

Leaf Anatomy and Morphology in South African Species of *Danthonia*.

By

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The genus *Danthonia* is variable and this is particularly true of the South African species (de Wet, 1954a and 1956). On the basis of anatomical and morphological evidence Nevski (1934)† removed *D. glauca* Nees and *D. forskalii* (Vahl.) R. Br. from *Danthonia* to form the basis of a new genus, *Asthenatherum*. It was suggested by Hubbard (1937) that some other South African species may be equally worthy of generic rank. A new genus *Alloeochaete* was described by Hubbard (1940) to include *D. andonensis* Rendle. The South African species were studied in detail in order to determine whether any other species should be removed from *Danthonia*.

MATERIAL AND METHODS

Anatomical slides were prepared from Herbarium material as indicated by Prat (1948) and de Wet (1956). Chromosome numbers were counted in root-tip sections. Root-tips were collected in the veld, fixed in Randolph's (1935) fluid, dehydrated and sectioned as indicated by de Wet (1953) and stained in Stockwell's (1934) solution. Drawings of chromosomes and vascular bundles were made with the aid of a camera lucida.

RESULTS

The anatomical study is confined to mature leaves. These data are presented in the form of a key in Table I. Only the lower epidermis surface has been studied. In *D. forskalii* (Vahl.) R. Br. the siliceous cells are in the shape of short dumbbells which often appear spherical.

TABLE I.—ANATOMICAL TRAITS

1. Chlorophyll localized around the vascular bundles; inner bundle sheath sclerenchymatous, outer bundle sheath parenchymatous; bicellular hairs present; siliceous cells dumbbell-shaped, localized above nerves; unicellular hairs form an arch over stomata. (Figs. 2 and 5).....	<i>D. forskalii</i> , <i>D. glauca</i> , <i>D. mossamedensis</i> , <i>D. suffrutescens</i> .
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† Ex, Hubbard (1937), page 135.

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| 7. Unicellular hairs do not form an arch over the stomata..... | 9 |
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| 9. Epidermis cells thin parenchyma; dumbbell-shaped siliceous cells localized above the nerves (Fig. 6). <i>D. brachyphylla</i> , <i>D. curva</i> , <i>D. macrantha</i> , <i>D. purpurea</i> , <i>D. tenella</i> . | |
| Epidermis cells thick parenchyma; spherical siliceous cells localized above the nerves (Fig. 7)..... | <i>D. dura</i> , <i>D. stricta</i> . |
| 10. Epidermis cells thick parenchyma; dumbbell-shaped siliceous cells localized above nerves..... | <i>D. pumila</i> . |
| 8. Epidermis cells thick parenchyma; halfmoon-shaped siliceous cells distributed all over the epidermis..... | <i>D. cincta</i> , <i>D. papposa</i> . |
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| Epidermis cells thick parenchyma; bicellular hairs absent; siliceous cells spherical, distributed all over the epidermis..... | <i>D. drakensbergensis</i> , <i>D. macowanii</i> . |
| 14. Epidermis cells thick parenchyma; bicellular hairs absent, siliceous cells spherical, distributed all over the epidermis (Fig. 8)..... | <i>D. disticha</i> . |
| 4. Leaves more or less spherical; chlorophyll localized in a continuous band 3-5 layers of cells thick directly below the epidermis; mesophyll in the middle lacks chloroplasts; inner bundle sheath sclerenchymatous, outer bundle sheath composed of thin parenchyma (Fig. 1); bicellular hairs absent; epidermis cells thick parenchyma; siliceous cells spherical, localized above nerves..... | <i>D. rangei</i> . |

