PART 3

GENERAL CONSIDERATIONS

3.1. General Discussion of the Leaf Anatomy of the Aristideae

The anatomical details included in the taxonomic descriptions are based only on the study of scrapes of the abaxial epidermis and cross-sections of the leaf-blade. For this reason a general account giving further details of the anatomical structure has been drawn up. In order to arrive at a better understanding of the anatomy, a thorough study was made ot a few representative species where, in addition to the epidermal scrapes and cross sections prepared for all species, the leaf in longitudinal section, and the leaf-tissues in a macerated state, were included.

Stipagrostis (Fig. 157)

The Epidermis. The long elements of the abaxial epidermis seen in surface view (Fig. 157, H) usually have strongly undulate, anticlinal walls, and cross sections show that the outer (tangential) walls are strongly thickened. In longitudinal section under

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high magnification the strong thickening of the outer walls is very evident and in this thickened portion faint concentric complete or interrupted circles can be seen. These concentric rings are the undulations of the anticlinal (radial) walls, which so clearly show up in surface view, seen end on (Fig. 157 F). From this it may be inferred that the faces of the anticlinal walls (those parallel to the longitudinal axis of the leaf) are strongly undulate mainly in their upper part, i.e. the area approaching the outer tangential wall of the cell concerned; the undulations, however, gradually become weaker and finally disappear as the anticlinal walls "approach" the inner tangential wall of the cell. The long ripple-walled cells of the adaxial epidermis are thin-walled and the anticlinal walls usually much less undulate. In some cases, however, their inner tangential walls are thickened whereas their outer walls are thin. Two types of epidermal hair occur: (1) Unicellular retrorse barbs more or less appressed to the surface of the epidermis occur in most species both ad- and abaxially. There is, however, a marked tendency for a more copious production of hairs adaxially and these hairs are usually less appressed to the surface thus forming a dense bristly layer. Appressed unicellular hairs are also present adaxially. In surface view these hairs are broadly oblong in outline when very short, and the apex can often be distinguished only with difficulty. They vary greatly in shape and length, viz. abruptly produced into an acute apex, to attenuate with an acuminate, very fine, sharp apex. In longitudinal section it is clearly seen that the base is often narrowed and inserted between the adjoining narrow ends of the long ripple-walled elements. In the species with long woolly hairs, the bases of these hairs are also narrowed, occupy the same position, and should therefore be regarded as homologous with the papilla-like hairs found

