INFORMATION TO USERS

This reproduction was made from a copy of a document sent to us for microfilming. While the most advanced technology has been used to photograph and reproduce this document, the quality of the reproduction is heavily dependent upon the quality of the material submitted.

The following explanation of techniques is provided to help clarify markings or notations which may appear on this reproduction.

1. The sign or "target" for pages apparently lacking from the document photographed is "Missing Page(s)". If it was possible to obtain the missing page(s) or section, they are spliced into the film along with adjacent pages. This may have necessitated cutting through an image and duplicating adjacent pages to assure complete continuity.

2. When an image on the film is obliterated with a round black mark, it is an indication of either blurred copy because of movement during exposure, duplicate copy, or copyrighted materials that should not have been filmed. For blurred pages, a good image of the page can be found in the adjacent frame. If copyrighted materials were deleted, a target note will appear listing the pages in the adjacent frame.

3. When a map, drawing or chart, etc., is part of the material being photographed, a definite method of "sectioning" the material has been followed. It is customary to begin filming at the upper left hand corner of a large sheet and to continue from left to right in equal sections with small overlaps. If necessary, sectioning is continued again—beginning below the first row and continuing on until complete.

4. For illustrations that cannot be satisfactorily reproduced by xerographic means, photographic prints can be purchased at additional cost and inserted into your xerographic copy. These prints are available upon request from the Dissertations Customer Services Department.

5. Some pages in any document may have indistinct print. In all cases the best available copy has been filmed.

University
Microfilms
International
300 N. Zeeb Road
Ann Arbor, MI 48106

8424002

Wright, Kay Louise Tomlinson

STUDIES IN THE DANTHONIEAE (POACEAE)

The University of Oklahoma PH.D. 1984

University
Microfilms
International 300 N. Zeeb Road, Ann Arbor, MI 48106

PLEASE NOTE:

In all cases this material has been filmed in the best possible way from the available copy. Problems encountered with this document have been identified here with a check mark _✓_.

1. Glossy photographs or pages ___✓___
2. Colored illustrations, paper or print _____
3. Photographs with dark background ___✓___
4. Illustrations are poor copy _____
5. Pages with black marks, not original copy _____
6. Print shows through as there is text on both sides of page _____
7. Indistinct, broken or small print on several pages ___✓___
8. Print exceeds margin requirements _____
9. Tightly bound copy with print lost in spine _____
10. Computer printout pages with indistinct print _____
11. Page(s) _____ lacking when material received, and not available from school or author.
12. Page(s) _____ seem to be missing in numbering only as text follows.
13. Two pages numbered _____. Text follows.
14. Curling and wrinkled pages _____
15. Other _____

University
Microfilms
International

THE UNIVERSITY OF OKLAHOMA

GRADUATE COLLEGE

STUDIES IN THE DANTHONIEAE (POACEAE)

A DISSERTATION

SUBMITTED TO THE GRADUATE FACULTY

in partial fulfillment of the requirements for the

degree of

DOCTOR OF PHILOSOPHY

By

KAY LOUISE TOMLINSON WRIGHT

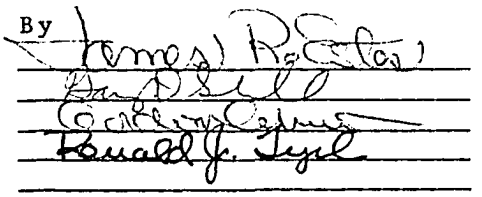
Norman, Oklahoma

1984

STUDIES IN THE DANTHONIEAE (POACEAE)

A DISSERTATION

APPROVED FOR THE DEPARTMENT OF BOTANY AND MICROBIOLOGY



ACKNOWLEDGMENTS

I would like to thank James R. Estes, Chairman of my Advisory Committee, for his assistance and support on all phases of this research. In addition, I thank the other members of my committee for their patience and understanding of the difficulties of completing a dissertation *in absentia*. I am grateful to a number of others as well: to John W. Wright, for putting up with an absent wife for six months; to R. F. Thorne, for allowing me the time to complete this paper, and not complaining about the sorry state of the east wing; to T. S. Elias, for his support and confidence, and for setting deadlines; to my staff in the workroom, for knowing when to stay out of my way, and being cheerful about it; to Sherwin Carlquist, who has shown himself to be a true friend, and without whose help the photography would have been a major trauma; to R. K. Benjamin for numerous discussions of format; to the rest of the staff of RSABG for their kindness and understanding; to Jim Smith for bailing me out in various ways on numerous occasions; to Susan Smith for putting up with a houseguest who appeared and disappeared virtually unannounced; to Rhonda Riggins and Richard Pimentel, for advice and counsel; and finally, to Debbie Kama, for the figures and plates, and most of all, for her friendship and unflagging belief in me.

TABLE OF CONTENTS

LIST OF TABLES

Part I

Part II

LIST OF ILLUSTRATIONS

PREFACE

This dissertation has three separate and independent parts, each with its own format and pagination. Part I, "Systematic Relationships in *Danthonia* s. lat. (Danthonieae: Poaceae)", will be submitted to *Systematic Botany* for possible publication, and is prepared in the appropriate style and format. Part II, "Comparative Anatomical Studies in the Danthonieae: *Danthonia* s. lat.", has been prepared for submission to *Aliso*. Part III, "*Arundo*, *Phragmites*, and *Danthonia* in the Southeastern United States", has been accepted for publication in *Vascular Flora of the Southeastern United States*, edited by L. Radford, et alia. Abstracts are not required for articles in *Aliso*, nor for the flora, and so were not prepared for Parts II and III. References in this dissertation to Wright (1984) refer to chapters of this document.

KAY L. TOMLINSON WRIGHT

James R. Estes, Chairman of Advisory Committee

STUDIES IN THE DANTHONIEAE (POACEAE)

ABSTRACT

The genus Danthonia s. lat. has long been recognized as a heterogeneous assemblage of taxa. In an effort to elucidate the systematic relationships within this genus, an anatomical investigation of the leaf anatomy and lodicule micromorphology was carried out on 15 taxa of Danthonieae (Danthonia, 12 of its segregate genera, Schismus, and Cortaderia). On the basis of these data, Centropodia, Dregeochloa, and Pseudopentameris appear to be isolated in the tribe. Danthonia s. str. is relatively uniform anatomically, and no clear-cut divisions can be made within it. Rytidosperma appears to be distinct from Danthonia s. str., but the separation of Erythranthera, Pyrranthera, and Monostachya from Rytidosperma is not strongly supported. Monachather is distinct from the rest of Danthonia s. lat., but its closest relationships apparently lie with Rytidosperma. A close relationship between Schismus and Karroochloa is supported, but suggestions of similarly close

relationships of Chionochloa and/or Merxmuellera with Cortaderia are not.

These anatomical and micromorphological data were then combined with other morphological data and a cladistic analysis was performed, using Wagner parsimony, character compatibility, and UPGMA cluster analysis. Major findings are that 1) Danthonia s. str. appears to represent a monophyletic group; 2) Cortaderia sect. Bifida consistently occurred within the clade comprising Danthonia s. str. and separate from the clade comprising the other sections of Cortaderia; 3) Rytidosperma and Merxmuellera appear to be polyphyletic taxa; 4) suggested close relationships between Cortaderia and Chionochloa and/or Merxmuellera were not supported; 5) evidence of cladistic relationship between Schismus and Karroochloa was not strong. Relationships among other segregate genera of Danthonia in the Southern Hemisphere were not clarified by this analysis.

Finally, treatments of the genera and species of Arundo, Phragmites, and Danthonia in the southeastern United States are presented.

STUDIES IN THE DANTHONIEAE (POACEAE)

PART I

SYSTEMATIC RELATIONSHIPS IN *DANTHONIA* S. LAT. (DANTHONIEAE: POACEAE)

SYSTEMATIC RELATIONSHIPS IN *DANTHONIA* S. LAT. (DANTHONIEAE: POACEAE)

KAY L. TOMLINSON WRIGHT

Rancho Santa Ana Botanic Garden
Claremont, California 91711

ABSTRACT. In order to examine the phylogenetic relationships in *Danthonia* s. lat., a cladistic analysis of representative species of 13 genera of Danthonieae (*Danthonia*, 10 of its segregate genera, *Schismus*, and *Cortaderia*) was performed based on morphological and anatomical data. Techniques employed include parsimony, character compatibility, and UPGMA cluster analysis. Major findings are that 1) *Danthonia* s. str. appears to represent a monophyletic group; 2) *Cortaderia* sect. *Bifida* consistently occurs within the clade comprising *Danthonia* s. str. and separate from the clade comprising the other sections of *Cortaderia*; 3) *Rytidosperma* and *Merxmuellera* appear to be polyphyletic; 4) suggested close relationships between *Cortaderia* and *Chionochloa* and/or *Merxmuellera*, and between *Schismus* and *Karroochloa*, are not supported. Relationships among the other segregate genera of *Danthonia* in the Southern Hemisphere were not clarified by this analysis.

Danthonia s. lat. is worldwide in distribution and has well over 100 named species. These are typically characterized by the two-lobed lemma with a geniculate awn arising from between these lobes; the awn is divided into a basal, often dark-colored and tightly spirally-twisted portion and an apical, straight or only slightly twisted part. There are two to many florets per spikelet, and the glumes are equal to or longer than the spikelet. This combination of characters occurs in a broad array of grasses.

Danthonia was placed in the tribe Aveneae by early authors (Hooker, 1867; Bentham, 1881; Stapf, 1917; Hitchcock, 1951), based on floret number, glume length, and the form of the awns. Two subtribes of Aveneae were generally recognized by these same authors: the Aveninae, mainly northern hemisphere species with membranous ligules and lemmas awned from the middle of the back, and the Danthoninae, primarily southern hemisphere taxa with ciliate ligules and lemmas awned from an apical notch. Comparative cytological investigations of Avdulov (1931) and leaf anatomical studies by Prat (1932, 1936) were followed by numerous other nontraditional studies (Reeder, 1957; Brown, 1958; Tateoka, 1954, 1957, 1967; inter alia) which led to the realization that the division in the Aveneae was fundamental, and validated Hubbard's (1948) description of

the tribe Danthonieae as a separate entity. This arrangement was further substantiated by Hilu and Wright (1982), who showed on the basis of UPGMA cluster analysis that the arundinoid-danthonioid grasses were distinct from the festucoid group.

DeWet (1954, 1956, 1960) pointed out that Danthonia itself was heterogeneous for a variety of features which had been used in recognizing tribes and subfamilies among the grasses. For example, features of leaf anatomy such as the arrangement and shape of the silica bodies and the structure of the mesophyll, as well as the chromosome base number, were found to differ among the species. DeWet therefore suggested that Danthonia represents a polyphyletic assemblage. Over a dozen genera have since been segregated from Danthonia by various authors; these are discussed below. However, the validity of these segregates and their relationship to other genera in the Danthonieae remain obscure.

In addition, the delimitation of the Danthonieae itself is problematic. Superficially, the genera of the Danthonieae appear to form a distinctive group. However, upon closer examination, the tribe can be seen to have extremely close ties to the Arundineae, and in fact may be inseparable from it (Renvoize, 1982). The closenesss of the relationship is particularly evident in the genera Chionochloa (Danthonieae) and Cortaderia (placed in the

Arundineae by most authors, but in the danthonioid group by Clifford and Watson (1977). Indeed, Danthonia archboldii from New Guinea was placed in Cortaderia by Connor and Edgar (1974), and transferred to Chionochloa by Conert (1975c), who apparently was unfamiliar with Connor and Edgar's paper. A major impediment to the understanding of relationships within the Danthonieae is the fact that Danthonia and its segregates have never been monographed on a worldwide basis, although a number of major regional works have been accomplished: Conert (1971: Africa), Connor and Edgar (1979: New Zealand), DeWet (1954, 1956, 1960: selected species, worldwide), Nicora (1973: Argentina and Chile), Vickery (1956: Australia), and Zotov (1963: New Zealand).

Thus, despite considerable study, the phylogenetic and taxonomic relationships within this group of grasses remain obscure. I set out to analyze these relationships in Danthonia s. lat. by performing an analysis of the characters used by others to define groups, seeking additional morphological and anatomical characters which might prove useful, and performing a cladistic analysis using these characters in order to assess the validity of the proposed taxonomic treatments.

MATERIALS AND METHODS

Anatomy and micromorphology. Representative specimens of 89 taxa were examined during the course of this investigation (Appendix A). Specimens were scored for the leaf anatomical and morphological characters listed in Table 1. Information on some species was supplemented from the literature.

Leaf material from the herbarium specimens to be prepared for anatomical investigation was taken from a section approximately midway between the ligule and the tip of the blade of mature leaves. Flag leaves on flowering culms were not used. The leaf material was first soaked in a 5% solution of Contrad 70 for approximately 24 hr, thoroughly rinsed in water, placed in a weak (ca. 5%) solution of acetic acid in 50% ethanol for 24-48 hr, then stored in 50% ethanol until examined (Schmid and Turner, 1977).

Preparations of the lower epidermis were prepared by placing the soaked leaf material on a microscope slide and scraping away the upper epidermis and mesophyll with a safety razor blade until only the lower epidermis itself remained (Metcalfe, 1960). This was then mounted in Hoyer's solution (Johansen, 1940) so that the outer surface of the epidermis faced the cover slip. Hoyer's solution has a sufficiently high refractive index to reveal silica bodies,

and has the additional advantage of being water-soluble, yet permanent. Leaf sections were cut freehand with a razor blade, stained with safranin and counterstained with fast green using Northen's variation of Foster's method (Johansen, 1940), dehydrated through an alcohol series to xylene, and mounted in Coverbond. Lodicules were dissected from florets in a drop of alcohol and mounted in Hoyer's solution. All voucher slides are deposited at OKL.

Cladistic Analysis. In order to obtain the best possible estimate of the phylogeny of this group, it was considered desirable to use more than one type of cladistic analysis. The program PHYSYS, written by S. J. Farris, was used. The program provides subroutines which generate fit and diagnostic statistics for any tree matrix. This permits the choice of the particular tree which best fits the original data matrix, and allows the character states to be plotted on each tree generated. Thus, analysis of state changes for any character on any tree can readily be performed, homoplasies detected and studied, and different phylogenetic methods can be compared. The following types of analysis were performed:

1. Parsimony analysis. The WAGNER.S subroutine in PHYSYS, which uses global branch-swapping, is a variation of Farris's (1970) implementation of Wagner's (1961) Groundplan Divergence Method. For comparative purposes, two outgroups were used in this portion of the analysis. First I selected

Arundo, a member of the Arundinoideae but not a member of the Danthonieae. Second, I constructed a hypothetical ancestor by using the character states which are postulated to be primitive for the Danthonieae.

Farris (1969) developed a successive approximations approach to character weighting, which was also employed in this analysis. Character weighting may be important to the estimation of relationships among taxa because not all characters can be expected to show the same degree of cladistic reliability, or agreement with actual phylogeny. Farris' algorithm allows the weights given to each character to be determined by the data themselves, thereby removing a subjective component from the analysis. The rationale for this procedure is that characters which are hierarchically correlated, or support the same estimate of phylogeny, are unlikely to be thus correlated purely by chance, though functionally related characters may covary. Using simulation tests, Farris was able to show that the successive weighting procedure was able to reproduce the true phylogeny even in cases where cladistically unreliable characters far outnumbered cladistically reliable ones.

In a successive weighting analysis, as implemented in PHYSYS, characters in the analysis are given a weight proportional to their assumed cladistic reliability; that is, the degree to which they agree with the estimated phylogeny as reflected in the tree diagram produced by

whichever phylogenetic algorithm is chosen. Characters which do not show homoplasy on the tree are considered reliable, and receive high weight; characters which show parallelisms or reversals on the tree are weighted proportionately less depending on the amount of homoplasy displayed. A new tree is generated based on these weighted characters, and another weighted character matrix produced. The cycle repeats until the weights produced by two successive iterations are the same.

2. Character Compatibility Analysis. This type of analysis permits no missing values; there are 7 missing values in the data set, involving 6 taxa. In order to resolve this, the data were handled in two separate runs, the first with the pertinent characters deleted (Run I), and the second with the taxa deleted (Run II).

One extremely useful attribute of character compatibility analysis is the information it provides about the minimum amount of homoplasy in the data set. Conflicting trees implied by pairs of incompatible characters cannot both be true; therefore, one character must be homoplasious. Thus, the number of characters in the maximal clique must represent the maximum possible number of characters which show no homoplasy on the true tree (Meacham, 1980; Estabrook, 1972).

3. UPGMA Cluster Analysis. Colless (1970) suggested that this technique might be useful in estimating

phylogenetic relationships. The analysis was performed on a Euclidean distance matrix calculated from unstandardized data. The dendrogram was then optimized using the subroutine DIAGNOSE, which established the optimal character states for the stem species at each node, allowing the dendrogram to be analyzed in the same manner as the trees generated by the other algorithms.

Analysis of trees. Trees generated by the various techniques were examined for consistency with the original data matrix using the FIT and LFIT subroutines. LFIT calculates the length, overall consistency (C-index: sum of all the character ranges divided by the total length of the tree), and homoplasies (F-ratio: similar to the F-statistic of Farris [1981] but calculated from the branch lengths of the tree) for each tree produced from a character data matrix. FIT generates a number of statistics, including the cophenetic correlation coefficient (Sneath and Sokal, 1973; Farris, 1969), which describes the fit of a tree to the distance matrix from which it was calculated.

Character state changes on each tree were examined using information provided by the subroutine DIAGNOSE, which lists point(s) of origin of each character state, apomorphies of each taxon, optimized character states for each hypothetical stem species, character ranges and consistencies for each tree, and mean consistencies for each character over all trees in the matrix.

Cladistic units. The data matrix of the characters ultimately chosen for use in the cladistic analysis (Table 1) was examined and, within genera, those taxa which could be coded identically were included in a single cladistic unit (CU). Where variation occurred in one or two characters among taxa otherwise identical, these characters were coded for the apomorphic condition. Table 2 lists CUs and their included species. Coding of characters for cladistic analysis and assignment of primitive states are detailed under Discussion of Characters.

DISCUSSION OF TAXA

Ideally, the study group in any taxonomic investigation should be a natural assemblage of individuals and taxa (i.e., monophyletic sensu Hennig [1966]). In practice, however, it is impossible to know a priori whether or not a group of organisms is monophyletic; this can only be postulated as result of the investigation. The closest a priori approximation to a natural group is one which is diagnosable, that is, can be defined on the basis of uniquely derived character states.

Danthonia s.lat. can be diagnosed on the basis of the form of the lemma; however, when so characterized, it contains many taxa which are clearly not closely related, and so becomes a highly unnatural assemblage. Certain

features, such as strongly radiate mesophyll, large and distinct outer bundle sheath cells, greatly enlarged and specialized bulliform cells, and highly modified fruits, are uncommon in Danthonia s. lat., and are generally correlated. Taxa which possess these specialized suites of characters do not appear to be closely related to the majority of these grasses. Other features which appear to unite most members of the group, such as mesophyll at most only indistinctly radiate, and unspecialized caryopses, represent primitive conditions and are found in many taxa throughout the grass family. This situation, where an apparently natural group lacks synapomorphic features, is not unique to Danthonia; indeed, it is typical of the Arundinoideae as a whole (Clayton, 1978).

Once the taxa most obviously misplaced in Danthonia are removed, the remaining core group of taxa appear to be more closely related to each other than to any other taxa. Yet the assertion that these taxa do in fact form a monophyletic group is difficult to establish conclusively because of the lack of synapomorphies. However, Watrous and Wheeler (1981) stated that the original groupings in an analysis need not necessaryly be monophyletic; rather, errors can be detected later by examination of the results. Thus, the investigation may shed considerable light on the real relationships within the Danthonia complex.

The following are taxa which have been segregated from

Danthonia. A summary of the reasons for the segregation of each is given. An asterisk precedes those whose closest relationships are considered to lie outside the core group of Danthonia and which therefore are not included in the present study.

*Alloeochaete Hubbard. Species of this genus have radiate chlorenchyma and the lowest floret of the spikelets is reduced, rather than the uppermost ones as in most members of this group (DeWet, 1954, 1956; Hubbard, 1937; Kabuye & Renvoize, 1975).

*Centropodia Reichb. (Asthenatherum Nevski). This genus also has radiate parenchyma and outer bundle sheath cells which are very large and distinct. The lower leaf surface is deeply grooved, with prickles overarching the grooves (Wright, 1984). It also has very small chromosomes, and 5-11 nerved glumes. This combination of specializations is not found elsewhere in the study group, and indicates that the closest relationships of this genus lie outside Danthonia (Conert, 1962; DeWet 1956).

Chionochloa Zotov. Chionochloa , with approximately 20 species, differs from Danthonia in having a dibasic chromosome number of x = 7 and 6, and in its lower leaf sheaths, which are persistent and indurate. Members of this genus are the widespread and important snowgrasses of Australia and New Zealand (Zotov, 1963).

*Dregeochloa Conert. The mature caryopsis in this small

South African genus of two species has a very large embryo, pericarp that is separate from the seed, and other peculiarities not found elsewhere in Danthonia. Features of the leaf anatomy, such as the large bulliform groups which occupy over half the leaf thickness, and the grooved lower surface, are quite distinctive (Conert, 1966; Ellis, 1977; Wright, 1984).

Erythranthera Zotov. The two species of this genus are small, alpine grasses from New Zealand. Their lemmas are unawned, minutely 3-lobed, with a relatively blunt callus (Zotov, 1963).

Karroochloa Conert and Türpe. Restricted to South Africa, this genus of four species was removed from Danthonia (Conert and Türpe, 1969, 1974) based on anatomical differences such as lack of bulliform cells, and on morphological grounds such as size of the caryopsis and embryo, and the form of the prophylla in two of the species. All of these features indicate a very close relationship to Schismus. Members of these two genera appear to form an intergrading series.

Merxmuellera Conert. This African genus was segregated from Danthonia based on differences in the arrangement of the hairs on the lemma; on tendencies toward 1-nerved glumes, indurate lower leaf sheaths, and lateral lemma lobes more or less united with the lower portion of the awn. Conert (1961) suggested that it has close ties with

Cortaderia and Chionochloa, based on these features. It consists of about a dozen species (Conert, 1970, 1975b).

*Metcalfia Conert. This monotypic Mexican genus was removed from Danthonia by Conert (1960). Tateoka (1964) investigated the embryo and lodicule anatomy and demonstrated convincingly that it is festucoid, probably a primitive member of the Aveneae.

Monachather Steudel. The Australian M. paradoxa Steud. (Danthonia bipartita F. Muell.) has long been recognized as an isolated species. Its indurate, broadly turbinate lemma with very large side lobes, the shape of the grain, the embryo which occupies nearly the length of the grain, and the woolly basal leaf sheaths set it apart (Vickery, 1956; Blake, 1972).

Monostachya Merrill. This monotypic genus differs from Danthonia in the reduction of the lateral lobes and central awn (Hitchcock, 1936), but otherwise it resembles Rytidosperma.

Plinthanthesis Steudel. The three species of this genus are small Australian alpine plants whose lemmas have a short callus and a short awn, and whose grains have a linear hilum (Blake, 1972).

*Pseudopentameris Conert. In this unusual genus, the very large spikelets are two- rather than several-flowered and the glumes strongly transversely-veined. In addition, the stigmatic hairs are decurrent and join over the top of

the ovary, and the seed is attached only loosely to the pericarp along the linear hilum (DeWet, 1956; Conert, 1971). The outer bundle sheath cells are large and distinct, and the cells of the abaxial epidermis are much larger than those of the adaxial epidermis, and often inflated (Wright, 1984). This combination of specializations suggests that the closest relationships of this genus lie outside the core group of Danthonia.

Pyrrhanthera Zotov. The New Zealand P. exigua (Kirk) Zotov, the only species, has minutely 3-toothed lemmas and the fruit is a nut (Zotov, 1963). Otherwise it closely resembles Rytidosperma.

Rytidosperma Steudel (Notodanthonia Zotov). This southern hemisphere segregate differs from Danthonia s. str. in having the hairs on the lemma arranged in tufts instead of scattered, and in the shape of the hilum, which is round to oval rather than linear (Nicora, 1973; Zotov, 1963).

Sieglingia Bernhardi. Included in Danthonia when that genus was originally described, S. decumbens, the sole species, differs from European Danthonia in the complete reduction of the awn. It has been shown to form a sterile hybrid with D. alpina (Conert, 1969).

Though never included in Danthonia s.l., two other taxa were investigated:

Schismus Beauv. This genus of five species has the central awn greatly reduced or absent, and the lemma hairs

scattered rather than tufted. In other respects, including its apparent South African origin, it resembles Karroochloa, and Conert and Türpe (1974) noted that there is some justification for combining the two genera. For this reason Schismus is included here.

