or complete, outer sheath of large more or less circular thin-walled cells, inner sheath of smaller cells of which the inner tangential walls are strongly thickened. *Chlorenchyma* cells large, circular or angular, forming a continuous tissue between the bundles; in longitudinal section somewhat irregular in arrangement and with intercellular spaces. *Stereome strands* present ad- and abaxially opposite all bundles, strongly developed opposite the first order bundles and less so opposite second order bundles, strands narrow abaxially, wider adaxially especially opposite first order bundles; all strands consisting of strongly thickened fibres with fairly large cell-lumen. *Motor cells* fairly well differentiated, all epidermal in origin. *Midrib* strongly projecting abaxially; midrib bundle surrounded by large thin-walled parenchyma cells (containing no or very few chloroplasts) additional to the parenchymatous outer sheath; inner sheath consisting of two layers of cells with strongly thickened walls whereas the other bundles

Awn: (Fig. 8, A & B). Column roughly triangular in outline with rounded angles, ventral side with a shallow depression in sections cut near the foot, furnished with three vascular bundles; central bundle large and surrounded by large cells with very strongly asymetrically lignified walls, of which those situated on the ventral and dorsal sides of the bundle much exceed the others in size; lateral bundles small and situated near the base of the central bundle, each subtending a large somewhat elongated group of chlorenchyma cells which flank the central bundle and lie directly below the epidermis; epidermis with the outer tangential walls very strongly lignified, furnished with stomata; seta essentially similar in structure to the column but cells surrounding the bundles less lignified and smaller, the lateral bundles disappearing towards the apex of the seta, the groups of chlorenchyma cells lying in close contact with the central bundle which in turn is surrounded by relatively thin-walled cells.

*Caryopsis: starch grains* compound, consisting of numerous granules; *embryo* in sagittal section showing the presence of a well-developed epiblast; the lower part of the scutellum fused to the coleorrhiza or absent, no cleft being present at the base of the coleorrhiza; the scutellum bundle diverging directly below the coleoptile (Fig. 2, E); cross-section of the coleoptile showing the first embryonic leaf with margins touching but not overlapping, and with three vascular bundles, one median and two lateral, the coleoptile with two lateral bundles and the scutellum with one median bundle. Anatomically no differences could be detected characterizing the varieties.

#### KARYOLOGY

The chromosomes are of the small type and 2n = 48 (Fig. 7 No. 21).

#### (a) var. dregeana.

S. dregeana Steud., Syn. Pl. Glum. 1: 132 (1855); Dur. & Schinz, Consp. Fl. Afr. 5: 811 (1895); Stapf, Fl. Cap. 7: 572 (1898); Chippindall, Grasses and Pastures S.A. 1: 289 (1955).

Lasiagrostis capensis Nees, Fl. Afr. Austr., 167 (1841); Trin. & Rupr., Gram Stip., 88 (1842).

Inflorescence dense, much elongated.

CAPE.—Riversdale: Oakdale, Liebenberg 5617 (a). Oudtshoorn: near Cango Caves, Bolus 12433. Uitenhage: Redhouse, Paterson 15946; Addo, Glennie s.n. Port Elizabeth: Koega, Fairdale 252. Alexandria: Boschhoek, Acocks 12089; Sandflats, Archibald 5433. Cradock: Mountain Zebra Park, Barnard 518; Brynard 30; Cradock, Holland s.n. Albany: Grahamstown, Godfrey & Story, S.H. 1351; Britten 2964. Bathurst: Port Alfred, Tyson s.n. Dep. Agric. No. 12601; Kowie West, Britten 5926; Kowie, Tyson, Tvl. Mus. 17070. King William's Town: Keiskama Valley, Story 3690.

The distribution of this variety is limited to the Cape Province where it occurs from the Peninsula to the King William's Town district (Fig. 3). It occurs mainly in shady places but often in habitats which are much more arid than those of the var. *elongata*. The large, hard tufts are found along forest margins as well as in xerophytic karroid scrub. It is well-grazed by game and stock. (b) var. elongata (Nees) Stapf in Fl. Cap. 7: 573 (1898); Chippindall in Grasses and Pastures S.A. 1: 289 (1955). Type: Uitenhage, Primeval forest at Krakakamma, Drege s.n. (B<sup>†</sup>; PRE, fragment of holo.!).

Lasiagrostis elongata Nees, Fl. Afr. Austr. 168 (1841). L. capensis var. elongata (Nees) Trin. & Rupr., Gram. Stip., 88 (1842).