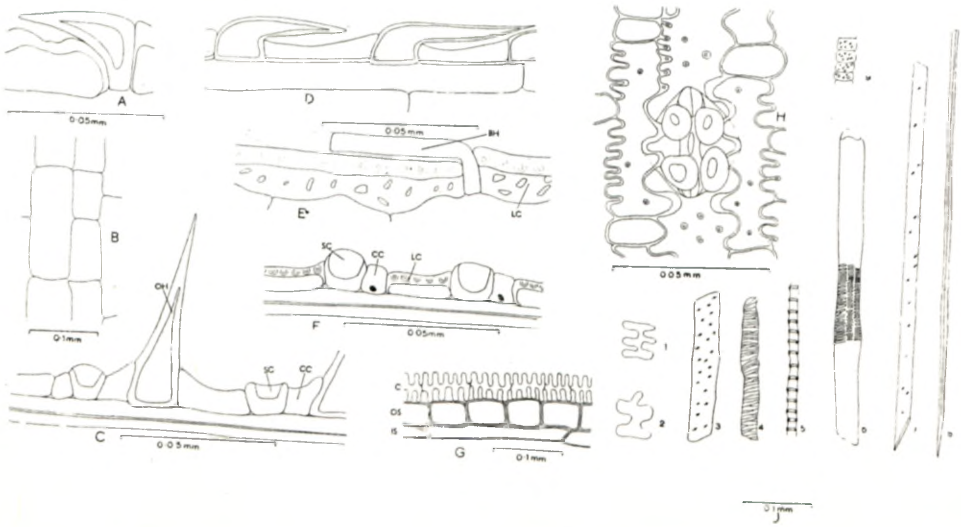

FIG. 157.—*Anatomical details of Stipagrostis: S. uniplumis* var. *neesii:* A, one-celled retrorse barb in longitudinal section in the stomatal area of abaxial epidermis; B, l.s. of motor cells; C, adaxial epidermis, adjacent to the stereome, in longitudinal section showing one-celled hair (OH), silicified cells (SC) and suberized cells (CC); D, l.s. of adaxial epidermis showing retrorse hairs subtended by parenchyma cells; E, l.s. of bicellular hair in the stomatal area of abaxial epidermis; F, l.s. of abaxial epidermis in silicified cell zone showing silicified cells (SC) accompanied by suberized cells (CC) as well as long ripple-walled cells (LC) and subtended by fibres; G, l.s. of bundle sheaths and chlorenchyma cells (*de Winter* 3204). *S. dregeana:* H, surface view of stoma and guard cells in abaxial epidermis, showing large papillae, formed by projections of the walls of the adjacent long ripple-walled cells, which project over the guard cells (*Kinges* 2572). *S. uniplumis* var. *neesii:* J, cell types: 1. chlorenchyma, 2. parenchyma cell supporting the chlorenchyma, 3. thick-walled pitted parenchyma cell from the xylem; 4. small mx vessel; 5. ring vessel from px; 6. large pitted vessel from mx; 7. transition fibre; 8. fibre; 9. inner bundle sheath cells.

in other species. A complete gradient between these extreme types is found (Fig. 157, A). (2) *Hairs of the bicellular linear type:* The bases of these hairs are likewise inserted between the adjoining narrow ends of long ripple-walled cells. In contrast to the unicellular hairs they are relatively thin-walled and terete; they lie closely appressed to the surface of the epidermis (Fig. 157, E). The *silicified cells* are strongly impregnated with silica. In longitudinal section the silicified cells are usually about as wide as deep, the anticlinal walls parallel or sloping inwards towards the inner walls so that the cells are narrowed towards the base (Fig. 157, C, F). The inner tangential walls as well as the anticlinal walls are much thickened, decreasing in thickness towards the outer thin tangential wall which is domeshaped (Fig. 157, F).

In a few annual species the silicified cells are dumb-bell-shaped in surface view and thus agree with the silicified cells of *Aristida* in general structure (see p. 392). The silicified cells in both the adaxial and abaxial epidermis are similar in shape and size. They are usually more numerous in the abaxial epidermis. The *suberized cells* can be recognized by the usually deeper staining of the contents of these cells which in the mature epidermis often have retained their nuclei. They are thin-walled throughout. In the majority of cases they are found in association with the silicified cells. Where they are small and associated with silicified cells which are narrowed towards the inner walls they are partially hidden and often appear kidney-shaped in surface view (Fig. 157, C, F). In the stomatal apparatus the cells subsidiary to the guard cells are triangular (Metcalfe 1960, p. 667). In a few species the thick outer tangential walls of the adjacent ripple-walled long cells are produced into large papilla-like structures projecting over the stomatal apparatus partially hiding the component cells (Fig. 157, H). Examples of this are found in the abaxial epidermis of *S. obtusa*, *S. lanipes* and *S. dregeana*. This phenomenon has also been reported by other authors for species such as *S. ciliata* and *S. pungens*.

The *motor cells* are large parenchymatous cells and do not exhibit any striking peculiarities (Fig. 157, B).

The *chlorenchyma*, however, presents an entirely different picture in longitudinal section compared with that in transverse section. The cells are elongated with the tangential walls deeply undulated thus creating a large number of intercellular spaces. The circular structures observed in these cells, when studied in cross section, represent the constricted portions of the cells seen in end view. This may be characteristic for all the tribes showing a radial arrangement of the chlorenchyma (Fig. 157, G). The *outer sheath of the vascular bundles*, which lies adjacent to the chlorenchyma, is composed of cells which are either thin-walled or the walls of these cells may be somewhat thickened. These cells are well supplied with chloroplasts and are larger or smaller than the cells of the inner sheath. Study of longitudinal sections shows that they are fairly short and occasionally approximately isodiametric. The length of the longitudinal walls, however, usually exceeds their width (Fig. 157, G). The cells of the inner sheath are usually rather elongated, thin-walled and devoid of chloroplasts. They are parenchymatous cells with slightly, or occasionally fairly strongly thickened walls. These are traversed by simple or funnel-shaped pits; if funnel-shaped, the openings are slit-like and lie obliquely.