Cortaderia Stapf. This genus has traditionally been placed with the reed grasses in the Arundineae because of its growth form and its apparent relationship to Lamprothyrsus and other undisputed members of that tribe. In recent years, however, a close relationship with the danthonioid taxa has been suggested by several authors (Conert, 1961; Clifford and Watson, 1977). Some of its species, notably those in section Bifida, have lemmas which are similar in form to those of Danthonia and, as mentioned above, C. archboldii was recently placed in Chionochloa (Conert, 1975c). Thus, it was considered necessary to include representative species from each of its sections in this study.

Cortaderia is the one genus in this study group which can be diagnosed on the basis of a synapomorphy: all known species, including C. archboldii, are gynodioecious, a condition which is extremely rare in the Poaceae (Connor, 1963, 1970, 1974, 1981).

CHARACTERS

Discussion of characters. During the course of this study, data were collected on 49 characters (Table 1 and Appendix A). These included the characters historically used in the diagnoses for these taxa. In addition, many others were investigated in an attempt to locate those with potential taxonomic usefulness. For anatomical data, the terminology of Ellis (1976, 1979) was followed whenever possible in order to standardize the descriptions. For the most part, measurements were made in a straightforward and self-explanatory manner. However, certain characters presented difficulties in assigning states, or require further explanation. These are discussed here in detail. Characters used in the cladistic analysis are marked with an asterisk, and assignment of primitive states is discussed only for these characters.

1. Adaxial furrows. This character indicates the shape of the furrows between the ribs on the adaxial surface. It was frequently difficult to assign a single state to a given specimen because intermediate forms were common; furthermore, since herbarium specimens were examined, the effect of drying on the shape of the furrows could not be assessed. Ellis (1977) noted considerable differences in the shape and size of furrows in fresh or preserved as opposed to herbarium material. Therefore, this character

may be less dependable than others whose states are more clear-cut.

4. Adaxial ribs--shape over primary vascular bundles. Massive ribs (state 2) protrude over the smaller ribs to either side (Wright, 1984, fig. 3). They are generally flat on top, but are distinguished from those coded as flat-topped by the size and shape difference between them and their neighbors.

6 and 7. Primary vascular bundle shape. Most species have round or elliptical primary vascular bundles. A few have bundles which are somewhat egg-shaped in outline, with the wider end adaxial. The occurrence of egg-shaped bundles is scattered among the taxa, and its significance is unclear. This character is also often difficult to score reliably because of the deformation of the sections. More detailed investigations using fresh or preserved material will be necessary before this character can be interpreted with confidence.

*8. Phloem. In most grasses, the phloem is not divided by fibers, but a few taxa, from different tribes and subfamilies, have fibrous intrusions into the phloem. These fibrous intrusions have different shapes in the different groups possessing them, and appear to represent parallel developments, perhaps in response to xeric environments (Ellis, 1976; Metcalfe, 1960). Within this study group, two distinct forms occur. In one, occurring in some

species of Merxmuellera and some South American Danthonia, the phloem is neatly and evenly divided into two nearly round groups of conductive cells (Wright, 1984, fig. 1). In the other form, found in some species of Cortaderia, the division is irregular and generally into more than two groups of conductive strands (Wright, 1984, fig. 8). Undivided phloem is considered the primitive condition, and the two categories of divided phloem are considered separate, specialized states.

9. Outer bundle, or parenchyma, sheath. All taxa within this group possess double bundle sheaths. An attempt was made to score each taxon for the completeness or incompleteness of the outer bundle sheath surrounding the primary vascular bundles. This was less variable within a specimen than was the completion of the sheaths around the smaller bundles, as well as being easier to determine from herbarium material. Poorly-preserved material was very difficult to score accurately.

11. Inner bundle sheath cells. In most taxa in the study group, these cells have the inner tangential and radial walls more heavily thickened than the outer tangential walls. This feature can be most easily seen in the region adjacent to the phloem, and it was cells in this region which were examined for coding this character. A few taxa regularly have these cells with evenly, often heavily-thickened walls.

13. Adaxial sclerenchyma--shape over primary vascular bundles. In scoring this character and character 15, I departed from Ellis in that I scored the shape of the entire structure linking the vascular bundle with the epidermis -- sclerenchyma and colorless cells forming bundle sheath extensions were considered together. The reason for this scoring was the fact that in many specimens, the extent of the bundle sheath extensions was quite variable, and these colorless cells tended to intergrade with the sclerenchyma, making any attempt to distinguish between the two very arbitrary.

15. Abaxial sclerenchyma--shape under primary vascular bundles. As explained under #13, the shape includes both colorless cells, if any, and sclerenchyma cells. A number of taxa have more or less continuous subepidermal sclerenchyma. Since in most cases this condition seemed to intergrade with T- or anchor-shaped abaxial sclerenchyma, and often was impossible to separate from this condition, the two were scored alike. This probably represents a loss of some information, but also avoids a great deal of subjectivity. Ellis (1976) noted that marked intraspecific variation may be expected in the distribution and amount of sclerenchyma accompanying vascular bundles, and this is borne out by the present study.

16. Mesophyll. Most of the taxa in the study group have non-radiate mesophyll, but a few belong in the category

for which, as Clifford and Watson (1977, p. 42) have said, "one would not wish to be forced to make a choice between the radiate and non-radiate conditions." These are coded as indistinctly radiate. This condition is often difficult to detect in herbarium material.

17. Colorless cells. This category refers to any such cells present in the leaf, including the bundle sheaths and extensions. In most of these taxa, these extensions are the only colorless cells present, but in others, colorless cells form a major portion of the mesophyll of the leaf. In some cases, such as Merxmuellera papposa (Wright, 1984, fig. 3) and Cortaderia araucana, their development is so extensive that the chlorenchyma is restricted to U-shaped bands around the adaxial furrows (state 3). In others, such as some species of Chionochloa, a more or less continuous band of these cells is present in the lower half of the leaf, but they do not occupy a major portion of the leaf volume (state 2). In many such cases these cells are filled with silica, and it may be that this deposition of silica is what causes them to take on the colorless appearance; for within some species some specimens show them and others lack them. Further investigation of this character is clearly needed.

18. Metaxylem vessels. The size of these cells was compared with the size of the outer bundle sheath cells. Often this was quite difficult, since in many specimens the outer bundle sheath was poorly preserved or unclear.

*21. Upper epidermis. In the original data table, this character is scored for the presence of four states. In many, such as the North American Danthonia, the cells of the upper epidermis are small and unspecialized. In many other taxa, notably Merxmuellera, many Chionochloa, and most Cortaderia, the epidermis is variously specialized. Cells in some are rounded and considerably inflated, though not obviously thickened. Others have most cells with broad, thickened papillae (Wright, 1984, fig. 4). These forms intergrade with the taxa which have long, finger-like, obviously thickened papillae on most cells, or on cells in the adaxial furrows (fig. 7). Many times these states appear quite distinct, but in some taxa it is difficult to decide which state to code for a given specimen. For this reason, in the cladistic analysis, all these apparently specialized states were coded alike. Again, this procedure necessarily results in some loss of information, but removes considerable subjectivity. However, if the states of the character have in fact arisen separately, then such coding will introduce misinformation, adding apparent homoplasy to the data. Only further study will clarify this character.

*22. Hypodermic prickle hairs. These intriguing structures (Wright, 1984, fig. 1), the shape of which is somewhat reminiscent of tiny syringes, are found only in two of the Merxmuellera species in this group. Judging from their appearance, they probably represent a specialization

for defense against insect predators. They appear to be hollow, but it is unknown whether or not they contain any repellant substance.

*23. Bulliform cells. Most species in this group have bulliforms in simple fan-shaped groups between the vascular bundles. In other taxa, bulliforms or bulliform-like groups of cells are found only on either side of the midrib, forming apparent hinges or are absent altogether. These taxa were scored as lacking bulliforms. Monachather was found to have bulliforms in fan-shaped groups, but with the central cell much enlarged relative to the others. Arundo also has a unique condition, where the fan-shaped bulliform groups are accompanied by other colorless cells directly beneath them. Simple fans of bulliforms are common throughout all subfamilies of the grasses, and they also occur in Joinvillea (Wright, unpublished); therefore, they are considered primitive. Loss of bulliforms thus represents a specialized condition, as do the two states found in Monachather and Arundo.

24. Microhairs. These were scored as either present on the abaxial epidermis, or not seen. An initial attempt was made to measure the lengths of the cells, but was abandoned for two reasons. First, the variation in size and shape of the basal cells is great. Rytidosperma, for instance, tends to have short basal cells, while Danthonia tends to have the basal cell elongate. However, the ranges for these lengths

overlap, and thus, while it might be a useful character within each genus, it is useless for distinguishing between them. Second, apical cells are generally thin-walled and poorly preserved or lost in herbarium material, making comparisons difficult.

26. Intercostal long cells--side walls. This character deals with the degree of sinuosity of these walls. There are many characteristics of the cell wall shape, such as pits, papillae, and so on, which on first sight appear to make excellent candidates for taxonomic characters. However, as Ellis (1979) and Watson (1942) have pointed out, these are very susceptible to environmental influence. Indeed, in different leaves from the same plant, or even on different portions of the same leaf, the degree of sinuosity may be found to vary. Standardization of the position on the leaf from which samples are taken will help to some extent, but such data must be viewed with extreme caution.

State 3 of this character (W-shaped undulations, Wright, 1984, fig. 5) is not illustrated by Ellis (1979), and is found in some Merxmuellera species and in Danthonia chaseana.

*27. Costal short cells. Most members of this study group have long rows of costal short cells, but a number of others have them exclusively in pairs or singly. Generally, when paired, one of the members of the pair is a cork-cell, and the other contains a silica body. Assignment of a

primitive state for this character is difficult, for both conditions occur commonly in taxa outside the study group as well. However, long files of short cells tend to occur in taxa which show other less specialized features, and so this arrangement is tentatively assumed to be the primitive condition in Danthonia.

*28. Costal silica body shape. In most of the taxa in this group at least some of the silica bodies are dumbbell- or cross-shaped. Others, however, appear to have exclusively round, oval, or crescent-shaped silica bodies. A few taxa have mainly crescent-shaped or tall-and-narrow silica bodies, but invariably they also have round ones as well. Because crescent-shaped and tall-and-narrow silica body shapes appear to intergrade with the round to oval state, they were coded as round to oval rather than as a separate category.

Stebbins (1982) stated that the primitive condition of this character is probably quadrate or elongate, and that both cross-to-dumbbell and rounded silica body shapes are specializations in the grasses as whole. Within the Danthonieae, DeWet (1956) assumed the primitive condition to be cross-dumbbell-shaped, because the North American species, whose floral anatomy he considered to be primitive, have silica bodies of this shape. This rationale is certainly suspect, since it involves both ingroup rather than outgroup comparison, and correlation of putatively

primitive features. However, because Arundo also has dumbbell-shaped silica bodies, I postulated that this represents the ancestral conditon.

*29. Lower leaf sheaths. Most of the taxa have unspecialized lower leaf sheaths, but some Merxmuellera, Chionochloa, and Cortaderia species have the sheaths indurate and often persistent. Monachather and some species of Merxmuellera, on the other hand, have the lower sheaths densely lanate. These latter two states are considered to have arisen separately from the unspecialized condition.

*30. Prophylla. One of the features separating Schismus from Danthonia is the membranous, distinctly-awned prophylla in Schismus. This type of structure is also found in the two annual species of Karroochloa, but nowhere else within the Danthonieae. Arundo has prophylla which are thick, triangular, and lanate on the keels. The putatively primitive condition, found in other members of the study group as well as in most other grasses, is prophylla which are similar in texture to the rest of the leaf sheaths.

31. Cleistogamous spikelets. Highly modified cleistogamous spikelets produced in the lower axils are reported for nearly all Danthonia s. str., and apparently do not occur in other taxa. Chase (1918) reported such cleistogenes from Rytidosperma semiannulare from New Zealand, but this has never been substantiated, though the New Zealand species have been thoroughly investigated

(Connor and Edgar, 1979). The production of cleistogenes is known in quite a number of grasses, many of which occur in rather dry habitats (Chase, 1918; Connor, 1981; Weatherwax, 1928). It probably represents a specialization for reproduction under these conditions.

This character was not included in the cladistic analysis because the fact that cleistogenes were not mentioned in the literature was not considered sufficiently reliable evidence of their absence, particularly for African species. A really thorough search for these structures often involves considerable damage to herbarium specimens, and thus was not carried out. Therefore, entries of state 0 in the data table for this character should be viewed with caution.

*33. Lemma hairs. These are scattered or only marginal in all Danthonia s.s., as well as Cortaderia, Chionochloa, and many other taxa throughout the grass family. This is considered to be the primitive condition (DeWet, 1954; Stebbins, 1982). The other states are considered specializations which have arisen separately from the primitive condition.

34. Lateral lobes. These may be distinct from the awn base, as in most taxa within the group, or united to a greater or lesser extent with the base of the awn. However, the degree of this union depends very much on the maturity of the specimen examined. Even in Danthonia s.s., very

young specimens can be found in which the lateral lobes have not yet separated from the awn base, although in mature florets the separation is always complete. Thus, this character is considered unreliable.

*35. Development of free portion of lateral lobes. This character is quite variable within the study group. In many cases is is difficult to decide where to draw the line as to what constitutes reduction. Within North American Danthonia, for example, the lateral lobes are distinct but not strongly developed in most D. spicata. In other species, such as D. californica, the lobes are relatively long and acuminate. There does seem to be a break or gap between the condition in D. spicata and that seen in the taxa which were coded as reduced. The major difficulty with this character occurred with Cortaderia, in those species which have poorly-developed side lobes. In most of these one can see the distinct base of the awn (i.e., the thickened rib formed by the fusion of the central nerves), but the free portion of the lobes is very small. I followed Conert (1961) in interpreting these cases as examples of reduction of the lobes.

37. Callus--development. Virtually all members of the group have a well-developed callus. However, among those species which were coded as having an elongate callus, there is a complete range of conditions from relatively short and unpointed, as in D. spicata, to some of the Merxmuellera and

Rytidosperma species, with calluses very elongate and sharp-pointed. All the North American Danthonia were coded as having an elongate callus, because of the evident transitional series.

38. Callus--vestiture. Nearly all taxa were found to have a hairy callus. In Danthonia spicata, the callus is occasionally glabrous, but in most specimens at least some hairs are present.

41. Palea/rachilla ratio. It was suggested by Nicora (1973) that a distinguishing characteristic between Rytidosperma and Danthonia s. str. was the length of the rachilla remaining attached to the floret above. In an effort to quantify this, I chose to compare its length to that of the palea. This ratio is not entirely satisfactory, because the relative length of the palea differs greatly in the various taxa; however, all other portions of the spikelet which could have been used vary to a similar degree. The figures in Appendix A represent the average of measurements of two or three middle florets from each taxon. Because of the extreme variability both within and between species was great. As can be seen from the amount of overlap in the figures (Appendix A), this is not a reliable way to separate any of the higher taxa in this group from one another. Therefore, no effort was made to obtain large samples or to calculate standard deviations.

*42. Lodicules--vestiture. The shape of the lodicules in all these taxa correspond more or less to the panicoid type (Stebbins, 1956), which is truncate or cuneate, thickened, and vascularized. Blake (1972) used lodicule vestiture in his key to the genera of the Australian Danthonieae; however, this study indicates that while many genera consistently have either glabrous or hairy lodicules, in others, such as Cortaderia, Chionochloa, and Schismus, both glabrous and hairy lodicules occur. The primitive condition here is assumed to be glabrous, though the evidence is slight: Danthonia s.str. regularly has glabrous lodicules, as does Arundo.

*43. Lodicules--microhairs. Microhairs on lodicules are particularly interesting because in all species examined they tend to be multicellular rather than bicellular (Wright, 1984, fig. 6). It is assumed that, as on the leaf surfaces, the presence of microhairs on lodicules is the primitive state.

*44. Hilum shape. Clifford and Watson (1977) reported on the shape of the hilum in 226 Australasian grass genera. According to their results, in virtually all eu-panicoids, andropogonoids, and chloridoids, the hilum is punctiform-elliptical; the festucoids are fairly evenly divided between linear and punctiform-elliptical hila; in Aristida, the oryzoids, and the relatively few bambusoids they considered, the hila are all linear. In the arundinoid-danthonioid

group, both hilum shapes occur; in Arundo the hilum appears to be narrowly elliptical to linear. Tentatively, the primitive state is considered to be linear.

45. Hilum spot. The appearance of a lighter-colored spot above the base of the hilum in fully mature caryopses is a characteristic which is regularly found in most but not all Danthonia, and occasionally in other taxa, such as Schismus. Its function and composition are unknown.

46. Hilum length/width ratio. This ratio was calculated for those specimens examined which had mature caryopses. Figures given are the mean plus or minus the standard deviation, and, in parentheses, the number of caryopses measured.

*48. Sex form. All species in the group, with the notable exception of Cortaderia, have normal, bisexual flowers. Cortaderia, on the other hand, is uniformly gynodioecious. As noted above, this condition is rare in the grasses, and surely must represent a uniquely derived feature of this genus.

49. Chromosome number. The base number for nearly all taxa in the study group is X = 6. Chionochloa has a dibasic number of X = 6 and X = 7, though all species represented in this study belong to the second group. Zotov (1963) noted that no anatomical or morphological features have been found which distinguish the two groups within the genus.

Choice of characters for cladistic analysis. A number of characters were ultimately rejected for the cladistic analysis. Characters 1-7, 9, 10, 14-16, 18, 25, 32, 34, 38, and 45 vary within species and/or were difficult to record unambiguously, and so were considered likely to have relatively many coding errors. Characters 11-13, 32, 36, and 39-41 show considerable and apparently random variation within taxa which otherwise appear uniform, and so were considered likely to be extensively homoplasious and therefore uninformative at the taxonomic level of this study. Characters 1, 17, 19, 20, 24, and 26 were considered likely to be environmentally plastic, and therefore of little value in assessing phylogenetic relationsips. Characters 31, 46, 47, and 49 have many missing values, due to the unavailability or unreliability of information from the literature or of herbarium material for investigation. Finally, character 37 is invariant except in one taxon, and thus would add no information.

Not all missing values and intra-taxon variation could be removed by deleting characters from the data set without a concomitant, unacceptable loss of information. Several missing values remain in the cladistic data set: Lower leaf sheaths (#29) were not seen for Merxmuellera papposa, and the available literature was not specific on their form. In addition, lodicule preparations were unavailable for Danthonia montana. Finally, hilum shape was not observed

for D. shrevei, D. domingensis, D. cachemyriana, and Monostachya oreoboloides, and information was unavailable from the literature.

CLADOGRAMS

Parsimony analysis. The PHYSYS subroutine WAGNER.S, using Arundo as the outgroup, produced two trees with a length of 81. The two trees have identical C-indices, but the tree shown in fig. 1 has an F-ratio of 63.66 as opposed to 68.71, indicating a slightly better fit to the data. Character consistency values, which would equal 100 if a character shows no homoplasy, are 50 or less on both trees, with the exception of character 10 (hypodermic prickle hairs).

Tree matrices for these two trees were then used in a successive weighting routine, which stabilized after six iterations and generated 12 trees of length 19.387. This length is calculated from the weighted data matrix and is based on step-lengths of less than one; therefore, it is not strictly comparable to the lengths of the other trees. C-indices were identical for all trees; the F-ratios ranged from 22.73 to 23.41. The tree with the lowest F-ratio is reproduced in fig. 2. Character consistencies for characters 2 (prophyllum), 3 (lemma hairs), 8 (phloem), 10

(hypodermic prickle hairs), and 14 (sex form) are above 50; thus these are major contributors to the structure of this tree.

Finally, a Wagner tree based on a data set with a hypothetical primitive ancestor was sought. WAGNER.S produced six trees of length 80. C-indices were again identical, and F-ratios ranged from 55.14 to 59.43. The tree with the lowest F-ratio is reproduced in fig. 3. This tree showed a slightly better fit to its data matrix than the tree generated using Arundo as an outgroup did to its data matrix, and the average character consistencies were slightly higher.

Character Compatibility Analysis. In Run I, in which the characters with missing values (1,5,6,7) were deleted, 4 maximal cliques were found, each with 3 characters. In Run II, with Danthonia shrevei, D. domingensis, D. montana, D. cachemyriana, Merxmuellera papposa, and Monostachya deleted because of missing values, 1 maximal clique, with 4 characters was found. Characters in each are shown in Table 4, and the tree produced by Run II is shown in fig. 4. The results of this character compatibility analysis indicate that at least 10 of the 14 characters in the data set are homoplasious.

UPGMA Cluster Analysis. The cophenetic correlation coefficient for the dendrogram (fig. 5) generated by this algorithm is 79.64. The dendrogram was then optimized using

the subroutine DIAGNOSE, which established the optimal character states for the stem species at each node of the dendrogram, and allowed the character state transformations to be plotted on the resulting tree (fig. 6). Length of the optimized tree was 102. Character consistencies were similar to those of the other trees.

COMPARISON OF CLADOGRAMS

Trees produced by a given algorithm tended to be similar in that certain large groupings appeared in all trees, with rearrangements of CUs within them. For example, the two trees produced by the WAGNER.S subroutine using Arundo as an outgroup show the following major similarities: clades MDURA through MDAVYI (node 56 in fig. 1), DANTHOSS through CSECTBIF (node 49), EPUMILA and EAUSTRAL (node 60), and PLINTHAN through CSECTCOR (node 68) appear in both. The main differences in the remainder of the trees are the positions of MONACHAT, RPALLIDE, and SARABICU, and the linkages directly involved with these CUs. A similar situation occurs with the 12 trees generated by the successive weighting program and the six trees produced using a hypothetical ancestral CU. Thus, although the discussion below deals specifically with the trees in figs. 1-6, its main features apply equally well to the trees not illustrated.

Donoghue (1983) suggested that a comparison of cladograms generated by different algorithms might be useful in pointing out which clades are most robust, and therefore most likely to represent true evolutionary lineages. In the following discussion, congruent groupings will be pointed out. The tree produced by character compatibility analysis (fig. 4), because of the lack of resolution, was not considered in assessing stable clades.

The position of most CUs on these trees is unstable. Three clades, however, were stable on all trees, with some rearrangements of CUs within them:

a. Cortaderia sections Cortaderia, Monoaristata, and Mutica. This clade was generally supported by characters 1 (lower leaf sheaths), 8 (phloem), 12 (costal short cell arrangement), and 14 (sex form).

b. Karroochloa purpurea and Danthonia cachemyriana. The character states for these two taxa are identical, except for a missing value (hilum shape) for the latter (table 3).

c. Merxmuellera macowanii, M. davyi, and M. stereophylla. Characters which support this clade vary from one tree to another. M. davyi and M. macowanii are the only CUs with hypodermic prickle hairs (10 state 1).

Clades which are less stable on these trees include the following:

a. Danthonia and Cortaderia section Bifida, including C. archboldii, appear as a clade on all trees except two. In fig. 3, this group is split and appears as an unresolved polychotomy with a clade comprising the other sections of Cortaderia plus Plinthanthesis; in fig. 2, it includes Merxmuellera dura.

b. Erythranthera australis and E. pumila form a clade except in the UPGMA analysis (figs. 5 and 6).

DISCUSSION

Systematically, the results of the cladistic analysis are inconclusive. A massive amount of homoplasy is shown by the characters in the data set; groups are supported not by synapomorphies but by convergences or reversals; even Cortaderia, the only included taxon which can be diagnosed by an apparently synapomorphous state (gynodioecy), appears as a polyphyletic group on all trees. These factors make it difficult to have confidence in the phylogenetic hypotheses supported by these trees. However, certain relationships are consistently indicated by the analyses, and deserve consideration.

Cortaderia sections Cortaderia, Monoaristata, and Mutica formed a stable clade on all trees, indicating that these taxa probably are a monophyletic group. This hypothesis agrees with morphological evidence, such as the

similarity in lemma shape, habit, and cytology (Conert, 1961; Connor and Edgar, 1974; Connor, 1983).

Danthonia also forms a robust clade. In spite of the fact that no true synapomorphies for the group exist in this data set, and all characters which support it are homoplasious, the fact that it is stable lends credibility to the hypothesis that Danthonia s. str. is a monophyletic group. However, the consistent inclusion of Cortaderia section Bifida (including C. archboldii) in this clade is problematic. The character states shared by these taxa are all primitive conditions, such as scattered lemma hairs, costal short cells in long rows rather than paired, undivided phloem, and the presence of bulliform cells. When the clade appears high on the tree, such as in fig. 1, the nodes which subtend it are characterized by many reversals in these characters. In addition, members of C. section Bifida, like all members of this genus, are gynodioecious, a condition rare in the Poaceae (Connor, 1981). A phylogenetic hypothesis which requires a multiple origin for this condition seems untenable, particularly when the character states on which the hypothesis is based are primitive.