Stipa elongata (Nees) Steud., Syn. Plant. Glum. 1: 132 (1855).

Oryzopsis keniensis Pilger, Notizbl. Bot. Gart & Mus. Berlin 9: 509 (1926).

Piptatherum keniense (Pilg.) Roshev. in Bot. Mater Herb., Kamarov, Bot. Inst., U.S.S.R. Acad. Sci., 14 (1951).

Inflorescence effuse and divaricate, not much longer than broad.

CAPE.—Cape Peninsula: Camps Bay, Strey 772; Orange Kloof, Adamson 881; Kirstenbosch, Bolus s.n.; Skeleton Ravine, Marloth 6048; Bolus s.n. Alexandria: Olifantshoek, Johnson 909. Victoria East: Hogsback, Johnson 1139. Cathcart: Liebenberg 5389. Stutterheim: Kologha Forest, Acocks 9020; Dohne Mtn., Galpin 2455. East London: near river, Galpin 6533. King William's Town: Sim 20251. Komga: Grass valleys near Komga, Flanagan 909; Kei Road Station, Ranger s.n. Kentani: Chippendall 325; Along stream, Pegler 1106. Mt. Frere: Story 939. Umzimkulu: Insikeni near Hoha, van Tonder 4.

NATAL.—Lion's River: Nottingham Road, Maclean 955. Estcourt: Little Tugela River, Pentz 178. Bergville: Cathedral Peak Forest Res. Station, Indumeni River valley, Killick 1675; The Cavern, in fern forest, Gemmel 5347. Mont. aux Sources, Mogg 5314.

TRANSVAAL.—Krugersdorp: Magalies River, Codd 522; Waterval 74, Mogg 23285. Soutpansberg: Malta Gorge, Junod 4432; Blaauwberg, Leipzig Mission, Schweickerdt 1818.

BRITISH EAST AFRICA: KENYA.—Ngong, van Someren AH 9548; Muguga, Verdcourt 1841; Nakuru, Eastern Mau Forest Reserve, Maas-Geesteranus 6102; Londiani, Tonderet Forest Reserve, Maas-Geesteranus 4915.

The variety *elongata* occurs in the coastal areas of the Cape from the Peninsula to the Transkei, along the Drakensberg escarpment in Natal and in a few areas of the Transvaal (Fig. 3). It is also found in the cool highlands of Kenya at altitudes of over 6,000 feet. Personal observation and collectors' notes indicate that it prefers cool, shady and moist conditions. These factors explain, to some extent, its very interrupted distribution; suitable habitats being rare and occurring at wide intervals. It is possible that it has been over looked in the cool mountainous areas of the Rhodesias, Uganda and Tanganyika where one would expect it to occur. The fact that it is usually not abundant in its known habitats is a point in favour of the latter view.

Stipa dregeana was described originally by Nees as Lasiagrostis capensis Fl. Afr. Austr., 167 (1841). The genus Lasiagrostis is regarded by most authors as synonymous with Stipa, but Roshevitz (1951) retains it as distinct. If regarded as synonymous with Stipa and retained as a section, the name of the section must be Achnatherum for nomenclatural reasons, as pointed out by Elias (1942, p. 62) and Hitchcock (1950, p. 216). Investigation, however, has shown that S. dregeana does not belong to this section sensu stricto, but probably, in agreement with Elias (1942, p. 64) is provisionally best placed in the section *Ptilagrostis*. Some modification here may eventually be desirable since the two lobes at the apex of the lemma, otherwise typifying the section, are lacking in S. dregeana. Oryzopsis keniensis Pilger, which is conspecific with Stipa dregeana var. elongata, is placed in the genus Piptatherum Beauv. of the subtribe Timouriinae Roschev. by Roshevitz (1951). The type species of Piptatherum Beauv. is Piptatherum coerulescens Desf. to which S. dregeana is not closely related. Piptatherum coerulescens has a glabrous, ovate lemma and an untwisted deciduous awn, whereas the palea is distinctly exposed at the base of the floret, the lemma only overlapping upwards: a typical characteristic of Oryzopsis sensu lato which includes