The Xylem. The protoxylem vessels are usually either ring or spiral vessels and are partially or wholly surrounded by thin-walled elongate proto-parenchyma cells. The large metaxylem vessels are somewhat angular with transverse elongate bordered pits on the longitudinal walls; the transverse walls of the original component cells of the vessels are usually only slightly oblique, often with only a single large perforation, and thus almost absent. The smaller cells between and adjoining the large metaxylem vessels in longitudinal section, are vessels of various sizes with the remains of the transverse walls usually more oblique than in the large metaxylem vessels, the ends with one very large or a few fairly large perforations (Fig. 157, J, 3, 4, 5, 6). The cells surrounding the phloem are fibres or occasionally parenchyma cells with somewhat thickened walls. Where parenchyma cells adjoin the xylem vessels the walls are pitted complementarily.

The adaxial stereome consists mostly of long, very thick-walled fibres, likewise the abaxial stereome but, in a few species the abaxial stereome consists of large cells which in longitudinal section are seen to be elongate somewhat thick-walled parenchymatous cells. Much elongated narrow cells, intermediate in shape between fibres and parenchyma cells, frequently occur among the thick-walled parenchymatous cells just mentioned (Fig. 157, J, 7).

Aristida (Fig. 158)

Aristida largely agrees with *Stipagrostis* in its general anatomical features, and the description of the latter thus also applies to the former except for the bundle sheaths and silicified cells. Both the outer and the inner bundle sheaths of *Aristida* contain chloroplasts in contrast to *Stipagrostis*, in which only the outer sheath contains these bodies. The silicified cells of *Aristida* are almost invariably dumb-bell-shaped varying from short and broad to much longer than wide with a slender elongated central constriction. In a few species, however, such as *A. sciurus* and *A. dasydesmis* the silicified cells frequently are sub-circular. In species where the silicified cells are well developed they often protrude strongly above the surface of the epidermis (Fig. 158, H).