The morphology of the South African species of *Danthonia* has been discussed by Stapf (1900), Hubbard (1937) and Chippindall (1955). It will suffice to discuss the main characteristics of each group into which *Danthonia* was subdivided on the basis of anatomical traits. The species *D. mossamedensis* Rendle and *D. suffrutescens* Stapf share with *Asthenatherum* (*D. glauca* Nees and *D. forskalii* (Vahl.) R. Br.) the following prominent characteristics of external morphology. The lower culms are shortly pubescent to tomentose; innovation shoots are extravaginal; glumes strongly chartaceous, the lower distinctly 7-11-nerved and the upper 5-9-nerved; lemmas 7-10-nerved with the hairs arranged in rows between the nerves, the outer rows ending in tufts of longer hairs just below the lobes and the inner rows ending just below the insertion of the awn; lodicules 2, cuneate, nerved and glabrous; callus acute. These characteristics are also descriptive of *D. pumila* Nees, except that in the latter species the callus is obtuse. *Danthonia glauca* Nees and *D. suffrutescens* Stapf resemble each other so closely that the latter species could perhaps be regarded as a variety of *D. glauca* Nees. As indicated by Stapf (1900) they differ from each other only in two characters. The spikelets of *D. suffrutescens* Stapf are slightly larger and more acuminate than those of *D. glauca* Nees and the plant is suffrutescens with the lower sheath coriaceous. In contrast *D. glauca* Nees has smaller spikelets, is herbaceous and has a thin lower sheath. The genus *Asthenatherum* is further characterized by the panicoid type of internal leaf anatomy and epidermis.

The typical *Danthonia* species with dumbbell-shaped siliceous cells may be subdivided into three groups on the basis of external morphological traits. *Danthonia macrantha* Schrad. and *D. brachyphylla* Nees resemble *Pentameris* in superficial appearance but are more typical of *Danthonia* in spikelet morphology (Chippindall, 1955). They differ from other species of *Danthonia* conspicuously only in having two florets per spikelet and in that the hairs of the stigma bend down to join over the top of the ovary.