I believe it is more likely that the inclusion of C. section Bifida within this clade is due to the extensive homoplasy in the data, and does not accurately reflect the evolutionary relationships of this group. However, further

investigation is required. The rejection of this portion of the hypothesis reduces the credibility of the rest. It is possible that the CUs comprising Danthonia are similarly misplaced, and that their apparent relationship is an artifact of the data set. I do not believe this to be the case, but only further study can resolve the question.

The two species of Erythranthera form a stable clade, separated only by the UPGMA clustering algorithm (fig. 5, 6), in spite of their differences in lemma hair arrangement, lodicules, and silica body shape. This provides good evidence of close relationship.

Merxmuellera appears, on the basis of these analyses, to be polyphyletic. Only Merxmuellera davyi, M. macowanii, and M. stereophylla form a stable clade; this grouping is plausible based on other features of anatomy and morphology not included in the cladistic data set (Appendix A; Chippindall, 1955; Conert, 1970; Wright, 1984). Conert's (1961) suggestion of a close relationship between Merxmuellera and Cortaderia is not supported by these results. The amount of variability within Merxmuellera is great (De Wet 1954, 1956, 1960; Wright, 1984), and more investigation of this group must be conducted before any firm taxonomic conclusions can be drawn.

Karroochloa does not form a stable monophyletic group on these trees, but K. tenella and K. purpurea frequently appear as sister groups. The fact that Danthonia

cachemyriana is identical to K. purpurea in all characters but one is interesting. Morphologically the two species are suffiently similar that a close relationship seems plausible. Danthonia exilis often appears as a sister group. Karroochloa curva is consistently separated from these other taxa, usually based on its lack of bulliform cells (char. 11). Further investigation of these taxa is underway.

Schismus species appear as a polyphyletic or paraphyletic group on all trees except fig. 3. The relationship between Schismus and Karroochloa postulated by Conert and Türpe (1969, 1974) is not supported by these results.

Rytidosperma also appears polyphyletic based on these analyses. The CUs comprising this genus show no stable relationships on the trees, and therefore there is no clear indication of their relationships. Similarly, the relationships of Chionochloa, Monachather, Monostachya, and Pyrranthera are unresolved because their positions on the trees are labile.

Based on the results of this study, no firm conclusions can be drawn as to the relationships of these taxa, because of the extensive homoplasy shown by the characters and the lack of truly robust groups. There are three possible reasons for these results:

First, the homoplasy shown on the trees may represent parallel evolution. Clayton (1981), in fact, has suggested that the Arundinoideae, as a whole, represent the isolated remnants of an ancient group whose center has become extinct. If this is the case, the Danthonieae would have a common ancestor within the primitive center of the subfamily, but the taxa included in Danthonia s. lat. might represent separate evolutionary lineages arising from this common ancestral complex. These lineages, evolving independently but subject to similar selective pressures, might be expected to develop identical or nearly identical features, because of the similarity of their overall genetic constitution (Cronquist, 1968; Cantino, 1982). In such a situation, one would anticipate similarity in most features of the organisms in question.

Second, convergent evolution could be responsible for the homoplasy observed in this study. The ancestors of taxa included in Danthonia s. lat. may have belonged to different ancestral complexes, but developed similar adaptations in certain features in response to similar selective pressures. In this case, one might expect that differences would remain in those features which were not subjected to these selective pressures. The more distantly related the ancestors, the greater the expected differences would be, and the easier the convergence would be to identify. Conversely, if the ancestral complexes were closely related,

perhaps in the same subfamily, then the existing differences would be fewer and more difficult to recognize.

Convergent evolution is well-known and widespread in the Poaceae. A good example is the occurrence of a geniculate and twisted awn, such as is found in many Danthonieae, Aveneae, Stipeae, and other groups. This feature has arisen independently in virtually every subfamily, and its significance in seed dispersal is apparent. The convergent nature of this character can be demonstrated in most cases by an examination of other characters, such as leaf and embryo anatomy, which are not subject to the same selective pressures. On the basis of this sort of evidence, Alloeochaete, Centropodia, Dregeochloa, Metcalfia, and Pseudopentameris were removed from this study group because the weight of evidence indicated that their resemblance to other members of Danthonia s. lat. was due to convergent evolution.

Third, the evolution of this group may have been wholly or partially reticulate. It is well-documented that amphidiploidy and autopolyploidy followed by diploidization are common phenomena in the grasses, and probably represent the dominant means of speciation in the grasses as a whole; perhaps 70-80% of the grass species are of polyploid origin. Hybridization is a likely factor in the origin of the majority of polyploid series (Stebbins, 1956; Carnahan and Hill, 1961). Speciation through polyploidy and/or

hybridization is known in the Danthonieae. Australian Rytidosperma, for instance, have been shown to form a polyploid series (Brock and Brown, 1961). Similarly, in New Zealand Chionochloa, hybrids, both natural and experimental, are readily produced (Connor, 1967). Thus, it is not difficult to imagine that lineages could have arisen by hybridization and polyploidy among the closely related ancestors of the modern Danthonieae.

Cladistic analysis does not permit inferences concerning the causes of homoplasy observed on the phylogenetic trees. Thus, I was unable to distinguish among parallel, convergent, and reticulate evolution. However, the taxa included in this study show broad similarities in both morphological and anatomical features, implying considerable similarity in genetic constitution. The most plausible explanation for this, in my opinion, is to assume close common ancestry (Cronquist, 1968), and therefore parallelism seems the most likely explanation for the observed homoplasy. However, if the ancestors of two separate evolutionary lineages were themselves closely related, it would be virtually impossible to sort out parallelism from convergence in their descendants. Reticulation, if it occurred, would further obscure the relationships, rendering the evolutionary history of the group undecipherable using present techniques and data.

Only further investigation will reveal whether or not this is the case in Danthonia.

Many workers have discussed the problems of using cladistic methods in plant groups (Crisci and Stuessy, 1980; Duncan, 1980; Bremer and Wanntorp, 1978). In groups such as grasses, where hybridization and polyploidy are known to be common, and parallelism and convergence widespread, the difficulties are magnified. In this study, the questions raised by Stuessy (1980) regarding the efficacy of cladistics in plant groups are major issues. It is clear that the cladistic approach, while it holds much promise, must be used with caution.

ACKNOWLEDGMENTS. I would like to thank J. R. Estes for advice on the project and helpful comments on the manuscript. I also thank S. Barber, G. Schnell, R. Tyrl, G. Uno, and L. Wallace for reviewing the manuscript; J. W. Wright for many fruitful discussions of the project; R. Pimentel, W. Presch, R. Riggins, J. D. Smith, and S. E. Smith for discussions and assistance with the cladistic analyses; and S. Carlquist and D. L. Kama for moral support and assistance with the figures. This work was supported in part by a National Science Foundation Graduate Fellowship, and forms part of a doctoral dissertation submitted to the Department of Botany and Microbiology of the University of Oklahoma.

LITERATURE CITED

Adams, E. N. 1972. Consensus techniques and the comparison of taxonomic trees. Syst. Zool. 21:390-397.

Avdulov, N. P. 1931. Karyo-systematische Untersuchung der Familie Gramineen. Bull. Appl. Pl. Breed. Suppl. 44: 1-428.

Bentham, G. 1881. Notes on Gramineae. J. Linn. Soc. Bot. 19:14-134.

Blake, S. T. 1972. Plinthanthesis and Danthonia and a review of the Australian species of Leptochloa (Gramineae). Contrib. Queensland. Herb. 14:1-19.

Bremer, K., and H.-E. Wanntorp. 1978. Phylogenetic systematics in botany. Taxon 27:317-329.

Brock, R. D., and J. A. M. Brown. 1961. Cytotaxonomy of Australian Danthonia. Austr. J. Bot. 9:62-91.

Brown, W. V. 1958. Leaf anatomy in grass systematics. Bot. Gaz. 119:170-178.

Calder, J. W. 1937. A cytological study of some New Zealand species and varieties of Danthonia. Bot. J. Linn. Soc. (London) 51(337):1-9.

Cantino, P. D. 1982. Affinities of the Lamiales: a cladistic analysis. Syst. Bot. 7:237-248.

Carnahan, H. L., and H. D. Hill. 1961. Cytology and genetics of forage grasses. Bot. Rev. 27:1-162.

Chase, A. 1918. Axillary cleistogenes in some American grasses. Amer. J. Bot. 5:254-258.

Chippindall, L. K. A. 1955. A guide to the identification of grasses in South Africa. Pp. 1-527 in The Grasses and Pastures of South Africa, D. Meredith, ed. New York: Hafner Publishing Company.

Clayton, W. D. 1978. Poaceae. Pp. 285-290 in Flowering Plants of the World, V. H. Heywood, ed. Oxford: Oxford Univ. Press.

_____. 1981. Evolution and distribution of grasses. Ann. Missouri Bot. Gard. 68:5-14.

Clifford, H. T., and L. Watson. 1977. Identifying Grasses: Data, Methods and Illustrations. St. Lucia: University of Queensland Press.

Colless, D. H. 1970. The phenogram as an estimate of phylogeny. Syst. Zool. 19:352-362.

Conert, H. J. 1960. Metcalfia, eine neue Gattung der Gramineen. Willdenowia 2:417-419.

_____. 1961. Die Systematik und Anatomie der Arundineae. Wienheim: J. Cramer.

_____. 1962. Über die Gramineen-Gattung Asthenatherum Nevski. Senckenberg. Biol. 43:239-266.

_____. 1966. Dregeochloa, eine neue Gattung der Gramineen (Gramineae, Arundinoideae, Danthonieae). Senckenberg. Biol. 47:335-343.

_____. 1969. Dreizahngras (Danthonia decumbens De Candolle) und Traubenhafer (Danthonia alpina Vest). Jb. Nassau. Ver. Naturk., 100:54-72.

_____. 1970. Merxmuellera, eine neue Gattung der Gramineen. Senckenberg. Biol. 51:129-133.

_____. 1971. The genus Danthonia in Africa. Mitt. Bot. Staatssamml. Munch. 10:299-308.

_____. 1975a. Uber Danthonia domingensis Hackel & Pilger. (Poaceae: Arundinoideae: Danthonieae) Senckberg. Biol. 56:293-313.

_____. 1975b. Merxmuellera guillarmodae Conert n. sp. (Gramineae: Arundinoideae). Senckenberg. Biol. 56:145-152.

_____. 1975c. Die Chionochloa-Arten von Australien und Neuguinea (Poaceae: Arundinoideae). Senckenberg. Biol. 56:153-164.

_____, and A. M. Türpe. 1969. Karroochloa, eine neue Gattung der Gramineen. Senckenberg. Biol. 50:289-318.

_____, and _____. 1974. Revision der Gattung Schismus (Poaceae: Arundinoideae: Danthonieae). Abh. Senckenberg. Naturforsch. Ges. 532:1-81.

Connor, H. E. 1963. Breeding systems in New Zealand grasses. IV. Gynodioecism in Cortaderia. New Zealand J. Bot. 1:258-264.

_____. 1967. Interspecific hybrids in Chionochloa (Gramineae). New Zealand J. Bot. 5:3-16.

_____. 1970. Gynodioecy in Danthonia archboldii. Aust. J. Bot. 18:233-236.

_____. 1974. Breeding systems in Cortaderia (Gramineae). Evolution 27:663-678.

_____. 1981. Evolution of reproductive systems in the Gramineae. Ann. Missouri Bot. Gard. 68:48-74.

_____. 1983. Names and types in Cortaderia Stapf (Gramineae) II. Taxon 32:633-634.

_____, and E. Edgar. 1974. Names and types in Cortaderia Stapf (Gramineae). Taxon 23:595-605.

_____, and _____. 1979. Rytidosperma Steudel (Notodanthonia Zotov) in New Zealand. New Zealand J. Bot. 17:311-337.

Crisci, J. F., and T. F. Stuessy. 1980. Determining primitive character states for phylogenetic reconstruction. Syst. Bot. 5:112-135.

Cronquist, A. 1968. The evolution and classification of flowering plants. New York: Allen Press.

DeWet, J. M. J. 1954. The genus Danthonia in grass phylogeny. Amer. J. Bot. 41:204-211.

_____. 1956. Leaf anatomy and phylogeny in the tribe Danthonieae. Amer. J. Bot. 43:175-182.

_____. 1960. Leaf anatomy and morphology in South African species of Danthonia. Bothalia 7:303-310.

Donoghue, M. J. 1983. A preliminary analysis of phylogenetic relationships in Viburnum (Caprifoliaceae s. l.). Syst. Bot. 8:45-58.

Duncan, T. 1980. Cladistics for the practicing taxonomist -- an eclectic view. Syst. Bot 5:136-148.

Ellis, R. P. 1976. A procedure for standardizing comparative leaf anatomy in the Poaceae. I. The leaf blade as viewed in transverse section. Bothalia 12: 65-109.

_____. 1977. Leaf anatomy of the South African Danthonieae (Poaceae). I. The genus Dregeochloa. Bothalia 12:209-213.

_____. 1979. A procedure for standardizing comparative leaf anatomy in the Poaceae. II. The epidermis as seen in surface view. Bothalia 12:641-671.

Estabrook, G. F. 1972. Cladistic methodology: a discussion of the theoretical basis for the induction of evolutionary history. Annual Rev. Ecol. Syst. 3:427-456.

Farris, J. S. 1969. A successive approximations approach to character weighting. Syst. Zool. 18:374-385.

_____. 1970. Methods for computing Wagner trees. Syst. Zool. 19:83-92.

_____. 1981. Distance data in phylogenetic analysis. Pp. 3-23 in Advances in Cladistics, vol. 1 [Proceedings of the first meeting of the Willi Hennig Society], eds. V. A. Funk and D. R. Brooks. New York: Columbia University Press.

Hennig, W. 1966. Phylogenetic Systematics. Transl. by D. W. Davis and R. Zangerl. University of Illinois Press, Urbana.

Hilu, K. W., and K. Wright. 1982. Systematics of Gramineae: a cluster analysis study. Taxon 31:9-36.

Hitchcock, A. S. 1936. Botanical results of the Archbold Expedition. No. 1. Papuan grasses collected by L. J. Brass. Brittonia 2:107-115.

_____. 1951. Manual of the grasses of the United States, 2nd ed. Revised by A. Chase. U. S. Dept. Agr. Misc. Publ. 200.

Hooker, J. D. 1867. Handbook of the New Zealand Flora. London: Reeve & Co.

Hubbard, C. E. 1937. Alloeochaete andongensis (Rendle) C. E. Hubbard. Gramineae. Tribus Aveneae. Hook. Icon. Plant. 5: tab. 3418.

_____. 1948. Gramineae. Pp. 284-348 in British Flowering Plants, J. Hutchinson, ed. London: P. R. Gawthorn Ltd.

Johansen, D. E. 1940. Plant Microtechnique. New York: McGraw-Hill.

Kabuye, C. H. S., and S. A. Renvoize. 1975. The genus Alloeochaete, tribe Danthonieae (Gramineae). Kew Bull. 30:569-577.

Meacham, C. A. 1980. Phylogeny of the Berberidaceae with an evaluation of classifications. Syst. Bot. 5:149-172.

Metcalfe, C. R. 1960. Anatomy of the Monocotyledons. I. Gramineae. Oxford: Clarendon Press.

Nicora, E. G. 1973. Novedades agrostologicas Patagonicas. Darwiniana 18:80-106.

Prat, H. 1932. L'épiderme des Graminées, étude anatomique et systématique. Ann. Sci. Nat. Bot. X. 13:117-325.

_____. 1936. La systématique des Graminées. Ann. Sci. Nat. Bot. X. 18:165-258.

Reeder, J. R. 1957. The embryo in grass systematics. Amer. J. Bot. 44:756-768.

Renvoize, S. A. 1982. The subfamily Arundinoideae and its position in relation to a general classification of the Gramineae. Kew Bull. 36:85-102.

Schmid, R., and M. D. Turner. 1977. Contrad 70, an effective softener of herbarium material for anatomical study. Taxon 26:551-552.

Sneath, P. H. A., and R. R. Sokal. 1973. Numerical Taxonomy. San Francisco: W. H. Freeman.

Stapf, O. 1934. Gramineae. Pp. 1-1132 in Flora of Tropical Africa, D. Prain, ed. Ashford: L. Reeve & Co., Ltd.

Stebbins, G. L. 1956. Cytogenetics and evolution of the grass family. Amer. J. Bot. 43:890-905.

_____. 1982. Major trends of evolution in the Poaceae and their possible significance. Pp. 3-36 in Grasses and Grasslands, J. R. Estes, et al., eds. Norman: University of Oklahoma Press.

Stuessy, T. 1980. Cladistics and plant systematics: problems and prospects. Introduction. Syst. Bot. 5:109-111.

Tateoka, T. 1954. On the systematic significance of starch grains of seeds in Poaceae. J. Jap. Bot. 29:341-346.

_____. 1957. Proposition of a new phylogenetic system of Poaceae. J. Jap. Bot. 32:275-287.

_____. 1964. Notes on some grasses XVII. Metcalfia, a primitive genus of the tribe Aveneae. Bot. Mag. (Tokyo) 77(909):69-72.

_____. 1967. Lodicules of the tribes Ehrharteae and Aristideae (Gramineae). Bull. Nat. Sci. Mus. Tokyo 10:443-453.

Vickery, J. W. 1956. A revision of the Australian species of Danthonia DC. Contrib. New South Wales Nat. Herb. 2: 249-325.

Wagner, W. H. 1961. Problems in the classification of ferns. Pp. 841-844 in Recent Advances in Botany. Toronto: University of Toronto Press.

Watrous, L. E., and Q. D. Wheeler. 1981. The out-group comparison method of character analysis. Syst. Zool. 30:1-11.

Watson, R. W. 1942. The effect of cuticular hardening on the form of cuticular cells. New Phytol. 41:223-229.

Weatherwax, P. 1928. Cleistogamy in two species of Danthonia. Bot. Gaz. 85:104-109.

Wright, K. L. Tomlinson. 1984. Studies in the Danthonieae (Poaceae). Part II. Comparative anatomical studies in Danthonia s. lat. (Danthonieae: Poaceae). PhD dissertation, Univ. of Oklahoma.

Zotov, V. D. 1963. Synopsis of the grass subfamily Arundinoideae in New Zealand. New Zealand J. Bot. 1:78-136.

TABLE 1. Characters and character states. An asterisk (*) marks characters used in cladistic analysis. VB = vascular bundle, 1° = primary, 2° = secondary, BS = bundle sheath.

LEAF CROSS-SECTION: 1. Adaxial furrows: 0 = open; 1 = narrow cleft; 2 = broad, steep-sided; 3 = none. 2. Adaxial ribs, presence: 0 = over all VBs; 1 = only over midrib; 2 = only over 1° and 2° VBs; 3 = none. 3. Adaxial ribs, shape: 0 = similar over all VBs; 1 = different. 4. Adaxial ribs, shape over 1° VBs: 0 = rounded; 1 = flat-topped; 2 = massive. 5. Midrib: 0 = median VB only; 1 = midrib. 6. 1° VB shape: 0 = round or elliptical; 1 = egg-shaped. 7. 2° VB shape: 0 = round or elliptical; 1 = egg-shaped. *8. Phloem: 0 = not divided by fibers; 1 = evenly divided into 2 groups; 2 = irregularly divided. 9. Outer BS: 0 = complete; 1 = incomplete above; 2 = incomplete below; 3 = incomplete above and below. 10. Outer BS size: 0 = cells equal to or smaller than parenchyma cells, inconspicuous; 1 = cells equal to or smaller than parenchyma cells, conspicuous; 2 = cells larger than parenchyma cells, conspicuous. 11. Inner BS cell walls: 0 = unevenly thickened; 1 = evenly thickened. 12. Adaxial sclerenchyma, presence: 0 = associated with all VBs; 1 = lacking over 3° VBs; 2 = none. 13. Adaxial sclerenchyma, shape over 1° VBs: 0 = strand; 1 = girder; 2 = girder narrower toward bundle; 3 = T or anchor. 14. Abaxial

sclerenchyma, presence: 0 = associated with all VBs; 1 = lacking under 3° VBs. 15. Abaxial sclerenchyma, shape under 1° VBs: 0 = strand; 1 = girder; 2 = girder narrower toward bundle; 3 = T or anchor. 16. Mesophyll: 0 = not radiate; 1 = indistinctly radiate. 17. Colorless cells: 0 = none; 1 = present as BS extensions only, not extensive; 2 = present in mesophyll, not extensive; 3 = extensive. 18. Metaxylem vessels: 0 = smaller than or equal to outer BS cells; 1 = larger than outer BS cells. 19. BS extensions, adaxial: 0 = present, connecting bundle to sclerenchyma; 1 = extensions only, no sclerenchyma; 2 = no extensions. 20. BS extensions, abaxial: 0 = present, connecting bundle to sclerenchyma; 1 = extensions only, no sclerenchyma; 2 = no extensions. *21. Upper epidermis: 0 = cells unspecialized; 1 = composed mainly of rounded cells, somewhat enlarged; 2 = composed mainly of broadly papillate cells; 3 = composed mainly of fingerlike cells. *22. Hypodermic prickle hairs: 0 = absent; 1 = present on adaxial epidermis. *23. Bulliform cells: 0 = present, simple fans; 1 = present, fan-shaped groups but center cell enlarged; 2 = absent; 3 = Arundo-type.

LOWER EPIDERMIS IN SURFACE VIEW: 24. Microhairs: 0 = present; 1 = none seen. 25. Intercostal long cells, shape: 0 = walls parallel; walls bowed out. 26. Intercostal long cells, side walls: 0 = undulating; 1 = deep, interlocking undulations; 2 = U-shaped undulations; 3 = W-shaped

undulations. *27. Costal short cells: 0 = in long (5+) rows; 1 = mainly paired or solitary. *28. Costal silica body shape: 0 = cross-dumbbell; 1 = mainly round-crescentic.

MORPHOLOGY: *29. Lower leaf sheaths: 0 = unspecialized; 1 = indurate, persistent; 2 = densely lanate. *30. Prophylla: 0 = unspecialized; 1 = membranous, long-awned; 2 = triangular, lanate on keels. 31. Cleistogamous spikelets: 0 = absent; 1 = present. 32. Spikelets: 0 = more than 2-flowered; 1 = 2-flowered. *33. Lemma hairs: 0 = scattered or only marginal; 1 = tufted; 2 = in distinct lines between nerves; 3 = scattered above a horizontal line; 4 = absent. 34. Lateral lobes: 0 = distinct from awn base; 1 = more or less adnate to awn base. *35. Lateral lobes, development: 0 = well-developed; 1 = reduced; 2 = absent. 36. Awn: 0 = well-developed; 1 = reduced. 37. Callus, development: 0 = blunt, transverse; 1 = elongate. 38. Callus, vestiture: 0 = glabrous; 1 = more or less long-hairy. 39. Lemma nerve number: 0 = 5-9; 1 = 11-13. 40. Glume nerve number: 0 = 1; 1 = 3-5; 2 = 5-9; 3 = 11-13. 41. Palea/rachilla ratio: (value). *42. Lodicules: 0 = glabrous; 1 = hairy. *43. Microhairs on lodicules: 0 = present; 1 = absent. *44. Hilum: 0 = linear; 1 = round to oval. 45. Hilum, spot appearing above base: 0 = no; 1 = yes. 46. Hilum length/width ratio: (value + 1 s. d.; n). 47. Hilum/caryopsis ratio: (value + 1 s. d.; n). *48. Sex form:

0 = perfect-flowered; 1 = gynodioecious. 49. Basic chromosome number: 0 = 6; 1 = 7; 2 = 10.

TABLE 2. Cladistic units and included taxa. See text for explanation.