*Piptatherum.* In S. dregeand the lemma is cylindric, and in the fruiting spikelet the palea is slightly exposed towards the base of, and between the practically parallel margins of the lemma. In mature specimens the awn is often twisted at the base and does not disarticulate. The following species are apparently close relatives of S. dregeana: Stipa sibirica from Europe, Stipa vaseyii from N. America, Achnatherum pekenense (Hance) Ohwi (= Stipa extremiorientalis) from Japan, and Orvzopsis aeguiglumis Duthie from the North-West Himalayas. All these species technically belong to the genus Oryzopsis according to Bor's delimitation (1960, p. 641) of Stipa and Oryzopsis. Bor separates Orvzopsis from Stipa as follows: "Lemmas elliptic, plump; awn eventually deciduous; not twisted but curved; callus short, obtuse, never long and pointed". If Bor's delimitation of these genera is accepted S. dregeana, although possessing a twisted persistent awn. could possibly be placed in Oryzopsis. Another fact which may be of significance is the shortness of the epiblast in the embryo of S. dregeana (Fig. 2, E). According to Reeder (1957, p. 764) Stipa has a very long epiblast which reaches to the tip of the coleoptile (cf. S. capensis, Fig. 4E) whereas Oryzopsis has a "rather small epiblast". The rather short epiblast of S. dregeana would again point to a closer affinity with Oryzopsis. The delimitation of the genera by different authors, however, varies to such a degree that at present a transfer of S. dregeana to Oryzopsis seems unjustified.

A new combination in *Stipa* based on *Lasiagrostis capensis* Nees, the oldest name for this species, is not possible due to the existence of an earlier homonym, *Stipa capensis* Thunb., and *S. dregeana* Steudel therefore is the valid name for the taxon when placed in the genus *Stipa*.

2. S. capensis *Thunb.*, Prodr. 19 (1794); Thunb., Fl. Cap. ed Schult. 106 (1823); Nees, Fl. Afr. Austr. 1: 170 (1841); Trin. & Rupr., Gram. Stip. 63 (1842); Steud, Syn. Pl. Glum. 1: 129 (1855); Tackholm & Drar, Fl. Egypt, 1: 354 (1941); Chippindall in Grasses & Pastures S. Afr. 1: 290 (1955). Type: Cape, *Thunb.* s.n. (UPS, holo.). *Stipa tortilis* Desf., Fl. Atlant. 1: 99 t. 31, Fig. 1 (1798); Kunth, Enum. 1 Suppl.: 134 (1835); Trin. & Rupr., Gram. Stip. 64 (1842); Steud., Syn. Pl. Glum. 1: 130 (1855); Boiss, Fl. Or. 5: 500 (1884); Durand & Schinz, Consp. Fl. Afr. 5: 812 (1895). Stapf in Fl. Cap. 7: 372 (1898).

Caespitose annual. Culms erect or geniculate, slender, hollow, 10-100 cm high, unbranched or branched from lowermost nodes, glabrous; internodes usually enclosed by the sheaths, or the upper exserted; nodes glabrous. *Leaf-sheaths* rather loose, often slipping from the culms, the upper wider and sheathing the base of the young panicles, sparsely pubescent to pilose or glabrous. Ligule a membranous ciliolate rim. Leaf-blades linear, tapering to a fine point, expanded or somewhat rolled, 5-20 mm long and up to 3 mm wide, glabrous or sparsely pubescent to pilose below, often scabrid above. Panicle spike-like, narrow, 3-15 cm long; rachis terete, slightly ribbed, scabrous with appressed hyaline spines; branches fascicled, scabrous, very unequal, branched or simple, up to 7 cm long; pedicels shorter than the spikelets. Spikelets linear in outline, silvery,  $1 \cdot 2 - 1 \cdot 6$  cm long. *Glumes* very narrowly lanceolate to linear, hyaline, silvery, tapering to a fine apex, 3-nerved, the lateral nerves short; lower usually exceeding the upper in length, up to 1.6 cm long; upper up to 1.5 cm long. Lemma cylindrical, margins convolute, tightly clasping the grain, indurated, 4-5 mm long excluding the callus, sparsely bristly, 5-7-nerved, dorsally constricted just below the awn; awn solitary, deciduous, articulated at apex of lemma, 5-8 cm long, column twice geniculate, tightly twisted, hairy; bristle short, scabrid; callus pungent, bearded, up to 2 mm long. Palea much shorter than the lemma, 1.25-1.5 mm long, obtuse, somewhat indurated, 2-nerved, glabrous. Lodicules 2, oblong, membranous, hyaline, up to 1.5 mm long. Stamens 3, anthers yellow, 2.0-2.3 mm long, penicillate. Ovary glabrous, styles distinct, stigmas plumose. Caryopsis spindle-shaped, shortly stalked, 3-3.5 mm long, brown; hilum linear, nearly as long as the grain; embryo about the length of the grain (Fig. 4, D).