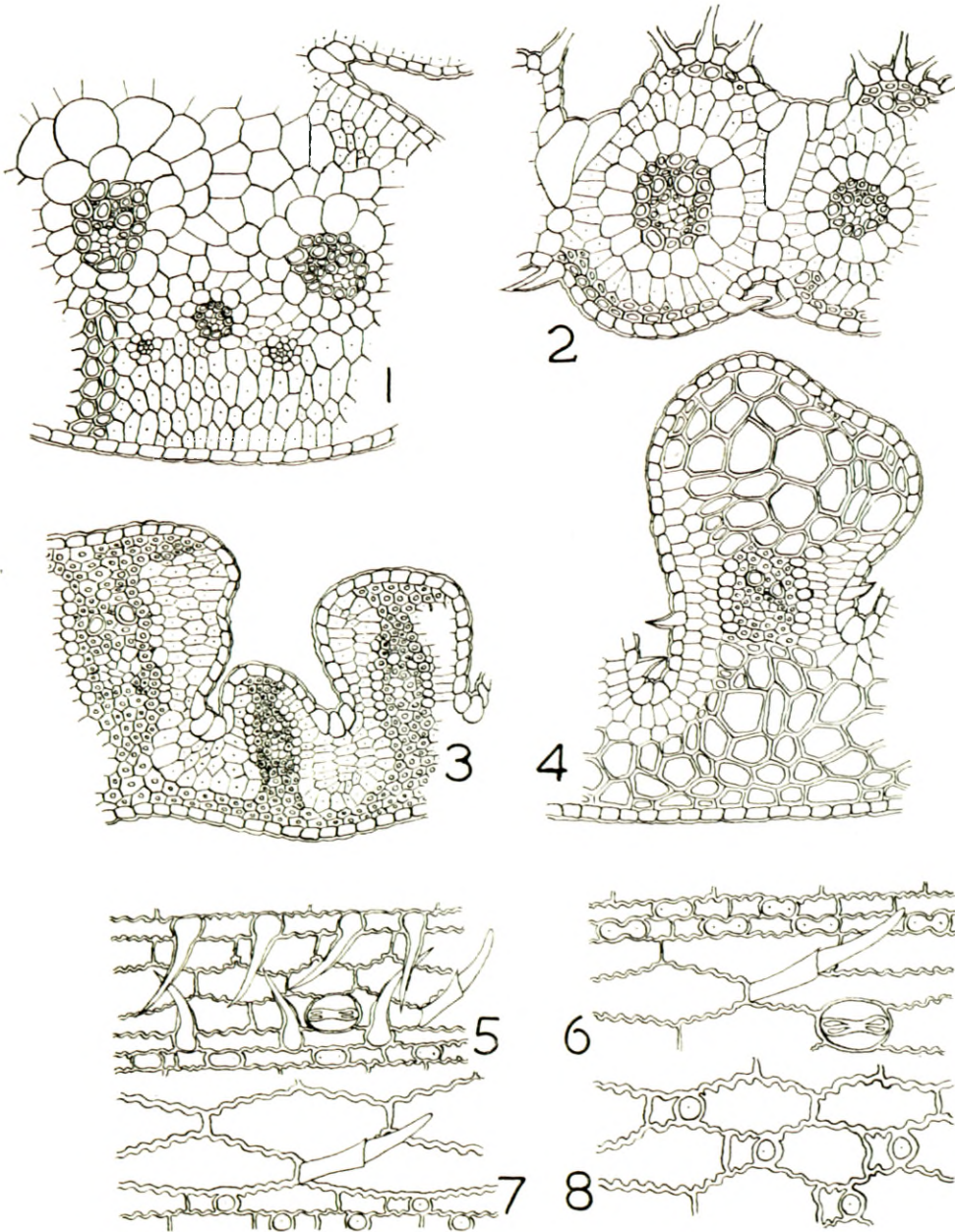


FIG. 1-4.—Internal leaf anatomy $\times 750$. 1. *D. rangei*; 2. *D. forskalii*; 3. *D. arundinacea*; 4. *D. cincta*.

FIG. 5-6.—Epidermis $\times 1000$. 5. *D. forskalii*; 6. *D. curva*; 7. *D. stricta*; 8. *D. disticha*.

Glumes that are 5-nerved; 9-nerved lemmas with a transverse fringe of tufts of long hairs below the insertion of the awn and several submarginal tufts below this fringe; distinctly 3-nerved lemma-lobes and 2 lodicules which are small, cuneate-obovate and ciliate are characteristic of *D. purpurea* Beauv. and the closely related annual *D. tenella* Nees.

Danthonia curva Nees with dumbbell shaped siliceous cells resemble *D. lanata* Schrad., *D. lupulina* (Thunb.) Roem. and Schult. and *D. zeyheriana* Steud. in spikelet morphology. These species have in common: glumes 3–5-nerved; lemmas 9-nerved with the hairs arranged in rows between the nerves ending just below the middle in a transverse fringe of long hairs; lobes of the lemma partly adnate to the awn; lodicules 2, obovate, ciliate, nerved.

Danthonia cincta Nees and *D. papposa* Nees differ from all other species of *Danthonia* in having 1–3-nerved glumes. Anatomically they are also quite distinct from other species of *Danthonia* (Figure 4). The cells between the bundles are sclerenchymatous except for two or more layers of cells along grooves of the upper epidermis. The chloroplasts are localized in these layers of parenchymatous cells.

Morphologically *D. dura* Stapf *D. stricta* Schrad., *D. drakensbergensis* Schweick. and *D. macowani* Stapf form a natural group with the following salient features: glumes 3–5-nerved; lemmas 7–9-nerved, with the hairs variously tufted; lemma-lobes partially adnate to the awn; callus obtuse; lodicules 2, obovate, ciliated, nerved.