CU	INCLUDED TAXA
ARUNDO	*Arundo donax*
CHIONOCL	*Chionochloa beddiei*, *C. bromoides*, *C. conspicua*, *C. flavescens*, *C. frigida*, *C. pallens*, *C. rigida*, *C. rubra*
COARCHBO	*Cortaderia archboldii*
CSECTBIF	*Cortaderia hapalotricha*, *C. pungens*
CSECTCOR	*Cortaderia araucana*
CSECTMON	*Cortaderia pilosa*
CSECTMUT	*Cortaderia modesta*
DANTHOSS	*Danthonia alpina*, *D. californica*, *D. compressa*, *D. decumbens*, *D. intermedia*, *D. parryi*, *D. secundiflora*, *D. sericea*, *D. spicata*, *D. unispicata*
DCACHEMY	*Danthonia cachemyriana*
DDOMINGE	*Danthonia domingensis*
DEXILIS	*Danthonia exilis*
DMONTANA	*Danthonia montana*
DSAMER1	*Danthonia cirrata*, *D. malacantha*
DSAMER2	*Danthonia dusenii*, *D. montevidensis*
DSHREVEI	*Danthonia shrevei*
EAUSTRAL	*Erythranthera australis*
EPUMILA	*Erythranthera pumila*
KCURVA	*Karroochloa curva*
KPURPURE	*Karroochloa purpurea*
KTENELLA	*Karroochloa tenella*
MARUNDIN	*Merxmuelllera arundinacea*
MDAVYI	*Merxmuellera davyi*
MDISTICH	*Merxmuellera disticha*

TABLE 2, continued.

CU	INCLUDED TAXA
MDRAKENS	Merxmuellera drakensbergiensis
MDURA	Merxmuellera dura
MGUILLAR	Merxmuellera guillarmodae
MLUPDECO	Merxmuellera lupulina, M. decora
MMACOWAN	Merxmuellera macowanii
MONACHAT	Monachather paradoxus
MONOSTAC	Monostachya oreoboloides
MPAPPOSA	Merxmuellera papposa
MRUFA	Merxmuellera rufa
MSTEREOP	Merxmuellera stereophylla
MSTRICTA	Merxmuellera stricta
PLINTHAN	Plinthanthesis paradoxus
PYRRANTH	Pyrranthera exigua
RAUSTRNZ	Rytidosperma acerosum, R. biannulare, R. caespitosum, R. clavatum, R. corinum, R. dimidiatum, R. erianthum, R. geniculatum, R. gracile, R. laeve, R. linkii, R. longifolium, R. nigricans, R. pauciflorum, R. penicillatum, R. pilosum, R. procerum, R. racemosum, R. richardii, R. semiannulare, R. setaceum, R. setifolium, R. unarede, R. violaceum
RPALLIDE	Rytidosperma pallide
RSAMERIC	Rytidosperma glabrum, R. virescens
RVESTITU	Rytidosperma vestitum
SARABICU	Schismus arabicus
SBARBATU	Schismus barbatus
SINERMIS	Schismus inermis
SSCABERR	Schismus scaberrimus

TABLE 3. Data matrix used in cladistic analysis (for key to CUs see table 2). 9 = missing observation. Character numbers at bottom refer to original data matrix.

	CLADISTIC CHARACTER NUMBER													
CU	1	2	3	4	5	6	7	8	9	10	11	12	13	14
ARUNDO	0	2	0	1	0	1	0	0	0	0	1	0	0	0
DANTHOSS	0	0	0	0	0	1	0	0	0	0	0	0	0	0
DSHREVEI	0	0	0	0	1	1	9	0	0	0	0	1	0	0
DDOMINGE	0	0	0	0	0	1	9	0	0	0	0	1	0	0
DSAMER1	0	0	0	0	0	1	0	1	0	0	0	1	0	0
DMONTANA	0	0	0	0	9	9	0	1	1	0	0	0	0	0
DSAMER2	0	0	0	0	0	1	0	0	1	0	0	0	0	0
DCACHEMY	0	0	1	0	1	0	9	0	0	0	0	0	0	0
DEXILIS	0	0	2	0	1	0	1	0	1	0	0	0	0	0
RSAMERIC	0	0	1	0	1	0	1	0	0	0	2	1	1	0
RAUSTRNZ	0	0	1	0	1	0	1	0	1	0	2	0	0	0
RPALLIDE	0	0	1	0	1	0	1	0	0	0	0	1	1	0
RVESTITU	0	0	1	0	1	0	1	0	1	0	2	0	1	0
MRUFA	2	0	2	0	1	0	1	0	0	0	0	1	1	0
MDURA	1	0	0	0	1	0	1	0	0	0	0	1	1	0
MLUPDECO	2	0	2	0	1	1	1	0	0	0	2	1	1	0
MPAPPOSA	9	0	3	0	1	1	1	0	1	0	0	1	1	0
MDISTICH	0	0	1	0	1	0	1	0	1	0	2	1	1	0
MSTRICTA	0	0	1	0	1	0	1	1	1	0	2	0	1	0
MDAVYI	0	0	1	0	1	1	1	1	1	1	0	1	1	0
MMACOWAN	1	0	1	0	1	0	1	1	1	1	0	1	1	0
MSTEREOP	1	0	1	0	1	1	1	1	1	0	0	1	1	0
MDRAKENS	1	0	1	0	1	0	1	1	0	0	2	1	1	0
MGUILLAR	0	0	0	0	1	0	1	1	1	0	2	0	0	0
MARUNDIN	1	0	2	0	1	0	1	0	0	0	0	1	1	0
CHIONOCL	1	0	0	0	1	0	0	0	1	0	2	1	1	0
CSECTBIF	1	0	0	0	0	0	0	0	1	0	0	0	0	1
CSECTCOR	1	0	0	1	1	1	0	2	0	0	2	1	0	1
CSECTMON	1	0	0	1	0	1	0	2	0	0	2	1	1	1
CSECTMUT	1	0	0	1	0	1	0	2	0	0	2	1	0	1
COARCHBO	1	0	0	0	1	1	0	0	1	0	0	0	0	1
SBARBATU	0	1	0	0	1	0	1	0	0	0	2	0	0	0
SARABICU	0	1	0	0	0	1	1	0	0	0	2	0	0	0
SSCABERR	0	1	0	2	1	0	1	0	0	0	0	0	0	0
SINERMIS	0	1	0	1	1	0	1	0	0	0	2	1	1	0

DSAMER2	0	0	0	0	0	1	0	0	1	0	0	0	0	0
DCACHEMY	0	0	1	0	1	0	9	0	0	0	0	0	0	0
DEXILIS	0	0	2	0	1	0	1	0	1	0	0	0	0	0
RSAMERIC	0	0	1	0	1	0	1	0	0	0	2	1	1	0
RAUSTRNZ	0	0	1	0	1	0	1	0	1	0	2	0	0	0
RPALLIDE	0	0	1	0	1	0	1	0	0	0	0	1	1	0
RVESTITU	0	0	1	0	1	0	1	0	1	0	2	0	1	0
MRUFA	2	0	2	0	1	0	1	0	0	0	0	1	1	0
MDURA	1	0	0	0	1	0	1	0	0	0	0	1	1	0
MLUPDECO	2	0	2	0	1	1	1	0	0	0	2	1	1	0
MPAPPOSA	9	0	3	0	1	1	1	0	1	0	0	1	1	0
MDISTICH	0	0	1	0	1	0	1	0	1	0	2	1	1	0
MSTRICTA	0	0	1	0	1	0	1	1	1	0	2	0	1	0
MDAVYI	0	0	1	0	1	1	1	1	1	1	0	1	1	0
MMACOWAN	1	0	1	0	1	0	1	1	1	1	0	1	1	0
MSTEREOP	1	0	1	0	1	1	1	1	1	0	0	1	1	0
MDRAKENS	1	0	1	0	1	0	1	1	0	0	2	1	1	0
MGUILLAR	0	0	0	0	1	0	1	1	1	0	2	0	0	0
MARUNDIN	1	0	2	0	1	0	1	0	0	0	0	1	1	0
CHIONOCL	1	0	0	0	1	0	0	0	1	0	2	1	1	0
CSECTBIF	1	0	0	0	0	0	0	0	1	0	0	0	0	1
CSECTCOR	1	0	0	1	1	1	0	2	0	0	2	1	0	1
CSECTMON	1	0	0	1	0	1	0	2	0	0	2	1	1	1
CSECTMUT	1	0	0	1	0	1	0	2	0	0	2	1	0	1
COARCHBO	1	0	0	0	1	1	0	0	1	0	0	0	0	1
SBARBATU	0	1	0	0	1	0	1	0	0	0	2	0	0	0
SARABICU	0	1	0	0	0	1	1	0	0	0	2	0	0	0
SSCABERR	0	1	0	2	1	0	1	0	0	0	0	0	0	0
SINERMIS	0	1	0	1	1	0	1	0	0	0	2	1	1	0
KCURVA	0	0	0	0	1	0	1	0	1	0	2	0	0	0
KTENELLA	0	1	1	0	0	0	1	0	0	0	0	0	0	0
KPURPURE	0	0	1	0	1	0	1	0	0	0	0	0	0	0
MONACHAT	2	0	1	0	0	1	1	0	0	0	1	0	0	0
PYRRANTH	0	0	0	1	1	0	1	0	1	0	2	0	0	0
PLINTHAN	0	0	0	1	0	1	0	0	0	0	2	0	0	0
EPUMILA	0	0	2	1	0	0	1	0	1	0	2	0	1	0
EAUSTRAL	0	0	4	1	0	1	1	0	1	0	2	0	0	0
MONOSTAC	0	0	1	2	1	0	9	0	1	0	2	1	1	0
	29	30	33	35	42	43	44	8	21	22	23	27	28	48

ORIGINAL CHARACTER NUMBER

TABLE 4. Results of character compatibility analysis.

RUN I (CHARACTERS 1,5,6,7 DELETED)
Clique 1: Characters 2,8,10
Clique 2: Characters 2,9,10
Clique 3: Characters 2,10,14
Clique 4: Characters 3,10,14
RUN II (6 CUs DELETED)
Clique 1: Characters 3,7,10,14

APPENDIX A. Anatomical and morphological data on 48 species of Danthonieae. See Table 1 for listing of characters and character states.

TAXON	CHARACTER																								
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27
Danthonia spicata	0	0	0	0	0	0	0	0	1	0	0	0	1	0	1	0	0	1	2	2	0	0	0	0	1	2	0
D. sericea	0,2	0	0,1	0,1	0	0	0	0	0,2	1,0	0	0,1	1	0,1	1	0	1	1	0	2	0	0	0	0	0,1	0,2	0
D. compressa	0	0	0	0	1	0	0	0	2	0	0	0	2	0,1	2	0	0	0	2	2	0	0	0	0	0	2	0
D. intermedia	0,2	0	0	1	0	0	0	0	1	0	0	0	1	1	1,2	0,1	0	0	2	2	0	0	0	0	0	2	0
D. parryi	2	0	0	1	0	0	0	0	1	0	0	0	1	1	1,2	0	2	1	2	2	0	0	0	0	0	2	0
D. californica	0	0	0	0	0,1	0	1	0	1	0	0	0	1	0	1	0	0,1	1	0,2	0,2	0	0	0	0	0	2	0
D. unispicata	0	0	0	0	1	0	0	0	1	0	0	0	1	0	1	0	0	1	2	2	0	0	0	1	0,1	2	0
D. decumbens	0	0	0	0	1	0	0	0	1	0	0	0	1	0,1	1	0	0	0	2	2	0	0	0	0	0	1	0
D. alpina	0	0	0	0	0	0	0	0	1	0	0	0	2	0	2	0	0	1	2	2	0	0	0	0	0	2	0
D. secundiflora	2	0	0	0	0	0	0	0	2	0	0	0	1	0	1,2	0	1	1	0	2	0,1	0	0	0	1	2	0
D. domingensis	1,2	0	0	1	0	1	1	0	1	1	0	0	1	0	1	0	2	1	2	2	0	0	0	0	0	2	1
D. shrevei	1,2	0	0	1	0	1	1	0	1	1	0	0	1	0	1	0	2	1	2	2	0	0	0	0	0	2	1
D. chaseana	2	0	0	0	1	0,1	0	0	1	0	0	1	1	0	1	0	0	1	2	2	1	0	2	1	0	1	0
D. cirrata	2	0	1	1	1	0	0	1	1	0	0	1	1	1	1	0	0	2	2	0	0	0	0	0	0	2	1
D. malacantha	2	0	1	1	1	0	1	1	1	0	0	0	1	0	2	0	0	0	2	2	0	0	0	1	0	2	1
D. montana	2	0	0	0	0	0	0	1	2	0	0	0	1	1	1,2	0	1	0	0	2	1	0	0	0	1	2	0
D. dusenii	2	0	0	0	1	0	0	0	2	0	0	0	1	0	1	0	1	1	0	2	1	0	0	0	1	1	0
D. montevidensis	2	0	0	1	1	0	0	0	2	1	0	0	1	1	1	0	2	0	0	2	0,1	0	0	0	0	2	0
D. cachemyriana	1	0	0	0	0	0	0	0	1	0	0	0	1	0	2,1	0	0	1	0	0	0	0	0	0	0	2	0
D. wallia	2	0	0	0	1	0	0	0	1	0	0	1	0	1	2	0	0	0	0	0	1	0	0		0	2	0
Rytidosperma virescens	2	0	0	1	1	0	0	0	0	0	0	0	1	0	2	0	1	1	0	2	0	0	2	0	0	2	1
R. glaucum	0	0	0	0	1	0	0	0	0	0	0	0,1	1	0	1	0	1	0	0	0	0	0	2	1	0	2	1
R. violaceum	2	0	0	1	0	0	0	0	2	0	0	0	1	0	2	0	0	0	2	2	0	0	0	0	0	2	0
R. acerosum	2	0	0	1	0	0	0	0	1	0	0	0	1	0	2	0	0	0	2	2	0	0	0	0	0	1	0
R. caespitosum	0	0	0	0	1	0,1	0	0	2,1	0	0	0	2,1	0	2	0	0	1	2	2	0	0	0	0	0	0	0
R. laeve	0	0	0	0	1	0	0	0	1	0	0	0	2	0	2	0	0	0	2	2	0	0	2	0	0	1	0
R. linkii	2	0	1	1	0	0	0	0	1	0	0	0	2	0	2	0	0	1	2	2	0	0	0	0	0	2	0
R. longifolium	2	0	0	0	1	1	0	0	1	0	0	0	2	0	2	0	0	1	2	2	0	0	0	1	0	1	0
R. penicillatum	1	1	9	9	1	0	0	0	2,1	0	0	0	1	0	2	0	1	0	0	2	0	0	2	0		2	0
R. pilosum	0	0	0	0	1	0	0	0	2,1	0	0	0	2	0	2	0	0	0	2	2	0	0	0	0	0	2	0
R. racemosum	0	0	0	0	1	0	0	0	1	0	0	0	2	0	2	0	0	1	2	2	1	1,0	0	0	1	2	0
R. semiannulare	2	0	0	1	0	0	0	0	1	0	0	0	1	0	2	0	0	1	2	2	0	0	0	0	0	2	0
R. setaceum	0	0	0	0	1	0	0	0	1	0	0	0	2	0	2	0	0	0	2	2	0	0	0	0	1	2	0
R. erianthum	0	0	0	0	1	0	0	0	1	0	0	0	2	0	2	0	0	0	2	2	0	0	0	0	0	2	0
R. geniculatum	0	0	0	0	1	0	0	0	1	0		0	1	0	1	0	0	0	2	2	0	0		0	1	2	0
R. pallide	0	0	0	1	1	0	0	0	2	0	0	1	2	0	2	0	0	0	2	2	0	0	0	0	0	0	1
R. pauciflorum	1	0	0	1	1	0	0	0	2	0	0	0	1	0	2	0	1	0	0	2	2,1	0	2	1	1	1	0
R. procerum	1	2	0	1	1	0	0	0	2	0	0	1	1	0	1	0	1	0	0	2	0	0	2	0	0	2	0
R. richardsonii	0	0	0	1	0	0	0	0	2	0	0	0	2	0	2	0	0	1	2	2	0	0	0	0	0	2	0
R. biannulare	0	0	0	0	0	0	0	0	1	0	0	1	1	0	1	0	0	1	2	2	0	0	0	0	1	2	0
R. clavatum	0	2	0	0	1	0	0	0	0	0	0	0	2	1	2	1	1	0	0	2	0	0	0	0	0	2	0
R. corinum	0	2	0	0	1	0	0	0	2	0	0	0,1	1	0	2	0	1	0	0	2	2,1	0	2	0	0	2	0
R. gracile	0	0	0	0	1	0	0	0	2	0	0	0	2	0	2	0	1	0	0	2	0	0	0	0	0	2	0
R. nigricans	1,2	0	0	1	1	0	0	0	0	0	0	0	1	0	2	0	1	0	0	2	0,1	0	0	0	0	0	0
R. setifolium	0	0	0	0	1	0	0	0	0,2	0	0	1	1	0,1	2	0	1	0	0	2	1	0	2	1	0	2	0
R. unarede	0	0	0	0	1	0	0	0	0	0	0	1	2	0	2	0	0	0	2	2	0	0	0	0	1	2	0
R. dimidiatum	0	0	0	0	1	0	0	0	1	0	0	0	1	0	1,2	0	0	0	2	2	0	0	0	0	0	2	0
R. vestitum	2	0	0	0	1	0	0	0	2	0	0	0	1	0	2	0	1	0	0	2	2,1	0	2	0	0	2	0
Merxmuellera arundinacea	1	0	1	2	0	1,0	0	0	1	0	1	0	1	0	1	0	0	1	2	2	0	0	0	1	0	2	1
M. davyi	1	0	0	0	1	0	0	1	2,1	0	1	0	1	0	1	0	0	0	2	2	1	0	1	0	1	1	1
M. decora	1	0	0	1	1	0,1	0	0	2,1	1	1	0	1	0	2	0	1	0	2	0	0	0	2	1	0	2	1
M. disticha	1	0	0	1	1	1	0	0	1	0	1	0	1	0	1	0	0	1	2	2	1	0	2	1	0	1	1
M. drakensbergiensis	1	0	0	0	1	0	0	1	1	0	0	0	1	0	1	0	0	0	2	2	0	0	2	1	0	1	1
M. dura	1	0	0	1	0	0	0	0	2,1	1	1	0	1	0	2	0	1	1	0	0	0	0	0	0	0	2	1
M. guillarmodae	1	1	9	9	1	0	0	1	2	1	0	1,2	1,9	0	1	0	1	0	0	2	1	0	2	0	0	1	0
M. lupulina	1	0	1	1	1	0	0	0	1	1	1	1	1	0	1	0	0	0	2	2	0	0	0	0	0	2	1
M. macowanii	1	0	1	1,2	1	0	0	1	2	1	0	0	1	0	1	0	0,1	1	0,2	2	2,1	1	0	1	0	1	1
M. pappose	1	0	0	2	1	1	0	0	0	1	0	0	0	0	0	0	1	1	0	0	1	0	0	1	0	0,2	1
M. rufa	0	0	0	0	1	0	0	0	0	1	1	0	1	0	1	0	0		2	2	0	0	0	1	0	2	1
M. stereophylla	1	0	0	0	1	0	0	1	1	0	0	0	1	0	1	0	0	0	2	2	2	0	0	1	0	1	1
M. stricta	0	0	0	0	1	0	0	1	2,1	1	0	0	1	0	2	0	1	0	0	2	2	0	2	0	0	2	0
Chionochloa buddiae	1	0	0	1	1	0	0	0	2	0,1	0	0	1	0	1	0	1	0	0	2	0,2	0	2	1	0	1	1
C. bromoides	1	0	0	1	1	1	0	0	2	0	0	0	1	0	1	1	1	0	0	2	2	0	2	1	0	2	1
C. conspicua	1	0	0	0	1	0	0	0	2	0	0	0	1	0	1	0	2	1	0	0	2	0	2	1	0	2	1
C. flavescens	1	0	0	0	1	0	0	0	2	0	0	0	1	0	1	1	2	1	0	0	2	0	2	1	0	2	1
C. frigida	1	0	0	1	0	0	0	0	2	0	0	0	2	0	2	0	1	0	0	2	2	0	2	1	0	2	1
C. pallens	1	0	0	0	1	0	0	0	2	0	0	0	1	0	1	1	1	0	0	0	2	0	2	1	0	2	1
C. rigida	1	0	1	2	0	0	0	0	2	0	0	0	1	0	2	0	1	1	0	0	2	0	2	1	0	2,1	1
C. rubra	1	0	0	0	1	1	0	0	0	0	0	0	1	0	1	0	2	1	0	0	2	0	2	1	0	2	1
Curtaderia archboldii	2	0	0	0	1	0	0	0	1	0	1	0	1	0	1	0	1	1	0	2	1	0	0	1	0	1	0
C. hapalotricha	1	0	0	1	0	0	0	0	1	0	0	0	1	0	1	0	0	0	2	2	0	0	0	1	0	2	0
C. pungens	1	0	0	1	0	0	0	0	2	0	0	0	1	0	1	0	0	0	2	2	2	0	2	1	0	2,1	0
C. araucana	1	0	0	1	0	0	0	0	2	0	1	0	1	0	2	0	1	0	0	0	0	0	2	1	0	1	1
C. mucronata	0	0	0	0	1	0	0	0	2	0	1	1	0	1	0	1	0	1	0	0	0	0	0	2	0	2	1