FIG. 4.—Stipa capensis: A, cross section of vascular bundles of the leaf-blade; B, diagram of leafblade in cross section; C, abaxial epidermis of the leaf-blade; D, caryopsis showing the embryo; E, longitudinal section of the embryo; F, cross section of the embryo (Acocks 18591).

### ANATOMY (Fig. 4, A & B)

Leaf-blade thin and flat, tapering towards the margins, abaxial surface with shallow depressions between the bundle units which are slightly raised, both surfaces with a few hairs; midrib only slightly protruding abaxially, not distinctly keeled; margins obtuse to acute. Abaxial epidermis: stomatal zones with a few stomata or stomata absent and zones consisting of elongate rectangular ripple-walled cells usually alternating with short elements; short elements single or paired, wider than long, occasionally giving rise to short unicellular papilla-like hairs, occasionally much enlarged, and producing very long soft unicellular hairs; bicellular hairs absent; silicified cells small, dumb-bell-shaped. Vascular bundle units: first order units about 9, trapezoid in outline, alternating with the second order units; second order bundle units broadly ovate in outline. Bundle sheaths: outer of large thin-walled parenchymatous cells, in the larger first order bundles supplemented by large cells both ab- and adaxially and these cells gradually decreasing in size as the walls increase in thickness; thus merging into the fibres of the stereome; inner sheaths of much smaller cells with the inner tangential walls strongly thickened, the outer walls, however, thin-walled. Chlorenchyma of irregular thin-walled cells forming a continuous tissue between the bundles. Stereome strands composed of small fibres, not very strongly developed, present both ab- and adaxially opposite all bundles or occasionally absent adaxially opposite the second order bundles, but always absent opposite the motor cells. Motor cells rather poorly differentiated, thin-walled, 5-8 in number, occupying only about  $\frac{1}{3}$  the thickness of the leaf.

Awn: column more or less square in outline, shallowly grooved ventrally, furnished with three vascular bundles; central bundle large and surrounded by large cells with very strongly asymmetrically lignified walls, those situated on the ventral and dorsal sides of the bundle much exceeding the others in size; lateral bundles small and situated near the base of the central bundle, each subtending a large somewhat elongated group of chlorenchyma cells which flank the central bundle and lie directly below

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the lateral epidermis; epidermis with the outer tangential walls strongly lignified, furnished with stomata opposite the chlorenchyma groups. *Seta* similar to the column but all cells with thinner walls, towards the apex the lateral bundles disappear and the chlorenchyma cells lie in close contact with the central bundle which is then surrounded by one or two layers of thin-walled cells.

Caryopsis: starch grains compound, composed of numerous granules; *embryo* in sagittal section showing the presence of an extremely elongated epiblast, the lower part of the scutellum fused to the coleorrhiza, no cleft present at the base of the coleorrhiza and the scutellum bundle diverging below the coleoptile. The cross-section of the first embryonic leaf (sheathed by the coeloptile) with margins touching but not overlapping; the coleoptile with two lateral vascular bundles and the scutellum with one median vascular bundle (Fig. 4 E & F).

CAPE.—George: Karoo in vicinity of Gauritz River, *Ecklon* s.n. Clanwilliam: *Schlechter* 8588; Welbedacht, *Maguire* 1855. Vanrhynsdorp: Ebenezer at Olifants River, *Drege* 8105; Zandkraal locally abundant in Marginal Strandveld, *Acocks* 14736; 2 m. N. of Vanrhynsdorp, *Schweickerdt* 2558; Wiedou River, *Barker* 9483. Calvinia: Groot Toring, *Acocks* 18591. Namaqualand: Doorn River Bridge, *Taylor* 997; Wallekraal, between Kamieskroon and Hondeklipbaai, *Schweickerdt* 2565. IRAQ.—Isbel Hamrin near Injana, *Guest* s.n. (N.H. 15797); Isbel Daramish-kan, *Guest* s.n. (N.H. 16003).

It occurs in the arid parts of the south western Cape in areas with winter rainfall (Fig. 3), and is widely distributed in North Africa and the Middle East. The interrupted distribution of *S. capensis* follows a pattern similar to that of many species in the Gramineae and various other families (see page 304). This annual species is adapted to desert conditions.

Guenzel (1921, p. 6) investigated the anatomy of the leaf-blade of *S. capensis* (as *S. tortilis* Desf.) and his observations agree fairly closely with the description given above. The specimen investigated by Guenzel was collected at El-Kantara in North Africa.