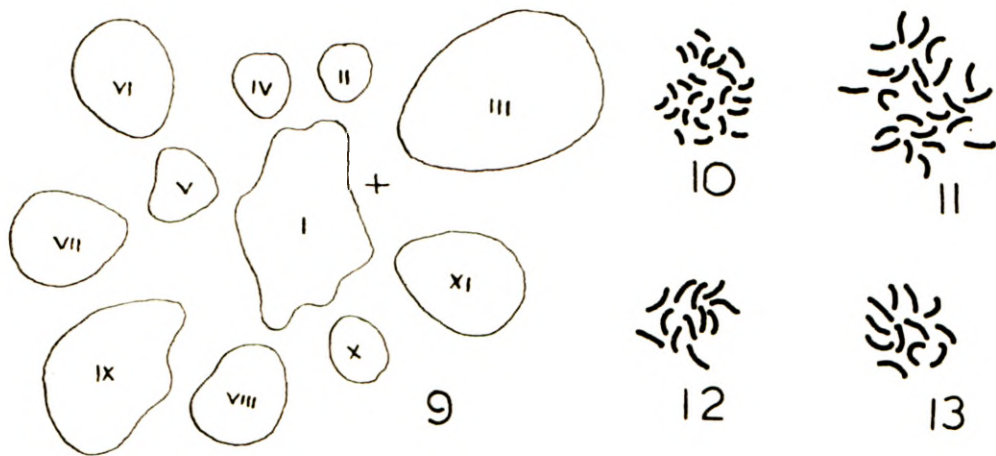


FIG. 9.—Diagram showing the relationships between species of *Danthonia*. The numbers represent groups of species as follows: Hypothetical ancestor; i. *D. curva*, *D. purpurea*, *D. tenella*; ii. *D. pumila*; iii. *Asthenatherum* (*D. forskalii*, *D. glauca*, *D. mossamedensis*, *D. suffrutescens*); iv. *D. rangei*; v. *D. arundinacea*; vi. *D. cincta*, *D. papposa*; vii. *D. lanata*, *D. lupulina*; viii. *D. dura*, *D. stricta*; ix. *D. drakensbergensis*, *D. macowanii*, *D. zeyheriana*; x. *D. disticha*, xi. *D. brachyphylla*, *D. macrantha*.

FIG. 10–11.—Chromosome numbers $\times 3000$. 10. *D. forskalii*, 11. *D. tenella*; 12. *D. arundinacea*; 13. *D. macowanii*.

Danthonia arundinacea (Berg.) Schweick. is a robust, tufted perennial with stout culms from 80 cm to more than 100 cm high; glumes 1-nerved; lemmas 7-9-nerved, villous all over and the lobes taper into a fine, short awn. *Danthonia disticha* Nees differs from all other species of *Danthonia* in having the inflorescence shaped into a distichous spike. An analysis of the spikelet reveals typical *Danthonia* characteristics. Glumes 3-nerved, lemmas 9-11-nerved, bilobed, with the hairs arranged in a tuft at the base and with a line of similar hairs on each side extending to the base of the lobes; lodicules 2, obovate, ciliated, nerved.

Danthonia rangei Pilger with its peculiar internal leaf anatomy resembles *Asthenatherum* in habit and superficial appearance. Spikelet morphology, however, is more typical of *Danthonia*, except that the florets are reduced to 2 per spikelet. Glumes are 3-nerved; lemmas 5-7-nerved, hairy all over, with three tufts of hairs, one each at the base of the lobes and the third at the insertion of the awn; lodicules 2, cuneate, minute; callus obtuse.

Three species, *D. macowanii* Stapf ($2n = 12$), *D. arundinacea* (Berg.) Schweick. ($2n = 12$) and *D. tenella* Nees ($2n = 24$), were studied for the first time cytologically. A number of other species were previously studied by Calder (1937), Stebbins and Love (1941) and de Wet (1954 b). Basic chromosome numbers appear to be $n = 6$ and $n = 7$. It was also indicated by de Wet (1954b) that the chromosomes of species belonging to *Asthenatherum* [*D. forskalii* (Vahl.) R. Br.] are smaller than those of more typical members of *Danthonia* (compare Figures 10-11).

DISCUSSION.

The trends of evolutionary progress in the family Gramineae were pointed out by Stebbins (1956). From this discussion it becomes evident that the complex panicoid-eragrostoid type of epidermal traits (siliceous cells variously shaped, bicellular hairs present) and the festucoid type of chlorophyll distribution (uniformly distributed throughout the mesophyll of the leaf), are the more primitive leaf anatomical characters. Members of the genus *Danthonia* exhibit a combination of primitive and advanced anatomical traits.