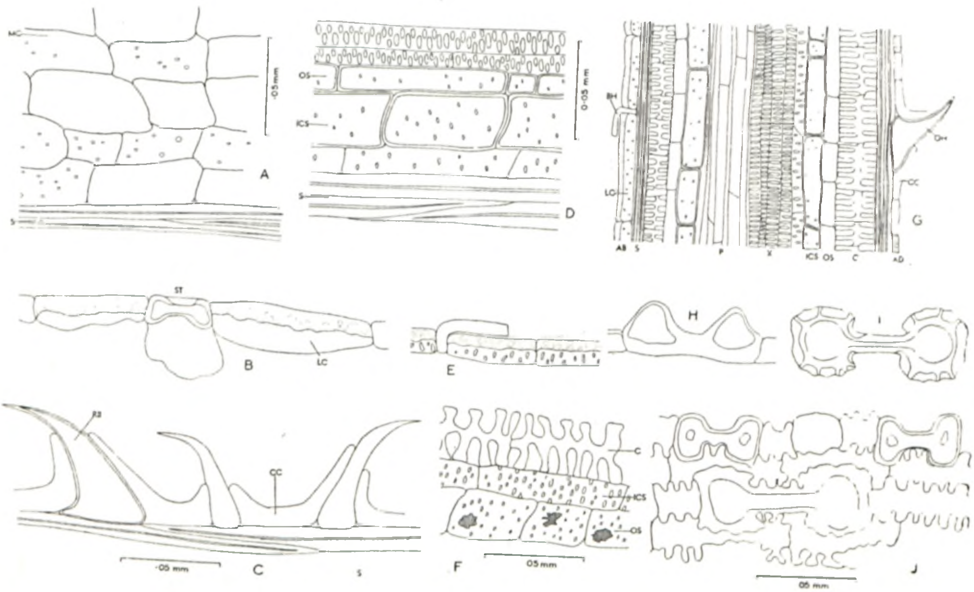

Fig. 158.—*Anatomical Details of Aristida: A. mollissima:* longitudinal section of: A, motor cells; F, abaxial epidermis cells and stoma; C, adaxial epidermis showing curved unicellular hairs sheathed at the base by enlarged suberized cells; D, bundle sheath cells (OS and ICS), fibres (S) and xylem vessels; E, bicellular appressed hair, and outer walls of epidermal cells showing circular patterns caused by undulate walls; F, *A. hordeacea*, inner and outer sheath cells (ICS and OS) and chlorenchyma cells (C) seen in longitudinal view (macerated material); G, *A. barbicollis*, longitudinal section through a third order vascular bundle: AB, abaxial epidermis; AD, adaxial epidermis; BH, bicellular hair; CC, suberized cell; C, chlorenchyma; ICS, inner bundle sheath; LC, long ripple-walled cell; OH, one-celled hair; OS, outer bundle sheath; P, phloem; S, stereome; X, xylem. *A. hordeacea*, macerated material: H, longitudinal section of silicified cell; I, silicified cell seen from below showing surfaces of attachment to other cells; J, epidermis in surface view showing ripple-walled and silicified cells.

The suberized cells on the adaxial epidermis are often very strongly developed adjacent to unicellular hairs, forming a sheath-like structure enclosing the base of the hair (Fig. 158, C, G). These cells are also described and depicted by Caceres (1961, p. 9). In Fig. 158 various tissues and individual cells as seen in longitudinal section are shown.

3.2. Silicification of the Leaf-Epidermis in the Aristideae

It is well known that grass leaves are often difficult to section due to silica deposited in the tissues. In order to obtain more information on the distribution of silica in the leaves of the *Aristideae*, material of several species was treated with acid to remove all organic material (see p. 204). The residue remaining after this treatment can readily be dissolved in hydrofluoric acid, and therefore represents the silicified parts of the leaf.

In some cases practically the whole of the epidermis was found to be silicified and fairly large pieces of recognizable epidermal "skeletons" were present in the residue. Two types of silicification were observed, viz. the impregnation of cell walls with silica, and the formation of solid or hollow "silica bodies" within cell cavities. The former was fairly general for all types of epidermal cells: even the cell walls of stomata were occasionally observed to be silicified, but the silica skeletons are extremely fine and fragile. The second type of silicification is found in "silicified cells" and some long ripple-walled cells. Here the cells contain silica bodies, which may be hollow or solid, in appearance and which fit tightly into the cell cavity. These bodies can be dissected from the cells leaving the cavity lined by the cell walls. In epidermal scrapes glass-like fractures are occasionally visible in the silica bodies. These fractures are probably caused by pressure exserted during scraping and do not extend to the cell walls as would be expected if the whole of the cell was silicified. This investigation has also indicated that the tissues of species growing in very dry areas are often more highly silicified than those of species growing under more temperate conditions.

SUMMARY

1. Anatomical, cytological and organographic data indicate that the *Stipeae* is a tribe of uncertain affinity.

2. The *Stipeae* should be limited to the genera *Stipa*, *Oryzopsis*, *Piptochaetium* and *Trikeraia*, of which only *Stipa* occurs in South Africa.

3. Of the four species of *Stipa* previously recorded from South Africa, only two are true species of *Stipa*, the other two being one-awned representatives of the *Aristideae*.

4. *Stipa parvula* Nees, is transferred to *Aristida* under the designation of *Aristida parvula* (Nees) de Winter, and *Stipa namaquensis* Pilger to *Stipagrostis* under the designation of *Stipagrostis anomala* de Winter.

5. The differences between the *Aristideae* and *Stipeae* are discussed. The *Aristideae* was justifiably separated from the *Stipeae* by Hubbard.

6. The phylogenetic position of the *Aristideae* is uncertain, but there are strong indications that this tribe is distantly related to the *Eragrosteae*.

7. The inclusion of *Amphipogon* and *Diplopogon* in the *Aristideae* (Pilger, 1956) cannot be supported. Both these genera could probably be better accommodated in the *Danthonieae*.