D. [illegible]	.	0	.	.	.	1	0,1	0	0	1	0	0	1	1	0	1	0	0	1	2	.	2	0	0	1	0	1	0				
D. [illegible]rsiata	2	0	1	1	1	0	0	1	1	0	0	1	2	1	1	1	0	0	2	2	0	0	0	0	2	1						
D. [illegible]delacartia	2	0	1	1	1	0	1	1	1	0	0	0	1	2	1	2	0	0	0	2	1	2	0	0	1	0	2	1				
D. [illegible]ardiana	2	0	0	0	0	0	0	1	2	0	0	0	1	1	1,2	0	1	0	0	2	1	0	0	0	1	2	0					
D. [illegible]weenii	2	0	0	0	1	0	0	0	2	0	0	0	1	0	1	0	1	1	0	2	1	0	0	0	1	1	0					
D. montevidensis	2	0	0	1	1	0	0	0	2	1	0	0	1	1	1	0	2	0	0	2	0,1	0	0	0	0	2	0					
D. cathcartiana	1	0	0	0	0	0	0	0	1	0	0	0	1	0	2,1	0	0	1	0	0	0	0	0	0	0	2	0					
D. exilis	2	0	0	0	1	0	0	0	1	0	0	0	1	0	1	2	0	0	0	0	1	0	0		0	2	0					
Rytidosperma virescens	2	0	0	1	1	0	0	0	0	0	0	0	1	0	2	0	1	1	0	2	0	0	2	0	0	2	1					
R. glabrum	0	0	0	0	1	0	0	0	0	0	0	0,1	1	0	1	0	1	0	0	0	0	0	2	1	0	2	1					
R. violaceum	2	0	0	1	0	0	0	0	2	0	0	0	1	0	2	0	0	0	2	2	0	0	0	0	0	2	0					
R. acervosum	2	0	0	1	0	0	0	0	1	0	0	0	1	0	2	0	0	0	2	2	0	0	0	0	0	1	0					
R. caespitosum	0	0	0	0	1	0,1	0	0	2,3	0	0	0	2,3	0	2	0	0	1	2	2	0	0	0	0	0	0	0					
R. laeve	0	0	0	0	1	0	0	0	1	0	0	0	2	0	2	0	0	0	2	2	0	0	2	0	0	1	0					
R. linkii	2	0	1	1	0	0	0	0	1	0	0	0	2	0	2	0	0	1	2	2	0	0	0	0	0	2	0					
R. longifolium	2	0	0	0	1	1	0	0	1	0	0	0	2	0	2	0	0	1	2	2	0	0	0	1	0	1	0					
R. penicillatum	3	3	9	9	1	0	0	0	2,3	0	0	0	1	0	2	0	1	0	0	2	0	0	2	0		2	0					
R. pilosum	0	0	0	0	1	0	0	0	2,3	0	0	0	2	0	2	0	0	0	2	2	0	0	0	0	0	2	0					
R. racemosum	0	0	0	0	1	0	0	0	1	0	0	0	2	0	2	0	0	1	2	2	1	1,0	0	0	1	2	0					
R. semiannulare	2	0	0	1	0	0	0	0	1	0	0	0	1	0	2	0	0	1	2	2	0	0	0	0	0	2	0					
R. setaceum	0	0	0	0	1	0	0	0	1	0	0	0	1	0	2	0	0	0	2	2	0	0	0	0	1	2	0					
R. erianthum	0	0	0	0	1	0	0	0	1	0	0	0	2	0	2	0	0	0	2	2	0	0	0	0	0	2	0					
R. geniculatum	0	0	0	0	1	0	0	0	1	0		0	1	0	1	0	0	0	2	2	0	0		0	1	2	0					
R. pallide	0	0	0	1	1	0	0	0	2	0	0	1	2	0	2	0	0	0	2	2	0	0	0	0	0	0	1					
R. pauciflorum	1	0	0	1	1	0	0	0	2	0	0	0	1	0	2	0	1	0	0	2	2,3	0	2	1	1	1	0					
R. procerum	1	2	0	1	1	0	0	0	2	0	0	1	1	0	1	0	1	0	0	2	0	0	2	0	0	2	0					
R. richardsonii	0	0	0	1	0	0	0	0	2	0	0	0	2	0	2	0	0	1	2	2	0	0	0	0	0	2	0					
R. biannulare	0	0	0	0	0	0	0	0	1	0	0	0	1	1	0	1	0	0	1	2	2	0	0	0	0	1	2	0				
R. clavatum	0	2	0	0	1	0	0	0	0	0	0	0	2	1	2	1	1	0	0	2	0	0	0	0	0	2	0					
R. corinum	0	2	0	0	1	0	0	0	2	0	0	0,1	1	0	2	0	1	0	0	2	2,3	0	2	0	0	2	0					
R. gracile	0	0	0	0	1	0	0	0	2	0	0	0	2	0	2	0	1	0	0	2	0	0	0	0	0	2	0					
R. nigricans	1,2	0	0	1	1	0	0	0	0	0	0	0	1	0	2	0	1	0	0	2	0,1	0	0	0	0	0	0					
R. setifolium	0	0	0	0	1	0	0	0	0,2	0	0	1	1	0,1	2	0	1	0	0	2	1	0	2	1	0	2	0					
R. unarede	0	0	0	0	1	0	0	0	0	0	0	0	1	2	0	2	0	0	0	2	2	0	0	0	0	1	2	0				
R. dimidiatum	0	0	0	0	1	0	0	0	1	0	0	0	1	0	1,2	0	0	0	2	2	0	0	0	0	0	2	0					
R. vestitum	2	0	0	0	1	0	0	0	2	0	0	0	1	0	2	0	1	0	0	2	2,3	0	2	0	0	2	0					
Merxmuellera arundinacea	1	0	1	2	0	1,0	0	0	1	0	1	0	1	0	1	0	0	1	2	2	0	0	0	1	0	2	1					
M. davyi	1	0	0	0	1	0	0	1	2,3	0	1	0	1	0	1	0	0	0	2	2	1	1	0	1	0	1	1					
M. decora	1	0	0	1	1	0,1	0	0	2,3	1	1	0	1	0	2	0	1	0	2	0	0	0	2	1	0	2	1					
M. disticha	1	0	0	1	1	1	0	0	1	0	1	0	1	0	1	0	0	1	2	2	1	0	2	1	0	2	1					
M. drakensbergiensis	1	0	0	0	1	0	0	1	1	0	1	0	1	0	1	0	0	0	2	2	0	0	2	1	0	1	1					
M. dura	1	0	0	1	0	0	0	0	2,3	1	1	0	1	0	2	0	1	1	0	0	0	0	0	0	0	2	1					
M. guillermodes	3	3	9	9	1	0	0	1	2	1	0	1,2	1,9	0	1	0	1	0	0	2	1	0	2	0	0	1	0					
M. lupulina	1	0	1	1	1	0	0	0	1	1	1	1	1	0	1	0	0	0	2	2	0	0	0	0	0	2	1					
M. macowanii	1	0	1	1,2	1	0	0	1	2	1	0	0	1	0	1	0	0,1	1	0,2	2	2,3	1	0	1	0	1	1					
M. papposa	1	0	0	2	1	1	0	0	0	1	0	0	0	0	0	0	1	1	0	0	1	0	0	1	0	0,2	1					
M. rufa	0	0	0	0	1	0	0	0	0	1	1	0	1	0	1	0	0		2	2	0	0	0	1	0	1	1					
M. stereophylla	1	0	0	0	1	0	0	1	1	0	0	0	1	0	1	0	0	0	2	2	1	0	0	1	0	1	1					
M. stricta	0	0	0	0	1	0	0	1	2,3	1	0	0	1	0	2	0	1	0	0	2	1	0	2	0	0	2	0					
Chionochloa beddiei	1	0	0	1	1	0	0	0	2	0,1	0	0	1	0	1	0	1	0	0	2	0,2	0	2	1	0	1	1					
C. bromoides	1	0	0	1	1	1	0	0	2	0	0	0	1	0	1	1	1	0	0	2	2	0	2	1	0	2	1					
C. conspicua	1	0	0	0	1	0	0	0	2	0	0	0	1	0	1	0	2	1	0	0	2	0	2	1	0	2	1					
C. flavescens	1	0	0	0	1	0	0	0	2	0	0	0	1	0	1	1	2	1	0	0	2	0	2	1	0	2	1					
C. frigida	1	0	0	1	0	0	0	0	2	0	0	0	2	0	2	0	1	0	0	2	2	0	2	1	0	2	1					
C. pallens	1	0	0	0	1	0	0	0	2	0	0	0	1	0	1	1	1	0	0	0	2	0	2	1	0	2	1					
C. rigida	1	0	1	2	0	0	0	0	2	0	0	0	1	0	2	0	1	1	0	0	2	0	2	1	0	2,1	1					
C. rubra	1	0	0	0	1	1	0	0	0	0	0	0	1	0	1	0	2	1	0	0	2	0	2	1	0	2	1					
Curtaderia archboldii	2	0	0	0	1	0	0	0	1	0	1	0	1	0	1	0	1	1	0	2	1	0	0	1	0	1	0					
C. hapalotricha	1	0	0	1	0	0	0	0	1	0	0	0	1	0	1	0	0	0	2	2	0	0	0	1	0	2	0					
C. pungens	1	0	0	1	0	0	0	0	2	0	0	0	1	0	1	0	0	0	2	2	2	0	2	1	0	2,1	0					
C. araucana	1	0	0	1	0	0	0	2	0	1	0	0	1	0	2	0	1	0	0	0	0	0	2	1	0	1	1					
C. modesta	0	0	0	0	1	0	0	2	0	1	1	0	1	0	1	0	1	0	0	0	0	0	2	0	0	2	1					
C. pilosa	0	0	0	1	1	0	0	2	0	1	0	0	1	0	1	0	1	0	0	0	0	0	2	1	0	2,1	1					
Schismus arabicus	0	0	0	0	0	0	0	0	0	0		1	0	1	0	0	0	0	2	2	0	0	2	0	0	2	0					
S. barbatus	0	0	0	0	1	0	0	0	0	0	0	2	9	1	0	0	0	0	2	2	0	0	2	0	0	1	0					
S. inermis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	2	0	0	2	1	0	2	1					
S. scaberrimus	0	2	0	0	0	0	0	0	2	0	1	1	0	0	1	0	0	0	2	2	0	0	0	0	0	2	0					
Karroochloa curva	2	0	0	0	1	0	0	0	1	0	0	0	1	0	2	0	0	1	2	2	1	0	2	0	0	2	0					
K. purpurea	0	0	0	0	1	0		0	1	0		0	2	0	2	0	0	0	2	2	0	0	0	0	0	2	0					
K. tenella	0	0	0	0	1	0		0	1	0		0	2	0	2	0	0	0	2	2	0	0	0	0	0	2	0					
Monachather paradoxus	0	0	0	1	1	0	0	0	2	1	1	0	1	0	2	0	1	0	0	2	0	0	1	0	0	0	0					
Pyrrhanthera exigua	0	2	0	0	1	0	0	0	2	0	0	1	1	1	2	0	1	0	0	2	1,2	0	2	0	0	2	0					
Plinthanthesis paradoxa	2	0	0	0	1	0	0	0	1	0	0	0	1	0	1	0	0	1	2	2	0	0	2	0	0	2	0					
Erythranthera australis	2	0	0	1	1	0	0	0	1	0	0	1	1	1	2	0	0	0	2	2	2	0	2	0	0	2	0					
E. pumila	0	0	0	0	1	0	0	0			0							0	0	2	2	1	0	2	0	0	2	0				
Monomtachya oreoboloides	0	0	0	0	1	0	0	0	2	0	0	1	1	0	2	0	1	0	0	2	1	0	2	1	0	2,1	1					
Arundo donax	0	0	0	0	1	0	0	0	1	1	0	0	1	0	1	0	0	1	0,2	2	0	0	1	0	0	2	0					

TAXON	CHARACTER 28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49
Xanthonia spicata	1	0	0	1	0	0	0	0,1	0	1	1	0	1	.18	0	1	0	1	6.70±1.67(130)	.36±.05	0	0
D. serrulata	1	0	0	1	0	0	0	0	0	1	1	0	1	.15	0	1	0	1	6.97±0.96(20)	.40±.05	0	0
D. compressa	1	0	0	1	0	0	0	0	0	1	1	0	1	.31			0	1	6.84±2.24(39)	.31±.06	0	0
D. intermedia	1	0	0	1	0	0	0	0	0	1	1	0	1	.06	0	1	0	1	11.73±2.02(106)	.51±.06	0	0
D. parryi	1	0	0	1	0	0	0	0	0	1	1	0	1	.15	0	1	0	0	27.40±4.79(5)	.63±.03	0	
D. californica	1	0	0	1	0	0	0	0	0	1	1	0	1	.12	0	1	0	0	24.10±6.36(73)	.70±.06	0	0
D. unispicata	1	0	0	1	0	0	0	0	0	1	1	0	1	.06	0	1	0	0	25.67±9.59(11)	.75±.10	0	0
D. decumbens	1	0	0	1	0	0	0	1	1	1	1	0	1,2	.18	0	1			8.94±1.36(10)	.42±.05	0	0
D. alpina	1	0	0	1	0	0	0	0	0	1	1	0	2	.17	0	0,1	0	1	10.49±1.34(3)	.49±.06	0	0
D. secundiflora	1	0			0	0	0	0	0	1	1	0	1	.11	0	1	0	1	4.56±0.83(15)	.29±.06	0	
D. domingensis	1	1		0	0	0	0	0	0	1	1	0	1	.12	0	1					0	
D. ahrevei	1	0,1		0	0	0	0	0	0	1	1	0	1	.12	1	1					0	
D. chaseana	1	0		0	0	0	0	0	0	1	1	0	1	.33	0	1	0	1	5.75±0.78(5)	.31±.01	0	
D. cirrata	1	0			0	0	0	0	0	1	1	0	1	.06			0	1	5.81±0.48(7)	.29±.04	0	0
D. malacantha	1	0			0	0	0	0	0	1	1	0	1	.32	0	1					0	
D. montana	1	0			0	0	0	0	0	1	1	0	1	.10			0	1	4.32±0.66(5)	.29±.01	0	
D. dusenii	1	0			0	0	0	0	0	1	1	0	1		0	1					0	
D. montevidensis	1	0			0	0	0	0	0	1	1	0	1	.17			0	1	6.32±1.96(8)	.29±.02	0	0
D. cachemyriana	1	0	0	0	0	1	0	0	0	1	1	0	1	.18	1	0					0	
D. exilis	1	0	0	0	0	2	0	0	0	1	1	0	1	.10	1	0	1	0	3.65±0.72(5)	.37±.06	0	
Rytidosperma virescens	2	0	0	0	0	1	0	0	0	1	1	0	2	.14	1	0	1	1,0	3.90±0.61(10)	.39±.03	0	
R. glabrum	2	0	0	0	0	1	0	0	0	1	1	0	2	.10	1	0	1	0	2.73±0.76(5)	.29±.09	0	
R. violaceum	1	0		0	0	1	0	0	0	1	1	0	2	.33	1	0					0	
R. acerosum	1	0	0	0	0	1	0	0	0	1	1	0	1	.07	1	0	1	0			0	0
R. caespitosum	1	0	0	0	0	1	0	0	0	1	1	0	2	.09	1	0	1	0			0	0
R. laeve	1	0	0	0	0	1	0	0	0	1	1	0	2,3	.12	1	0	1	0	3.42±0.36(5)	.32±.02	0	0
R. linkii	1	0	0	0	0	1	0	0	0	1	1	0	1	.06	1	0	1	0			0	0
R. longifolium	1	0	0	0	0	1	0	0	0	1	1	0	2	.18	1	0	1	0			0	0
R. penicillatum	1	0	0	0	0	1	0	0	0	1	1	0	2	.18	1	0	1	0	3.37±0.79(14)	.29±.02	0	0
R. pilosum	1	0	0	0	0	1	0	0	0	1	1	0	2	.10	1	0	1	0	3.58±0.42(12)	.31±.02	0	0
R. racemosum	1	0	0	0	0	1	0	0	0	1	1	0	2	.08	1	0	1	0	3.26±0.28(10)	.28±.02	0	0
R. semiannulare	1	0	0	0	0	1	0	0	0	1	1	0	2	.10	1	0	1	0	2.66±0.25(8)	.27±.04	0	0
R. setaceum	1	0	0	0	0	1	0	0	0	1	1	0	1	.08	1	0	1	0	1.99±0.40(5)	.35±.01	0	0
R. erianthum	1	0	0	0	0	1	0	0	0	1	1	0	1	.05	1	0					0	0
R. geniculatum	1	0	0	0	0	1	0	0	0	1	1	0	2		1	0					0	0
R. pallida	2	0	0	0	0	1	0	0	0	1	1	0	2	.25	1	0	1	0	3.61±0.44(5)	.38±.02	0	0
R. pauciflorum	1	0	0	0	0	1	0	0	0	1	1	0	1	.10	1	0					0	
R. procerum	1	0	0	0	0	1	0	0	0	1	1	0	2								0	0
R. richardsonii	2	0	0	0	0	1	0	0	0	1	1	0	2		1	0					0	0
R. biannulare	1	0	0	0	0	1	0	0	0	1	1	0	2	.14	1	0					0	
R. clavatum	1	0	0	0	0	1	0	0	0	1	1	0	2		1	0	1	1	4.75 (1)	.38	0	
R. corinum	1	0		0	0	1	0	0	0	1	1	0	2	.20	0	0	1	0			0	
R. gracile	1	0		0	0	1	0	0	0	1	1	0	1,2	.39	1	0	1	0	2.47±0.44(5)	.24±.03	0	
R. nigricans	1	0		0	0	1	0	0	0	1	1	0	1	.29	1	0	1	0	3.18±0.50(4)	.31±.02	0	0
R. setifolium	1	0	0	0	0	1	0	0	0	1	1	0	1,2	.24	1	0	1	0			0	
R. unarede	1	0		0	0	1	0	0	0	1	1	0	2	.11	1	0	1	0	3.48±0.27(5)	.31±.02	0	
R. dimidiatum	1	0		0	0	1	0	0	0	1	1	0	2	.08							0	
R. vestitum	2	0	0	0	0	1	0	0	0	1	1	0	0		1	0					0	
Merxmuellera arundinacea	2	1		0	0	2	0	0	0	1	1	0	0	.31	1	1,0	1				0	0
M. davyi	2	0	0	0	0	1	1	0	0	1	1	0	0		1	1	1				0	
M. decora	2	2		0	0	2	0	0	0	1	1	0	1		1	1	1				0	
M. disticha	2	0	0	0		1	0	0	0	1	1	0	1		1	0	1	0			0	0
M. drakensbergensis	2	1		0	0	1	1	0	0	1	1	0	0		1	0	1				0	
M. dura	2	1		0	0	0	1	0	0	1	1	0	1	.11	1	0	1				0	
M. guillarmodae	1	0	0	0	0	0	0	0	0	1	1	0	1	.10	1	0	1				0	
M. lupulina	2	2		0	0	2	0	0	0	1	1	0	1	.17	1	1	1	0			0	
M. macowanii	2	1		0	0	1	1	0	0	1	1	0	0	.13	1	1,0	1				0	0
M. papposa	2			0	0	3	1	0	0	1	1	0	0	.17	1	1	1				0	
M. rufa	2	2		0	0	2	0	0	0	1	1	0	1	.22	1	0	1				0	
M. stereophylla	2	1		0	0	1	1	0	0	1	1	0	0		1	1	1				0	
M. stricta	2	0	0	0	0	1	1	0	0	1	1	0	1,2	.16	1	0	1				0	
Chionochloa beddiei	2	1	0	0	0	0	0	0	0	1	1	0	0		1	0	0				0	
C. bromoides	2	1		0	0	0	1	0	0	1	1	0	0	.10	1	1	0				0	
C. conspicua	2	1		0	0	0	0,1	0	0	1	1	0	0,1	.08	1	1	0				0	1
C. flavescens	2	1		0	0	0	0,1	0	0	1	1	0	0	.12	1	0	0				0	1
C. frigida	2	1		0	0	0	1	0	0	1	1	0	0,1	.16	1	0	0				0	1
C. pallens	2	0		0	0	0	1	0	0	1	1	0	0,1	.08	1	1	0				0	
C. rigida	2	1		0	0	0	0,1	0	0	1	1	0	0,1	.14	0	0	0				0	1
C. rubra	2	1		0	0	0	0,1	0	0	1	1	0	0	.27	1	1	0				0	1
Cortaderia archboldii	1	1	0	0	0	0	0	0	0	1	1	0	1	.12	1	1	0				1	
C. hapalotricha	1	1		0	0	0	0	0	0	1	1	0	0	.14	0	0	0	0			1	
C. pungens	1	1		0	0	0	0	0	0	1	1	0	0	.16	1	0	0				1	
C. araucana	1	1	0	0	0	0	1	1	0	1	1	0	0	.11	1	1	0				1	
C. modesta	1	1		0	0	0	1	1	1	1	1	0	0	.11	0	1	0				1	
C. pilosa	2	1	0	0	0	0	1	1	0	1	1	0	0	.04	0	1	0				1	0
[illegible]	1	0	1	0	0	0	0	0	1	1	1	0	1	.10	0	1	1				0	0

D. [illegible]	1	0			0	0	0	0	0	1	1	0	1	.12	0	1													0	
D. montana	1	0			0	0	0	0	0	1	1	0	1	.10			0	1	6.33±0.66(5)		.69±.01	0								
D. tuberis	1	0			0	0	0	0	0	1	1	0	1		0	1													0	
D. [illegible]ensis	1	0			0	0	0	0	0	1	1	0	1	.17			0	1	6.33±1.96(8)		.79±.02	0	0							
D. [illegible]hoeyiana	1	0	0	0	0	1	0	0	0	1	1	0	1	.18	1	0													0	
O. setifolia	1	0	0	0	0	2	0	0	0	1	1	0	1	.10	1	0	1	0	3.65±0.72(5)		.37±.06	0								
Rytidosperma virescens	2	0	0	0	0	1	0	0	0	1	1	0	2	.16	1	0	1	1,0	3.90±0.61(10)		.39±.03	0								
R. glabrum	2	0	0	0	0	1	0	0	0	1	1	0	2	.10	1	0	1	0	2.73±0.76(5)		.49±.09	0								
R. violaceum	1	0		0	0	1	0	0	0	1	1	0	2	.33	1	0						0								
R. acernum	1	0	0	0	0	1	0	0	0	1	1	0	1	.07	1	0	1	0				0	0							
R. caespitosum	1	0	0	0	0	1	0	0	0	1	1	0	2	.09	1	0	1	0				0	0							
R. laeve	1	0	0	0	0	1	0	0	0	1	1	0	2,3	.12	1	0	1	0	3.62±0.36(5)		.33±.02	0	0							
R. linkii	1	0	0	0	0	1	0	0	0	1	1	0	1	.06	1	0	1	0				0	0							
R. lunglifolium	1	0	0	0	0	1	0	0	0	1	1	0	2	.18	1	0	1	0				0	0							
R. penicillatum	1	0	0	0	0	1	0	0	0	1	1	0	2	.18	1	0	1	0	3.37±0.79(14)		.49±.02	0	0							
R. pilosum	1	0	0	0	0	1	0	0	0	1	1	0	2	.10	1	0	1	0	3.58±0.42(12)		.31±.02	0	0							
R. racemosum	1	0	0	0	0	1	0	0	0	1	1	0	2	.08	1	0	1	0	3.26±0.28(10)		.28±.02	0	0							
R. semiannulare	1	0	0	0	0	1	0	0	0	1	1	0	2	.10	1	0	1	0	2.64±0.25(8)		.17±.04	0	0							
R. setaceum	1	0	0	0	0	1	0	0	0	1	1	0	1	.08	1	0	1	0	1.99±0.40(5)		.35±.01	0	0							
R. strianthum	2	0	0	0	0	2	0	0	0	2	2	0	3	.05	2	0						0	0							
R. geniculatum	1	0	0	0	0	1	0	0	0	1	1	0	2		1	0						0	0							
R. pallide	2	0	0	0	0	1	0	0	0	1	1	0	2	.25	1	0	1	0	3.61±0.44(5)		.38±.02	0	0							
R. pauciflorum	2	0	0	0	0	1	0	0	0	1	1	0	1	.10	1	0						0								
R. procerum	1	0	0	0	0	1	0	0	0	1	1	0	2									0	0							
R. richardsonii	1	0	0	0	0	1	0	0	0	1	1	0	2		1	0						0	0							
R. biannulare	2	0	0	0	0	1	0	0	0	1	1	0	2	.14	1	0						0								
R. clavatum	1	0	0	0	0	1	0	0	0	1	1	0	2		1	0	1	1	4.75 (1)		.38	0								
R. corinum	1	0		0	0	1	0	0	0	1	1	0	2	.20	0	0	1	0				0								
R. gracile	2	0		0	0	1	0	0	0	1	1	0	1,2	.39	1	0	1	0	2.47±0.44(5)		.24±.03	0								
R. nigricans	1	0		0	0	1	0	0	0	1	1	0	1	.29	1	0	1	0	3.18±0.50(4)		.31±.02	0	0							
R. setifolium	1	0	0	0	0	1	0	0	0	1	1	0	1,2	.24	1	0	1	0				0								
R. unarede	2	0		0	0	1	0	0	0	1	1	0	2	.11	1	0	1	0	3.48±0.27(5)		.31±.02	0								
R. dimidiatum	1	0		0	0	1	0	0	0	1	1	0	2	.08								0								
R. vestitum	2	0	0	0	0	1	0	0	0	1	1	0	0		1	0						0								
Heramuellera arundinacea	2	1		0	0	2	0	0	0	1	1	0	0	.31	1	1,0	1					0	0							
M. davyi	2	0	0	0	0	1	1	0	0	1	1	0	0		1	1	1					0								
M. decora	2	2		0	0	2	0	0	0	1	1	0	1		1	1	1					0								
M. disticha	2	0	0	0		1	0	0	0	1	1	0	1		1	0	1	0				0	0							
M. drakensbergiensis	2	1		0	0	1	1	0	0	1	1	0	0		1	0	1					0								
M. dura	2	1		0	0	0	1	0	0	1	1	0	1	.11	1	0	1					0								
M. guillarmodae	1	0	0	0	0	0	0	0	0	1	1	0	1	.10	1	0	1					0								
M. lupulina	2	2		0	0	2	0	0	0	1	1	0	1	.17	1	1	1	0				0								
M. macowanii	2	1		0	0	1	1	0	0	1	1	0	0	.13	1	1,0	1					0	0							
M. papposa	2			0	0	3	1	0	0	1	1	0	0	.17	1	1	1					0								
M. rufa	2	2		0	0	2	0	0	0	1	1	0	1	.22	1	0	1					0								
M. stereophylla	2	1		0	0	1	1	0	0	1	1	0	0		1	1	1					0								
M. stricta	2	0	0	0	0	1	1	0	0	1	1	0	1,2	.16	1	0	1					0								
Chionochloa beddiei	2	1	0	0	0	0	0	0	0	2	2	0	0		1	0	0					0								
C. bromoides	2	1		0	0	0	1	0	0	1	1	0	0	.10	1	1	0					0								
C. conspicua	2	1		0	0	0	0,1	0	0	1	1	0	0,1	.08	1	1	0					0	1							
C. flavescens	2	1		0	0	0	0,1	0	0	1	1	0	0	.12	1	0	0					0	1							
C. frigida	2	1		0	0	0	1	0	0	1	1	0	0,1	.16	1	0	0					0	1							
C. pallens	2	0		0	0	0	1	0	0	1	1	0	0,1	.08	1	1	0					0								
C. rigida	2	1		0	0	0	0,1	0	0	1	1	0	0,1	.14	0	0	0					0	1							
C. rubra	2	1		0	0	0	0,1	0	0	1	1	0	0	.27	1	1	0					0	1							
Cortaderia archboldii	1	1	0	0	0	0	0	0	0	1	1	0	1	.12	1	1	0					1								
C. hapalotricha	2	2		0	0	0	0	0	0	2	2	0	0	.16	0	0	0	0				1								
C. pungens	1	1		0	0	0	0	0	0	1	1	0	0	.16	1	0	0					1								
C. araucana	1	1	0	0	0	0	1	1	0	1	1	0	0	.11	1	1	0					1								
C. modesta	1	1		0	0	0	1	1	1	1	1	0	0	.11	0	1	0					1								
C. pilosa	2	1	0	0	0	0	1	1	0	1	1	0	0	.04	0	1	0					1	0							
Schismus arabicus	1	0	1	0	0	0	0	0	0	1	1	1	0	1	.30	0	1	1				0	0							
S. barbatus	1	0	1	0	0	0	0	0	0	1	1	1	0	1	.21	1	0	1	1			0	0							
S. inermis	2	0	1	0	0	0	0	1	1	1	1	1	0	1	.33	1	0	1	0			0								
S. scaberrimus	1	0	1	0	0	0	0,9	1,9	1,9	1	1	0	1	.23	1	0	1					0								
Karroochloa curva	1	0	0	0	0	0	0	0	0	1	1	0	1	.20	0,1	0	1	1				0	0							
K. purpurea	1	0	0	0	0	1	0	0	0	1	1	0	1	.14	1	0	1	0				0								
K. tenella	1	0	1	0	0	1	0	0	0	1	1	0	1	.25	0	0	1	0				0	0							
Monachather paradoxus	1	2	0	0	0	1	0	0	0	1	1	0	3	.38	0	1	1					0	0							
Pycranthera exigua	1	0		0		0	1	1	1	0	0	0	1		1	0	1					0								
Plinthanthesis paradoxa	1	0		0	0	0	0	1	1	1	1	0	1		0	1	0					0								
Erythranthera australis	1	0	0	0	0	4	0	1	1	1	0	0	1	.42	0	1	1					0								
E. pumila	2	0	0	0		2	0	1	1	1	1	0	1	.32	0	0	1					0								
Monostachya oreuboloides	2	0	0	0	1	1	9	9	0	1	1	0	0	.19	0,1	0,1						0	2							
Arundo donax	1	0	2	0	0	0	1	1	1	1	1	0	1		0	1	0					0	0							

FIGURE CAPTIONS

FIG. 1. Wagner parsimony analysis of Danthonia s. lat. In this and following figs., character state changes are indicated by bars. R = reversal, C = convergence or parallelism. See text for explanation of F-ratio, C-index, and character consistencies.