The known diploid species are confined to southern Africa. On the basis of stomatal size it would appear as if these, *D. curva* Nees, *D. disticha* Nees, *D. arundinacea* (Berg.) Schweick. and *D. macowanii* Stapf, are the only diploid representatives of the genus. The stomata of these species vary in size from 23-30 μ to 25.00 μ . Other species with relatively small stomata are present in South America: *D. lechleri* Steud. (26.40 μ) and *D. secundiflora* Presl. (27.69 μ), but they resemble in stomatal size the known tetraploid species *D. tenella* Nees (26-30 μ) and *D. purpurea* Beauv. (26.40 μ) more closely (de Wet, 1954b).

The known diploids exhibit the primitive type of chlorophyll distribution. The epidermis is of the primitive type in *D. curva* Nees, but more advanced (bicellular hairs are absent and the siliceous cells are spherical) in the remaining three diploids. The lemma-lobes are well developed in these diploids, with the lemmas hairy all over in *D. arundinacea* (Berg.) Schweick. and variously tufted and fringed in the others.

In respect of spikelet morphology the North American species, together with some from South America and the European species, *D. calycina* Roem. and Schult., appear to be the most primitive. These are characterized by relatively poorly developed lemma-lobes and lemmas are hairy along the margins only, or also sparsely so on the back. The North American species with these characteristics are hexaploids ($2n = 36$) according to Stebbins & Love (1941). South American species which exhibit these primitive floral characteristics: *D. chilensis* Desv. has $2n = 36$, *D. oresigena* Phil.

has $2n = 48$, *D. cirrata* Hack. and Arech. has $2n = 72$ and the remaining species *D. malacantha* (Steud) Pilger, *D. montana* Doell., *D. montevidensis* Hack. and Arech., *D. secundiflora* Presl. and *D. tandilensis* Kotze are unknown cytologically. All these presumed primitive species are characterized by an epidermis with dumbbell-shaped siliceous cells and linear bicellular hairs. The chlorophyll is uniformly distributed throughout the mesophyll of the leaf and the outer bundle sheath is parenchymatous.

From this discussion it would appear as if the most primitive characters exhibited by present day species of *Danthonia* are as follows: Lemma-lobes poorly developed; hairs on the lemma not tufted or fringed and confined to the margins and the back; inner bundle sheath of the vascular bundles of the leaf sclerenchymatous, outer bundle sheath composed of parenchymatous cells; chlorophyll uniformly distributed throughout the mesophyll of the leaf; epidermis with dumbbell-shaped siliceous cells and linear bicellular hairs. No South African species exhibit all of these assumed primitive characters.

Two dominant lines of phylogenetic specialization are evident in the South African species of *Danthonia*. The first line gave rise to the genus *Asthenatherum*. The latter genus is regarded in this discussion to include the following species: *D. forskalii* (Vahl.) R. Br., *D. glauca* Nees, *D. mossamedensis* Rendle and *D. suffrutescens* Stapf. Morphologically they resemble the more typical species of *Danthonia* in many respects (Hubbard, 1937). Anatomically they retained the primitive epidermal characters but became specialized in respect of chlorophyll distribution. Only one of these species, *D. forskalii* (Vahl.) R. Br. is known cytologically, but it has been pointed out by de Wet (1954b) that although the basic chromosome number is, as in *Danthonia*, $n = 6$ or 12 the chromosomes are significantly smaller than those of typical representatives of *Danthonia*. It is of interest to note that all the species here included in *Asthenatherum* are adapted to grow exclusively in dry sandy areas. The second line of phylogenetic development retain the primitive type of chlorophyll distribution, but the outer bundle sheath became sclerenchymatous, bicellular hairs are absent from the epidermis and the siliceous cells are spherical. This group includes the species *D. disticha* Nees, *D. drakensbergensis* Schweick., *D. macowanii* Stapf and *D. zeyheriana* Steud. Three more species, *D. lanata* Schrad., *D. lupulina* (Thunb.) Roem. and Schult., and *D. arundinacea* (Berg.) Schweick., resemble the above species in leaf anatomical characters except that the outer bundle sheath is parenchymatous.