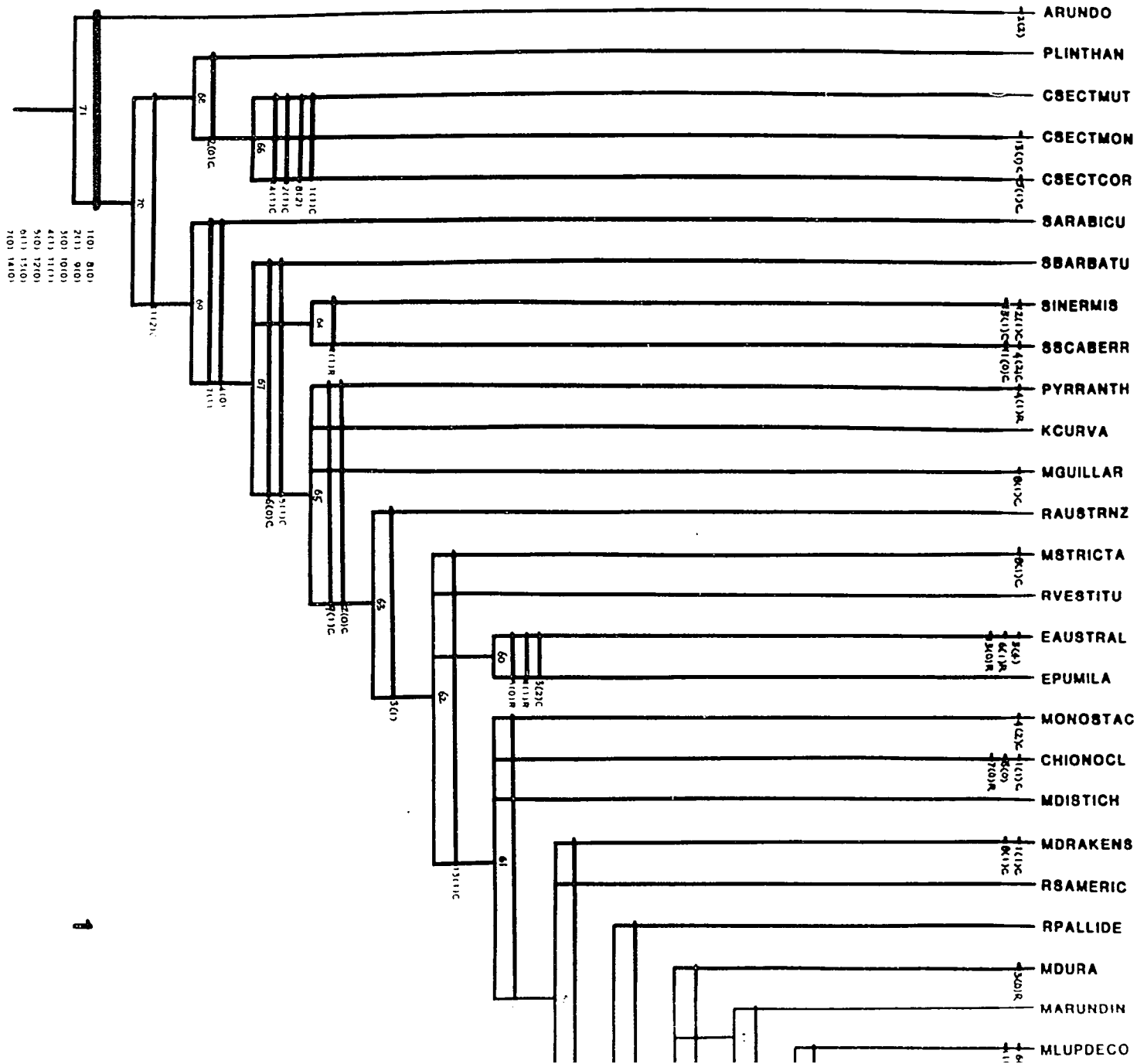
FIG. 2. Wagner parsimony analysis of Danthonia s. lat., using successive weighting of characters. R = reversal, C = convergence or parallelism.

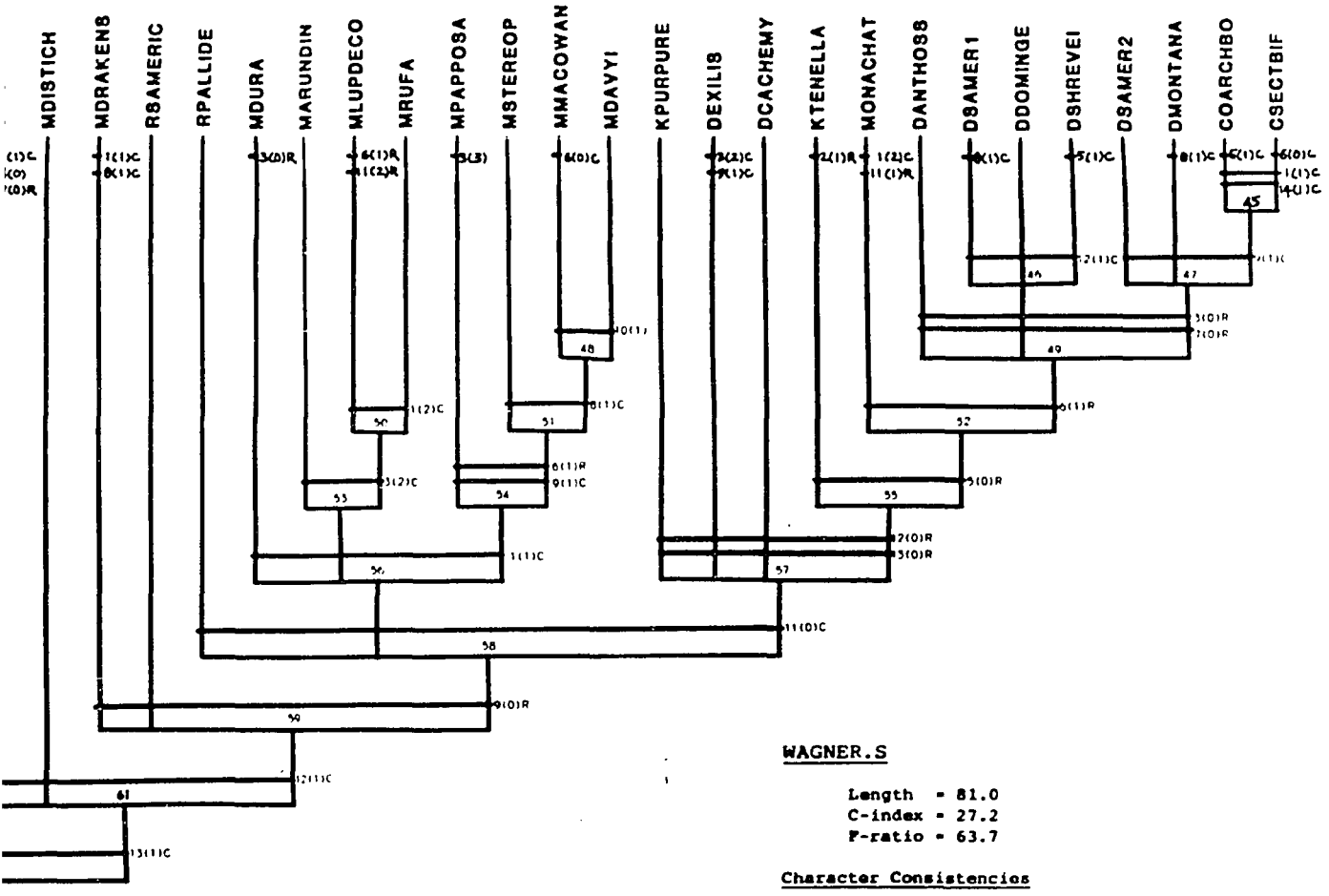
FIG. 3. Wagner parsimony analysis of Danthonia s. lat., with hypothetical ancestor used as outgroup. R = reversal, C = convergence or parallelism.

FIG. 4. Character compatibility analysis of Danthonia s. lat. See text for explanation.

Fig. 5. UPGMA cluster analysis of Danthonia s. lat.

FIG. 6. Dendrogram from fig. 5 with ancestral nodes optimized and character state changes plotted. See text for explanation.


ARUNDO
PLINTHAN
CSECTMUT
CSECTMON
CSECTCOR
SARABICU
SBARBATU
SINERMIS
SSCABERR
PYRRANTH
KCURVA
MGUILLAR
RAUSTRNZ
MSTRICTA
RVESTITU
EAUSTRAL
EPUMILA
MONOSTAC
CHIONOCL
MDISTICH
MDRAKENS
RSAMERIC
RPALLIDE
MDURA
MARUNDIN
MLUPDECO

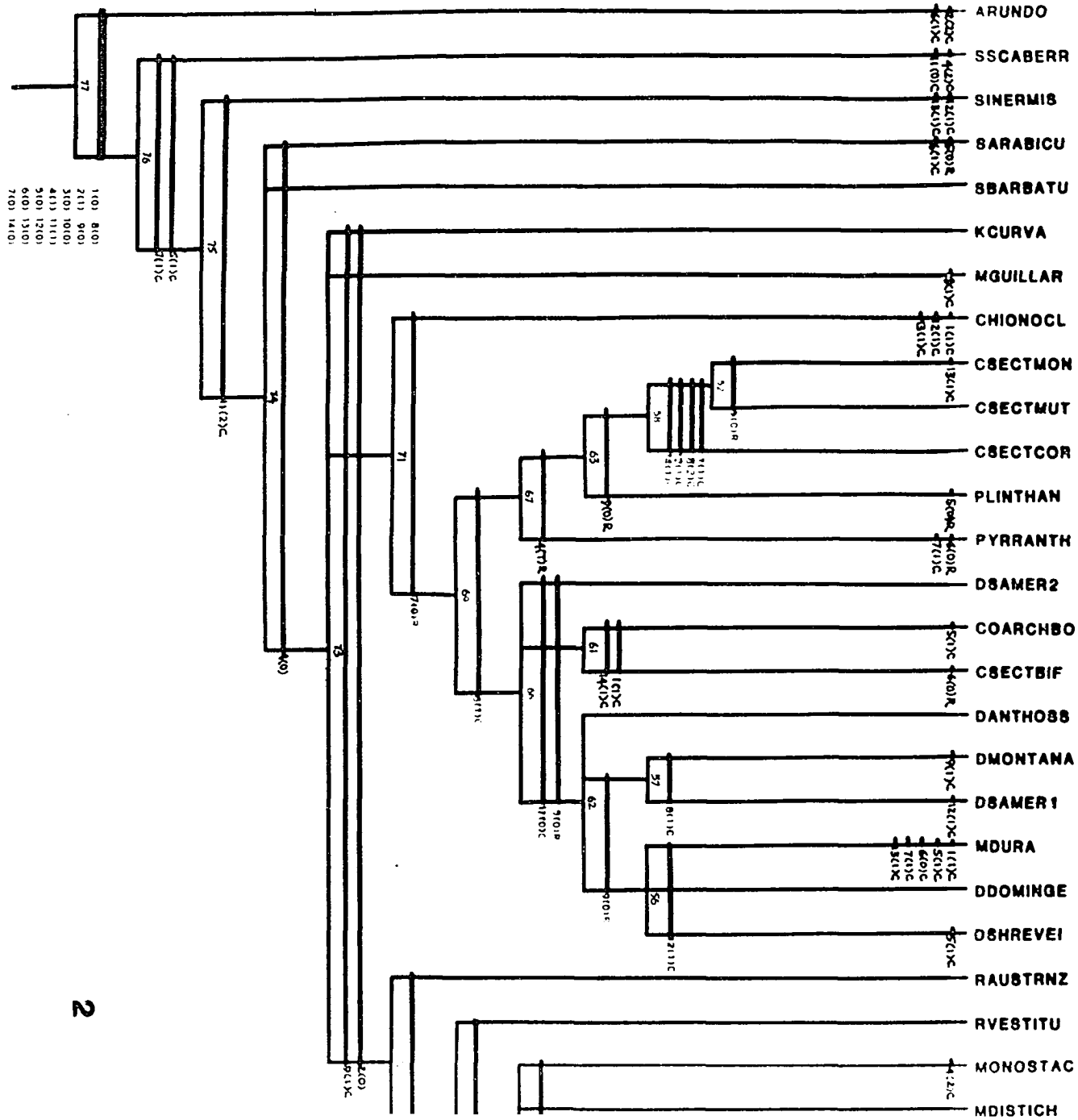


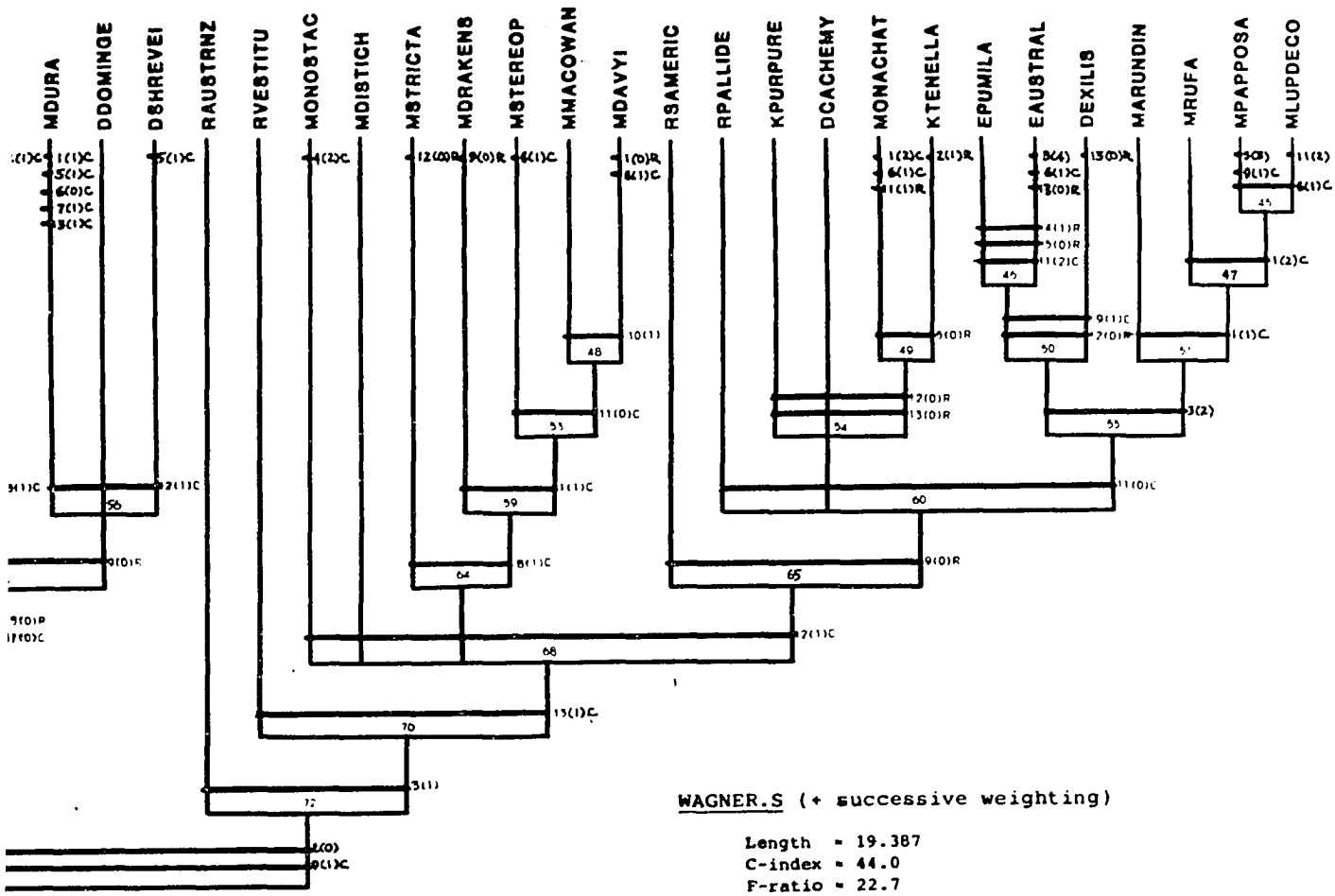
WAGNER.S

Length = 81.0
C-index = 27.2
F-ratio = 63.7

Character Consistencies

1	22.2	8	25.0
2	50.0	9	20.0
3	36.4	10	100.0
4	28.6	11	25.0
5	16.7	12	20.0
6	14.3	13	20.0
7	33.3	14	50.0


ARUNDO
SSCABERR
SINERMIS
SARABICU
SBARBATU
KCURVA
MGUILLAR
CHIONOCL
CSECTMON
CSECTMUT
CSECTCOR
PLINTHAN
PYRRANTH
DSAMER2
COARCHBO
CSECTBIF
DANTHOSS
DMONTANA
DSAMER1
MDURA
DDOMINGE
DSHREVEI
RAUSTRNZ
RVESTITU
MONOSTAC
MDISTICH

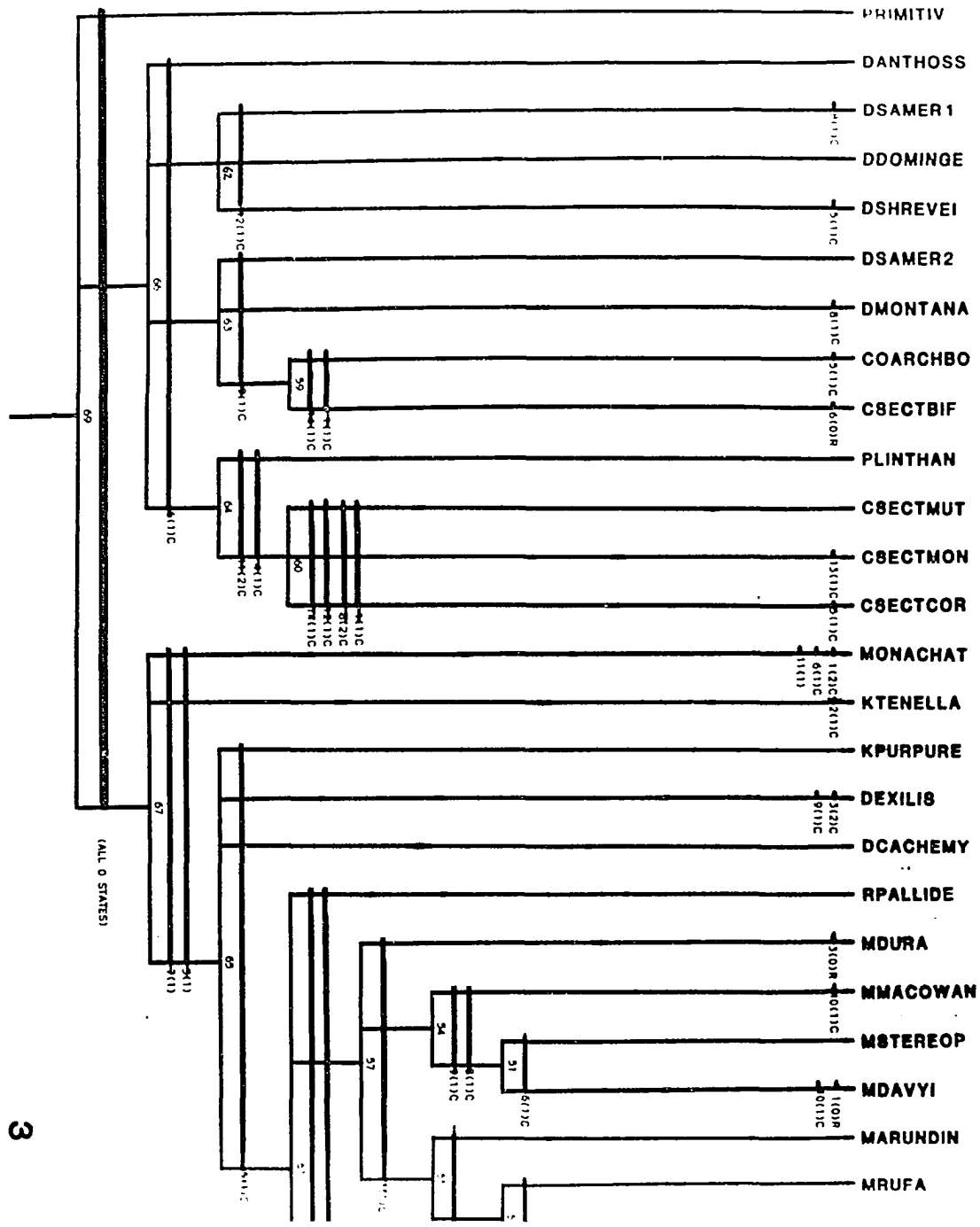


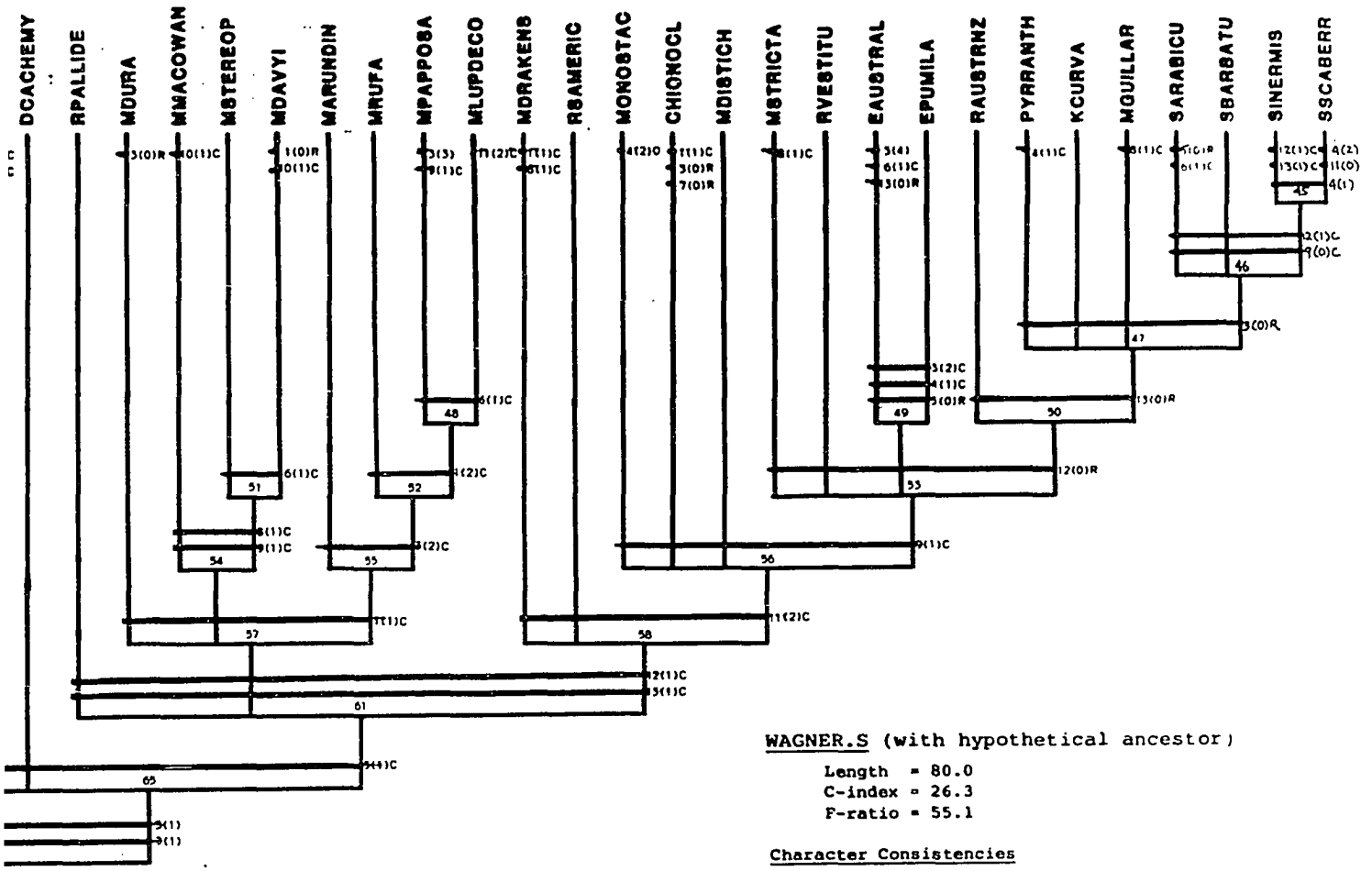
WAGNER.S (+ successive weighting)

Length = 19.387
C-index = 44.0
F-ratio = 22.7

Character Consistencies

1	20.0	8	40.0
2	66.7	9	12.5
3	80.0	10	100.0
4	33.3	11	15.4
5	10.0	12	11.1
6	9.1	13	12.5
7	25.0	14	50.0


PRIMITIV
DANTHOSS
DSAMER1
DDOMINGE
DSHREVEI
DSAMER2
DMONTANA
COARCHBO
CSECTBIF
PLINTHAN
CSECTMUT
CSECTMON
CSECTCOR
MONACHAT
KTENELLA
KPURPURE
DEXILIS
DCACHEMY
RPALLIDE
MDURA
MMACOWAN
MSTEREOP
MDAVYI
MARUNDIN
MRUFA
(ALL 0 STATES)



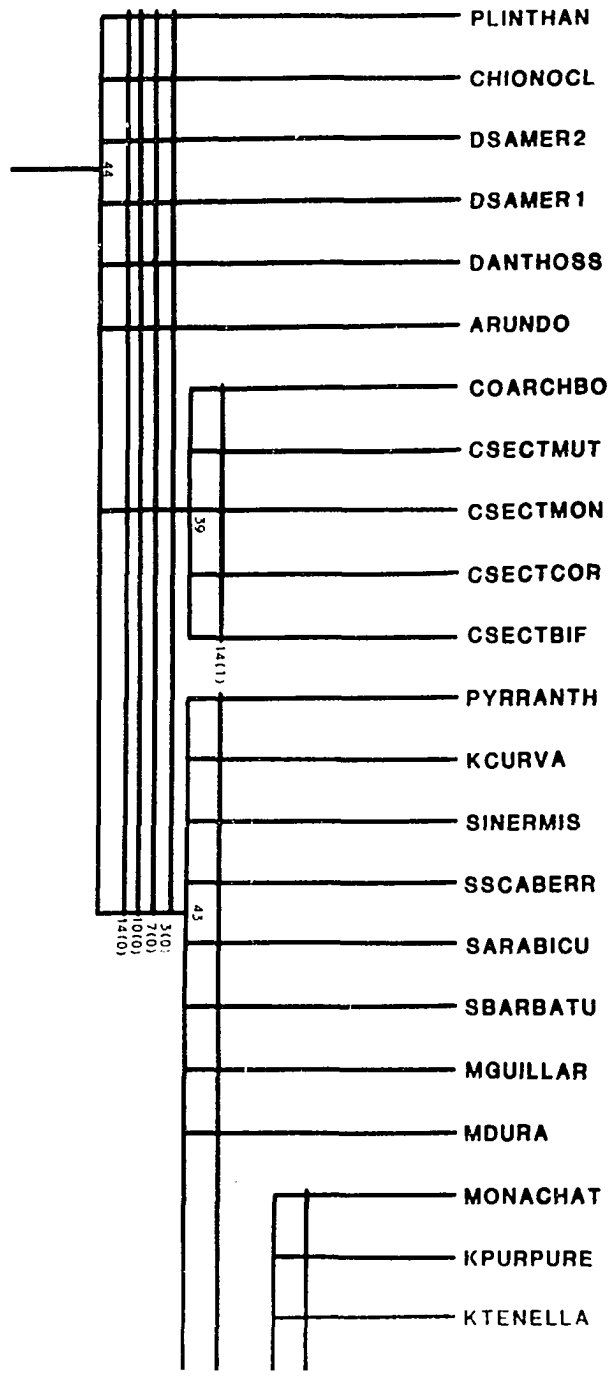
(ALL 0 STATES)

WAGNER.S (with hypothetical ancestor)

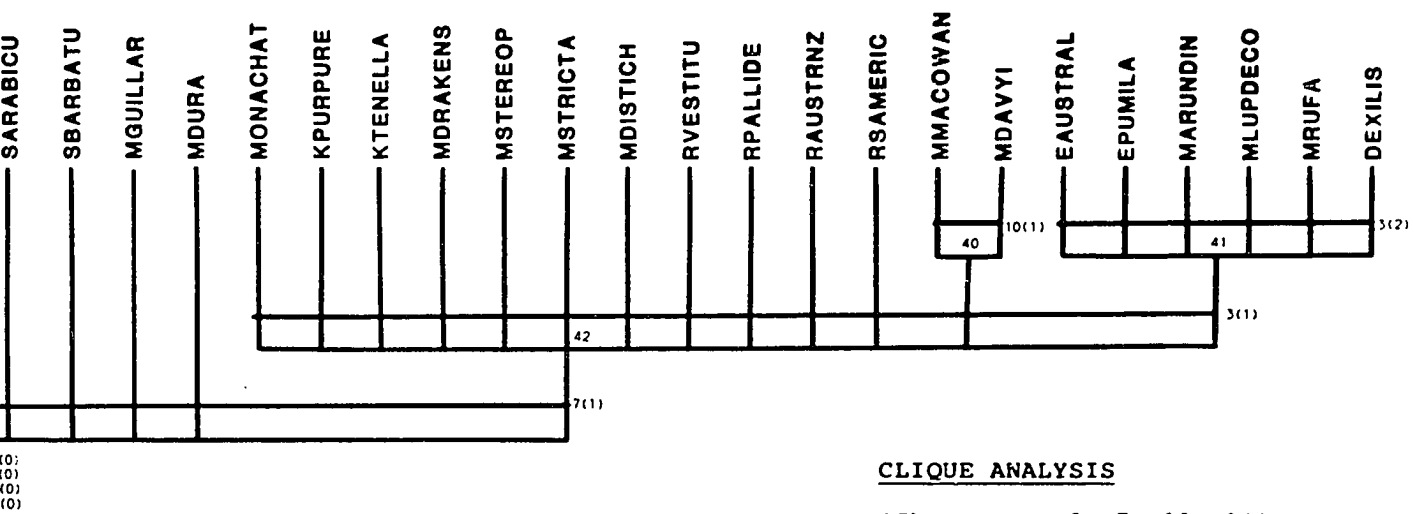
Length = 80.0
C-index = 26.3
F-ratio = 55.1

Character Consistencies

1	22.2	8	25.0
2	50.0	9	16.7
3	40.0	10	50.0
4	28.6	11	22.2
5	16.7	12	20.0
6	14.3	13	20.0
7	50.0	14	50.0


PLINTHAN
CHIONOCL
DSAMER2
DSAMER1
DANTHOSS
ARUNDO
COARCHBO
CSECTMUT
CSECTMON
CSECTCOR
CSECTBIF
PYRRANTH
KCURVA
SINERMIS
SSCABERR
SARABICU
SBARBATU
MGUILLAR
MDURA
MONACHAT
KPURPURE
KTENELLA
44
39
14(1)
43
5(0)
7(0)
10(0)
14(0)

4



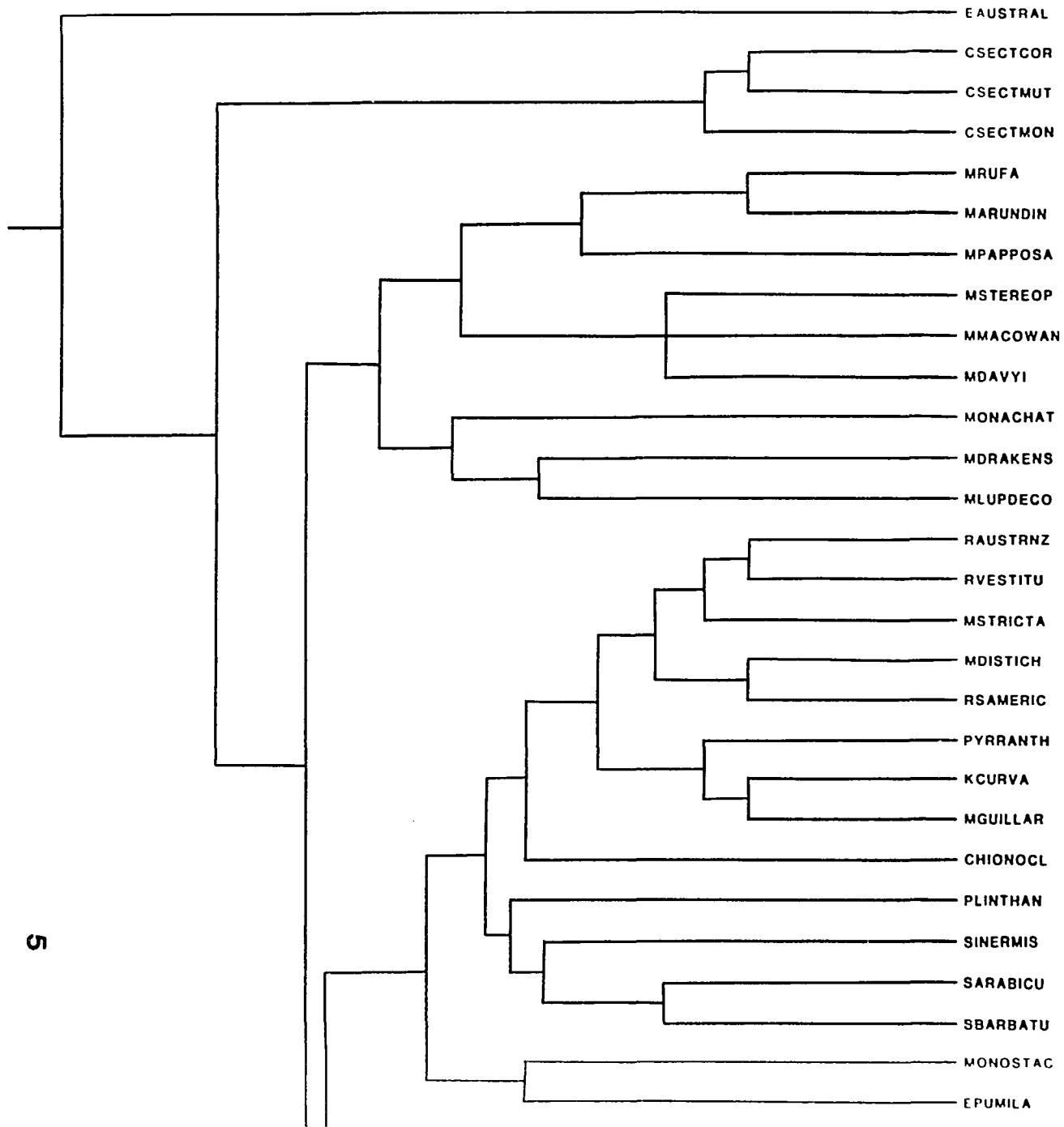
CLIQUE ANALYSIS

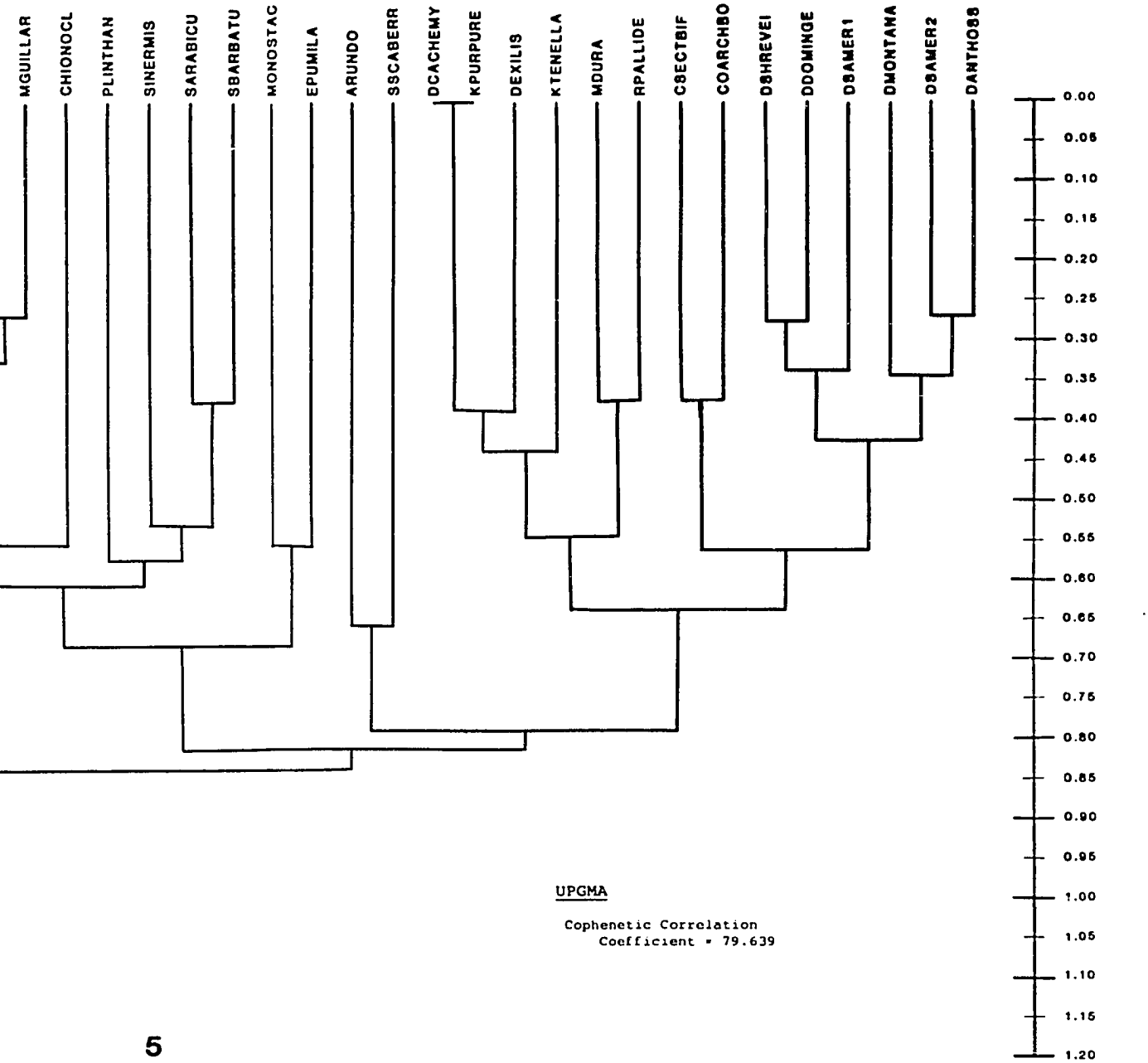
(Characters 3, 7, 10, 14)

Length = 143.0
C-index = 15.4
F-ratio = 47.2

Character Consistencies

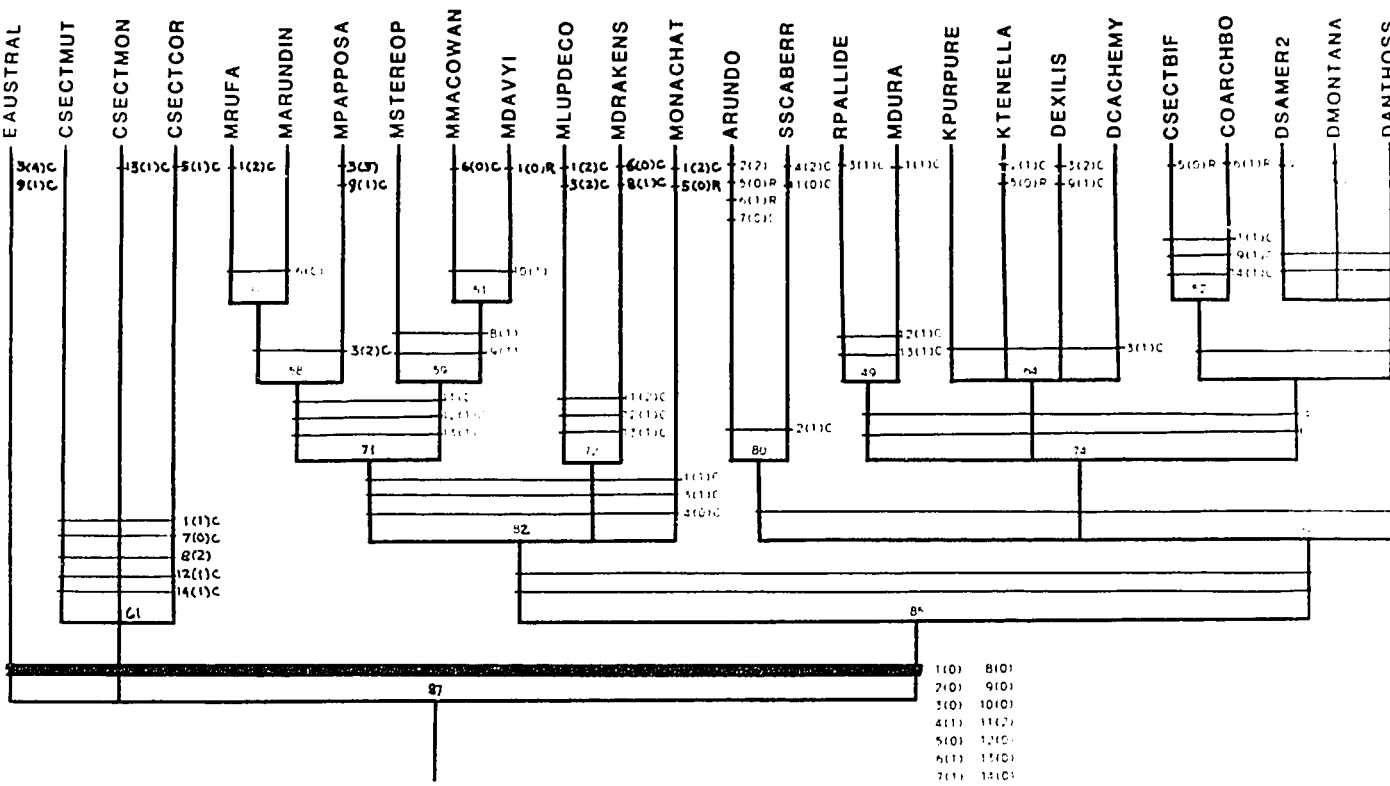
1	15.4	8	16.7
2	28.6	9	6.3
3	100.0	10	100.0
4	18.2	11	6.3
5	11.1	12	6.3
6	11.1	13	9.1
7	100.0	14	100.0

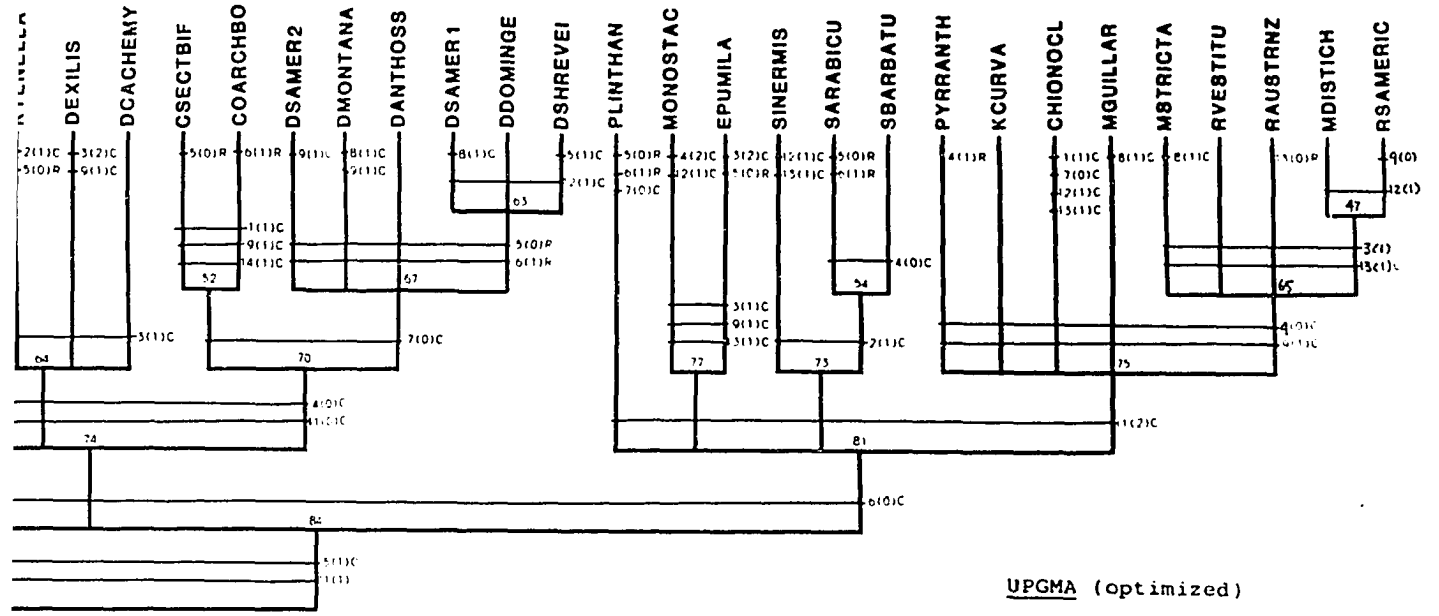

EAUSTRAL
CSECTCOR
CSECTMUT
CSECTMON
MRUFA
MARUNDIN
MPAPPOSA
MSTEREOP
MMACOWAN
MDAVYI
MONACHAT
MDRAKENS
MLUPDECO
RAUSTRNZ
RVESTITU
MSTRICTA
MDISTICH
RSAMERIC
PYRRANTH
KCURVA
MGUILLAR
CHIONOCL
PLINTHAN
SINERMIS
SARABICU
SBARBATU
MONOSTAC
EPUMILA



UPGMA

Cophenetic Correlation
Coefficient = 79.639


EAUSTRAL
CSECTMUT
CSECTMON
CSECTCOR
MRUFA
MARUNDIN
MPAPPOSA
MSTEREOP
MMACOWAN
MDAVYI
MLUPDECO
MDRAKENS
MONACHAT
ARUNDO
SSCABERR
RPALLIDE
MDURA
KPURPURE
KTENELLA
DEXILIS
DCACHEMY
CSECTBIF
COARCHBO
DSAMER2
DMONTANA



UPGMA (optimized)

Length = 102.0
C-index = 20.6
F-ratio = 56.6

Character Consistencies

1	22.2	8	25.0
2	50.0	9	10.0
3	28.6	10	100.0
4	28.6	11	33.3
5	9.1	12	11.1
6	11.1	13	11.1
7	20.0	14	50.0

STUDIES IN THE DANTHONIEAE (POACEAE)

PART II

COMPARATIVE ANATOMICAL STUDIES IN *DANTHONIA* S. LAT. (DANTHONIEAE: POACEAE)

COMPARATIVE ANATOMICAL STUDIES IN *DANTHONIA* S. LAT. (DANTHONIEAE: POACEAE)

Kay L. Wright

INTRODUCTION

Danthonia s. lat. comprises well over 100 species, distributed throughout both hemispheres (Wright, 1984; Conert, 1971). De Wet (1954, 1956, 1960) demonstrated that *Danthonia* is heterogeneous in many of the features that are now used to distinguish subfamilies of grasses, such as the arrangement and shape of the silica bodies and the structure of the mesophyll. He further suggested that the genus should be subdivided. Since then, more than a dozen segregate genera have been proposed (summary in Wright, 1984). Most of these segregates have been maintained in the Danthonieae. However, the patterns of generic relationships within the group are still unclear. I examined the leaf anatomy and lodicule morphology of representative species of all available segregate genera, in the hope of elucidating the complex evolutionary relationships of these taxa (Cronquist, 1978; Metcalfe and Chalk, 1979).