Danthonia stricta Schrad. and *D. dura* Stapf combine in their epidermis a peculiar combination of primitive and advanced characters. The siliceous cells are spherical, but linear bicellular hairs are always present.

Three species with the festucoid type of epidermal traits appear to represent specialized lines of development in respect of internal leaf anatomy. The chlorophyll bearing tissue is localized but not as in the highly developed panicoid type. These are *D. rangei* Pilger on the one side and *D. cincta* Nees and *D. papposa* Nees on the other side.

Among the species which retained the primitive type of epidermal traits, *D. brachyphylla* Nees and *D. macrantha* Schrad. exhibit a reduction in the number of fertile florets to two per spikelet. In these species the glumes are much enlarged and could serve as a means of seed dispersal.

The relationships of the species groups into which *Danthonia* may be subdivided on the basis of leaf anatomical and morphological characters are indicated in Figure 9. The actual connections between the species will only be known after a complete cytogenetical study of the genus has been undertaken. For this reason the type of diagrammatic presentation discussed by Stebbins (1956) has been adopted.

The various theories about centre of origin and plant migration have been discussed by Cain (1944). Although the greatest concentration of species is found in the south western tip of Africa, it would appear as if the genus migrated from the North. The species *D. calycina* Roem. and Schult. from Eastern Europe was shown to have retained many primitive characters and could perhaps be regarded as a relic. The tropical African species are characterized by the primitive type of anatomical characters and could perhaps be regarded as relics which have adapted themselves to their mountain existence in a tropical climate.

Small colonies of one or more species are also localized along the mountain ranges of the summer rainfall areas of southern Africa with a greater concentration of species in the winter rainfall area. The genus *Asthenatherum* extends from south east Asia into North Africa and along the arid areas of the west coast to South Africa. The presence of a species like *D. pumila* Nees along the arid west coast of South Africa is difficult to explain. As was pointed out earlier, this species resembles *Asthenatherum* very closely except for chlorophyll distribution of the leaf. In this respect it appears to form a direct link between *Danthonia* and *Asthenatherum*. If this species were present in south eastern Asia or North Africa it could have been regarded as a left-over of the original *Asthenatherum* type. Its presence in South Africa could be explained in any one of many ways. The most obvious although unlikely explanation is that *Asthenatherum* originated in South Africa, with *D. pumila* Nees forming a direct link between *Danthonia* and *Asthenatherum*. It is also possible that *D. pumila* Nees represents such a link and migrated south with *Asthenatherum*. It could also be regarded as a specialized line of development from *Asthenatherum*. The latter statement is hardly likely because it is difficult to imagine that the advanced type of chlorophyll distribution should change back to the more primitive one, especially as there is no obvious advantage in such a process. Another possibility is that *D. pumila* Nees represents a hybrid between a species of *Asthenatherum* and *Danthonia* or some other closely related genus. To the author the most likely explanation appears to be that *D. pumila* Nees represents a specialized line of phylogenetic development which came about after *Danthonia* had reached South Africa. It would appear as if the genera *Danthonia* and *Asthenatherum* had their origin in a common ancestor. The latter genus, being better adapted to dry conditions migrated south along the arid regions of the west coast of Africa. *Danthonia* migrated along the mountain ranges of the tropics and subtropics to reach the winter rainfall area of southern Africa.

SUMMARY

Leaf anatomy and morphology of the South African species of *Danthonia* were studied in detail. These data were correlated to trace the relationships of species. The problem of what is primitive and what is advanced has been related to leaf anatomy. Species with a combination of the panicoid type of epidermis and the festucoid type of internal leaf anatomy appear to represent the more primitive types. The possible direction of migration of the South African species of *Danthonia* was discussed. The chromosome numbers of *D. macowanii* Stapf ($2n = 12$), *D. arundinacea* (Berg.) Schweick. ($2n = 12$) and *D. tenella* Nees ($2n = 24$) are reported for the first time. Three species, *D. mossamedensis* Rendle, *D. pumila* Nees and *D. suffrutescens* Stapf should be transferred to *Asthenatherum*. The latter species could be regarded as a variety of *A. glauca* (Nees) Nevski.

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