MATERIALS AND METHODS

Leaf anatomy and lodicule morphology were examined for representative species of 15 genera (Table 1; Wright, 1984: Appendix A). In addition to taxa comprising Danthonia s. lat., species of Cortaderia and Schismus were investigated for comparative purposes. Although never included within Danthonia, a close relationships between these two genera and Danthonia has been suggested by several authors (Conert, 1961; Clifford and Watson, 1977; Wright, 1984). Two other genera segregated from Danthonia were not investigated here: (1) No specimens of the tropical African genus Alloeochaete were available for study. Its internal leaf anatomy is described by De Wet (1956) as panicoid (i. e., with radiate mesophyll). (2) Embryo and lodicule anatomy of Metcalfia mexicana, the sole species of this genus, was investigated by Tateoka (1964), who showed conclusively that it is festucoid, probably a primitive member of the Aveneae.

From herbarium specimens to be prepared for anatomical investigation I selected leaf material from a section approximately midway along the blade of mature leaves. Flag leaves on flowering culms were not used. The leaf material was first soaked in a 5% solution of Contrad 70 for approximately 24 hr, thoroughly rinsed in water, placed in a weak (ca. 5%) solution of acetic acid in 50% ethanol for 24-

48 hr, and then stored in 50% ethanol until examined (Schmid and Turner, 1977).

Preparations of the lower epidermis were made by placing the soaked leaf material on a microscope slide and scraping away the upper epidermis and mesophyll with a razor blade until only the lower epidermis itself remained (Metcalfe, 1960). The preparation was then mounted in Hoyer's solution (Johansen, 1940) so that the outer surface of the epidermis faced the cover slip. Hoyer's solution has a sufficiently high refractive index to reveal silica bodies, and has the additional advantage of being water-soluble, yet permanent.

Leaf sections were cut freehand with a razor blade, stained with safranin and counterstained with fast green using Northen's variation of Foster's method (Johansen, 1940), dehydrated through an alcohol series to xylene, and mounted in Coverbond. Lodicules were dissected from the florets in a drop of alcohol and mounted in Hoyer's solution. Slides are deposited at OKL.

OBSERVATIONS

Terminology used in descriptions of leaf anatomical features follows Ellis (1976, 1979) whenever possible. One major departure, however, is in the description of the shape of the adaxial and abaxial sclerenchyma. Ellis described the sclerenchyma and bundle sheaths separately, whereas I

found that in most of the taxa examined these two types of cells intergrade, making any distinction between the two structures arbitrary and frequently misleading.

Stomatal subsidiary cell shape was recorded for most taxa. All shapes were within the triangular to dome-shaped category; however, the range of shapes within a species and even within a given specimen was great. Furthermore, I was unable to detect meaningful differences between taxa. Another feature examined was the shape and size of the microhairs on the leaf surface. Again, the range of variation within and between species was quite large. In addition, the apical cells of microhairs are only rarely preserved intact in herbarium material, and thus uniform comparisons cannot be made. For these reasons, information on subsidiary cell and microhair shape is not included in the taxon descriptions.

Centropodia

Leaf Cross-section.--Adaxial furrows generally wide and open; adaxial ribs present, rounded, similar in shape over all vascular bundles (VBs). Midrib absent. VBs round to elliptical. Outer bundle sheath (OBS) complete, cells much larger than parenchyma cells, conspicuous. Inner bundle sheath (IBS) cell walls not thickened, or very slightly and evenly thickened. Metaxylem vessels much smaller than OBS cells. Phloem not divided. Adaxial and abaxial

sclerenchyma associated with all VBs, as strands (abaxially T-shaped in C. glauca). Bundle sheath (BS) extensions and colorless cells absent. Mesophyll poorly preserved in available material, but reported by DeWet (1954, 1956) to be radiate. Upper epidermal cells unspecialized; hypodermic prickle hairs (Fig. 1) absent. Bulliform cells in fan-shaped groups with the center cell enlarged (Fig. 2).

Leaf Abaxial Epidermis.--Microhairs apparently absent. Intercostal long cell side walls difficult to observe because they lie in deep grooves overarched by prickles, but apparently parallel, with interlocking undulations. Costal short cells mainly paired, with rounded or occasionally cross-shaped silica bodies.

Lodicule Morphology.--Lodicule preparations unavailable.

Chionochloa

Leaf Cross-section.--Adaxial furrows narrow clefts; adaxial ribs present and similar over all VBs, rounded or flat-topped (massive [Fig. 3] in C. frigida). Midrib present (absent in C. frigida and C. rigida). Primary VBs round to elliptical (egg-shaped in C. bromoides and C. rubra); secondary VBs round to elliptical. OBS incomplete below (complete in C. rubra), cells equal to or smaller than parenchyma cells, generally inconspicuous. IBS unevenly thickened. Metaxylem vessels smaller or larger than OBS

cells. Phloem not divided. Adaxial sclerenchyma present over all VBs, T- or anchor-shaped (girder in C. beddiei, girder narrower toward the bundle in C. frigida); abaxial sclerenchyma present under all VBs, T- to anchor-shaped or forming girders. BS extensions present adaxially, present or absent abaxially. Colorless cells present as BS extensions only, or a layer of colorless, usually silica-filled cells present just above the lower epidermis. Mesophyll not radiate or indistinctly radiate. Upper epidermis composed of broadly papillate cells (Fig. 4); hypodermic prickle hairs absent. Bulliform cells absent.

A number of species show a more or less complete abaxial band of subepidermal sclerenchyma. Zotov (1963) used this as a key character; however, the degree of completeness appears to vary within species.

Abaxial Leaf Epidermis.--Microhairs apparently absent. Intercostal long cell side walls parallel; undulations U-shaped (W-shaped [Fig. 5] in C. beddiei and sometimes in C. rigida). Intercostal short cells paired, with rounded silica bodies.

Zotov (1963) reported dumbbell-shaped silica bodies in C. bromoides. In coontrast, I found only elongate, rounded silica bodies.

Lodicule Morphology.--Lodicules cuneate to diamond-shaped or apically lingulate (Fig. 6), hairy (glabrous in C. rigida

and occasionally in C. rubra). Microhairs present in C. beddiei, C. flavescens, C. frigida, and C. rigida, 2-4 celled; absent in C. bromoides, C. conspicua, and C. pallens.

Danthonia s. str. (including Sieglingia)

Leaf Cross-section.--Adaxial furrows broad and open or steep-sided; adaxial ribs present, rounded or flat-topped, generally similar in shape over all VBs. Midrib present or absent. Primary and secondary VBs round or occasionally egg-shaped. OBS generally incomplete, sometimes complete above, cells equal to or smaller than parenchyma cells, inconspicuous. IBS unevenly thickened. Metaxylem vessels smaller or larger than outer bundle sheath cells. Phloem not divided (divided into two even groups [Fig. 1] in D. cirrata, D. malacantha, and D. montana). Adaxial sclerenchyma present over all VBs (absent over third order VBs in D. chaseana, D. cirrata, and occasionally in D. sericea); T- or anchor-shaped or forming girders; abaxial sclerenchyma present under all VBs or lacking under third order VBs; T- or anchor-shaped or forming girders. Adaxial and abaxial bundle sheath (BS) extensions present or absent. Colorless cells absent or present only as BS extensions (a few colorless, generally silica-filled cells sometimes present in mesophyll in D. parryi, D. domingensis, and D. montevidensis). Mesophyll not radiate (sometimes

inconspicuously radiate in D. intermedia and D. cirrata). Upper epidermal cells generally unspecialized (somewhat enlarged in D. montana, D. dusenii, and occasionally in D. secundiflora and D. montevidensis; broadly papillate in D. chaseana); hypodermic prickle hairs absent. Bulliform cells present as simple fan-shaped groups (absent in D. chascana).

Abaxial Leaf Epidermis.--Microhairs present (none seen in D. unispicata, D. chaseana, and D. malacantha). Intercostal long cell side walls parallel or bowed, with variously-shaped undulations. Costal short cells usually in long rows (mainly paired in D. domingensis, D. cirrata, and D. malacantha); costal silica bodies cross- to dumbbell-shaped.

Lodicule Morphology.--Lodicules generally cuneate, glabrous, (hairy, diamond-shaped with thinner apical portion in D. shrevei), and without microhairs. A single, 2-celled microhair was found on one otherwise typical lodicule of D. alpina. This appears to be an abnormal development, but more extensive investigation should be conducted.

Danthonia cachemyriana and D. exilis

Leaf Cross-section.--Adaxial furrows broad and steep-sided or narrow clefts; adaxial ribs present, rounded, similar over all VBs. Midrib present or absent. VBs round to elliptical. OBS incomplete, cells equal to or smaller than parenchyma cells, inconspicuous. IBS cells unevenly

thickened. Metaxylem vessels smaller than (D. exilis) or larger than (D. cachemyriana) OBS cells. Phloem not divided. Adaxial and abaxial sclerenchyma associated with all VBs, T- to anchor-shaped in D. cachemyriana; lacking in association with third order VBs in D. exilis, forming strands adaxially and girders narrower toward the bundles abaxially. BS extensions and colorless cells lacking. Mesophyll not radiate. Upper epidermal cells unspecialized or slightly enlarged; hypodermic prickle hairs absent. Bulliform cells present as simple fan-shaped groups.

Leaf Abaxial Epidermis.--Microhairs present in D. cachemyriana, not seen in D. exilis. Intercostal long cell walls parallel, with U-shaped undulations. Costal short cells in long rows, with cross- to dumbbell-shaped silica bodies.

Lodicule Morphology.--Lodicules cuneate, hairy, with 2-3 celled microhairs.

Dregeochloa

Leaf Cross-section.--Adaxial furrows wide, shallow, open; adaxial ribs present, similar over all VBs, very tall and narrow, rounded to flat-topped. Midrib absent. VBs round or elliptical. OBS complete, cells larger than parenchyma cells, conspicuous. IBS not thickened. Metaxylem vessels smaller than OBS cells. Phloem not divided. Adaxial

and abaxial sclerenchyma associated with all VBs, forming strands. BS extensions and colorless cells absent. Mesophyll indistinctly radiate. Upper epidermal cells unspecialized; hypodermic prickle hairs absent. Bulliform cells present, center cell very large, straight-sided; bulliform groups occupying more than half the leaf thickness.

Leaf Abaxial Epidermis.--Microhairs not seen. Intercostal long cells difficult to observe because of deep adaxial grooves between veins overarched by prickles; side walls apparently parallel, straight or slightly undulating. Costal short cells mostly paired or in short rows, silica bodies cross- to dumbbell-shaped.

Lodicule Morphology.--Lodicule preparations unavailable; lodicules reported by Conert (1966) to be cuneate and glabrous.

Erythranthera

Leaf Cross-section.--Adaxial furrows wide, open (E. pumila) or broad, steep-sided (E. australis); adaxial ribs present, similar over all VBs, rounded (E. pumila) or flat-topped (E. australis). Midrib present. VBs round to elliptical. OBS incomplete above and below, cells smaller than or equal to parenchyma cells, inconspicuous. IBS unevenly thickened. Metaxylem vessels smaller than or equal to OBS cells.

Phloem not divided. Adaxial sclerenchyma lacking over third order VBs, forming girders; abaxial sclerenchyma lacking under third order VBs, forming girders narrower toward bundles. BS extensions absent. Colorless cells apparently absent. Mesophyll not radiate. Upper epidermal cells rounded, slightly inflated (E. pumila) or broadly papillate (E. australis); hypodermic prickle hairs absent. Bulliform cells absent.

Leaf Abaxial Epidermis.--Microhairs present. Intercostal long cell walls parallel, with U-shaped undulations. Costal short cells in long rows, with cross- to dumbbell-shaped (E. australis) or rounded (E. pumila) silica bodies.

Available leaf material of E. pumila was poorly preserved and leaf cross-section preparations unclear, so observations of this species are ambiguous. Epidermal preparations were adequate.

Lodicule Morphology.--Lodicules glabrous, with 2-celled microhairs (E. pumila) or without microhairs (E. australis).

Karroochloa

Leaf Cross-section.--Adaxial furrows wide, open (broad, steep-sided in K. curva); adaxial ribs present, similar, and rounded over all VBs. Midrib present. VBs round to elliptical. OBS incomplete above and below, cells equal to or smaller than parenchyma cells. IBS evenly thickened.

Metaxylem vessels smaller than or equal to OBS cells (larger in K. curva). Phloem not divided. Adaxial and abaxial sclerenchyma associated with all VBs, forming girders narrower toward the bundles (T- or anchor-shaped adaxially in K. curva). BS extensions and colorless cells absent. Mesophyll not radiate. Upper epidermis unspecialized (mainly of rounded, slightly inflated cells in K. curva); hypodermic prickle hairs absent. Bulliform cells absent (K. curva) or present as simple fan-shaped groups.

Leaf Abaxial Epidermis.--Microhairs present. Intercostal long cell walls parallel, with U-shaped undulations. Costal short cells in long rows, with cross- to dumbbell-shaped silica bodies.

Lodicule Morphology.--Lodicules more or less cuneate, hairy in K. purpurea, hairy or glabrous in K. curva, and glabrous in K. tenella. 2-3 celled microhairs present in all species.

Merxmuellera

Leaf Cross-section.--Adaxial furrows narrow clefts (broad and open in M. rufa and M. stricta, absent in M. guillarmodae); adaxial ribs present and generally similar in shape over all VBs (none in M. guillarmodae), rounded or flat-topped (massive in M. arundinacea, M. papposa, and sometimes in M. macowanii). Midrib present (absent in M.

arundinacea and M. dura). Primary VBs round to elliptical or egg-shaped; secondary VBs round to elliptical. OBS complete to incomplete; cells equal to or smaller than parenchyma cells, conspicuous or inconspicuous. IBS cells evenly or unevenly thickened. Metaxylem vessels smaller or larger than OBS cells. Phloem not divided or evenly divided into two groups (M. stricta, M. davyi, M. macowanii, M. stereophylla, M. drakensbergiensis, and M. guillarmodae). Adaxial sclerenchyma present over all VBs (lacking over third order bundles or absent in M. guillarmodae), mainly T- or anchor-shaped (strands in M. papposa; girders in M. stricta); abaxial sclerenchyma present under all VBs, T- or anchor-shaped (girders in M. rufa, M. drakensbergiensis, and M. guillarmodae; girders narrower toward bundles in M. dura, M. decora, and M. stricta). BS extensions present or absent adaxially and abaxially. Colorless cells absent or present as BS extensions only (extensive in M. papposa). Mesophyll not radiate. Upper epidermal cells unspecialized (M. rufa, M. dura, M. decora, M. drakensbergiensis, and M. arundinacea), slightly inflated (M. guillarmodae), broadly papillate (M. stricta and M. stereophylla), broadly papillate or finger-like (M. macowanii; fig. 7), or finger-like (M. papposa, M. disticha, and M. davyi); hypodermic prickle hairs absent (present in M. davyi and M. macowanii). Bulliform cells present as simple fan-shaped groups or absent.

Leaf Abaxial Epidermis.--Microhairs apparently absent (present in M. dura, M. stricta, and M. guillarmodae). Intercostal long cell walls parallel, undulations W-shaped (M. davyi, M. macowanii, M. stereophylla, and M. drakensbergiensis) or mainly U-shaped. Costal short cells mainly paired (in short to long rows in M. stricta and .PA M. guillarmodae), with rounded silica bodies (dumbbell-shaped in M. guillarmodae).

Lodicule Morphology.--Lodicules quite variable; cuneate to diamond-shaped or apically lingulate; hairy (hairs very sparse and prickle-like in M. papposa). Microhairs present in some species, absent in others (either present or absent in M. macowanii and M. arundinacea).

Monachather

Leaf Cross-section.--Adaxial furrows wide, open; adaxial ribs present, similar, flat-topped over all VBs. Midrib present. VBs round to elliptical. OBS incomplete above, cells equal to or smaller than parenchyma cells, inconspicuous. IBS cells evenly thickened. Metaxylem vessels smaller than or equal to OBS cells. Phloem not divided. Adaxial sclerenchyma present over all VBs, T- or anchor-shaped; abaxial sclerenchyma present under all VBs, forming girders narrower toward bundle. BS extensions present adaxially, absent abaxially. Colorless cells

present as BS extensions only. Mesophyll not radiate. Upper epidermal cells unspecialized; hypodermic prickle hairs absent. Bulliform cells in fan-shaped groups, with center cell of each group enlarged (Fig. 2).

Leaf Abaxial Epidermis.--Microhairs present on lower leaf epidermis; intercostal long cell walls parallel, with undulating walls. Costal short cells in long rows, with cross- to dumbbell-shaped silica bodies.

Lodicule Morphology.--Lodicules cuneate, glabrous, without microhairs.

Monostachya

Leaf Cross-section.--Adaxial furrows wide, open; adaxial ribs present, similar, rounded over all VBs. Midrib present. VBs round to elliptical. OBS incomplete below, cells smaller than or equal to parenchyma cells. IBS unevenly thickened. Metaxylem vessels smaller than or equal to OBS cells. Phloem not divided. Adaxial sclerenchyma lacking over third order VBs, forming girders; abaxial sclerenchyma present under all VBs, forming girders narrower toward the bundles. BS extensions present adaxially, lacking abaxially. Colorless cells present as BS extensions only. Mesophyll not radiate. Upper epidermal cells fingerlike; hypodermic prickle hairs absent. Bulliform cells absent.

Leaf Abaxial Epidermis.--Microhairs not seen. Intercostal long cell walls parallel, with U-shaped or interlocking undulations. Costal short cells mainly paired, with rounded silica bodies.

Lodicule Morphology.--Lodicules variable in this monotypic genus, generally cuneate, hairy or glabrous, with or without 2-celled microhairs.

Plinthanthesis

Leaf Cross-section.--Adaxial furrows broad, steep-sided; adaxial ribs present, similar, rounded over all VBs. Midrib present. VBs round to elliptical. OBS incomplete above and below, cells smaller than or equal to parenchyma cells, inconspicuous. IBS unevenly thickened. Metaxylem vessels larger than OBS cells. Phloem not divided. Adaxial sclerenchyma present over all VBs, T- or anchor-shaped. Abaxial sclerenchyma present under all VBs, forming girders. BS extensions lacking. Colorless cells absent. Mesophyll not radiate. Upper epidermis unspecialized; hypodermic prickle hairs absent. Bulliform cells absent.

Leaf Abaxial Epidermis.--Microhairs present on abaxial epidermis. Intercostal long cell walls parallel, with U-shaped undulations. Costal short cells in long rows, with cross- to dumbbell-shaped silica bodies.

Lodicule Morphology.--Lodicules cuneate, glabrous, without microhairs.

Pseudopentameris

Leaf Cross-section.--Adaxial furrows broad, steep-sided; adaxial ribs present, rounded, similar in shape over all VBs. Midrib present. VBs round to elliptical. OBS complete, cells larger than parenchyma cells, conspicuous. IBS evenly thickened. Metaxylem vessels smaller than or equal to OBS cells. Phloem not divided. Adaxial sclerenchyma lacking over third order VBs, present under all VBs, forming girders. BS extensions present or absent. Colorless cells absent or present only as BS extensions. Upper epidermal cells unspecialized. Bulliform cells present as simple fan-shaped groups.

Seen in cross-section, the abaxial epidermal cells in this genus are considerably larger than those of the adaxial epidermis, and are often somewhat inflated.

Leaf Abaxial Epidermis.--Microhairs not seen. Intercostal long cell side walls thin, bowed out and inflated in P. brachyphylla, more or less parallel and not inflated in P. macrantha, with U-shaped undulations. Costal short cells in long rows, with cross- to dumbbell-shaped silica bodies.

Lodicule Morphology.--Lodicule preparations unavailable.

Pyrranthera

Leaf Cross-section.--Adaxial furrows wide, open; adaxial ribs lacking over third order VBs, similar in shape, rounded. Midrib present. VBs round to elliptical. OBS incomplete below, cells equal to or smaller than parenchyma cells. IBS unevenly thickened. Metaxylem vessels smaller than or equal to OBS cells. Phloem not divided. Adaxial sclerenchyma lacking over third order VBs, forming girders; abaxial sclerenchyma lacking under third order VBs, forming girders narrower toward the bundles. BS extensions present adaxially, absent abaxially. Colorless cells present as BS extensions only. Mesophyll not radiate. Upper epidermal cells unspecialized or rounded and somewhat enlarged; hypodermic prickle hairs absent. Bulliform cells absent.

Leaf Abaxial Epidermis.--Microhairs present on abaxial leaf epidermis; intercostal long cells with walls parallel and with U-shaped undulations; costal short cells in long rows, silica bodies cross- to dumbbell-shaped.

Lodicule Morphology.--Lodicules cuneate, glabrous, with 2-celled microhairs.

Rytidosperma

Leaf Cross-section.--Adaxial furrows of various shapes; adaxial ribs present over all VBs (absent in R. penicillatum, absent over third order VBs in R. procerum, R.

clavatum, and R. corinum); rounded or flat-topped, generally similar in shape over all VBs. Midrib present or absent. Primary VBs round to elliptical (egg-shaped in R. longifolium and occasionally in R. caespitosum); secondary VBs round to oval. OBS complete to incomplete, cells smaller than or equal to parenchyma cells, inconspicuous. IBS unevenly thickened. Metaxylem vessels smaller or larger than OBS cells. Phloem not divided. Adaxial sclerenchyma associated with all VBs or lacking over third order VBs; T- to anchor-shaped or forming girders; abaxial sclerenchyma associated with all VBs or (lacking under third order VBs in R. clavatum and occasionally in R. setifolium); forming girders or a girders narrower toward the bundle. BS extensions present or absent adaxially, absent abaxially (present in R. glabrum). Colorless cells absent or present only as BS extensions. Mesophyll not radiate (indistinctly radiate in R. clavatum). Upper epidermal cells unspecialized, rarely slightly inflated (broadly papillate to finger-like in R. pauciflorum, R. corinum, and R. setifolium); hypodermic prickle hairs absent. Bulliform cells present as simple fan-shaped groups or absent.

Leaf Abaxial Epidermis.--Microhairs present or apparently absent. Intercostal long cell side walls parallel or bowed, with variously-shaped undulations. Costal short cells in long rows, with cross- to dumbbell-shaped silica bodies

(mainly paired, with rounded silica bodies in R. virescens, R. glabrum, and R. pallide).

Lodicule Morphology.--Lodicules cuneate or diamond-shaped, hairy (glabrous in R. corinum), microhairs present, 2-3(-4) celled.

Cortaderia

Leaf Cross-section.--Abaxial furrows variously shaped; adaxial ribs present and similarly shaped over all VBs; flat-topped (rounded in C. modesta and C. archboldii). Midrib present or absent. VBs round to elliptical. OBS complete, cells equal to or smaller than parenchyma cells but conspicuous (C. araucana, C. pilosa, and C. modesta); or incomplete, cells equal to or smaller than parenchyma cells, inconspicuous (C. hapalotricha, C. pungens, and C. archboldii). IBS cells unevenly thickened (evenly thickened in C. modesta and C. archboldii). Metaxylem vessels smaller than or equal to OBS cells. Phloem not divided by fibers (C. archboldii, C. hapalotricha, and C. pungens), or divided irregularly into 2 or more groups (fig. 8). Adaxial sclerenchyma present over all VBs, T- or anchor-shaped; abaxial sclerenchyma present under all VBs, T- or anchor-shaped (girder narrower toward bundle in C. araucana, girder in C. archboldii). BS extensions present adaxially except in C. hapalotricha and C. pungens; extensions present abaxially except in C. hapalotricha, C. pungens, and C.

archboldii. Colorless cells absent or present as BS extensions only (extensive in C. araucana). Mesophyll not radiate. Upper epidermal cells unspecialized (broadly papillate in C. pungens, finger-like in C. archboldii); hypodermic prickle hairs absent. Bulliform cells absent (present as simple fan-shaped groups in C. hapalotricha and C. archboldii).

Leaf Abaxial Epidermis.--Microhairs apparently absent (present in C. modesta). Intercostal long cells with parallel side walls and generally U-shaped or interlocking undulations (occasionally W-shaped in C. pungens and C. modesta). Costal short cells in long rows (C. hapalotricha, C. pungens, and C. archboldii) or mainly paired (C. araucana, C. pilosa, C. modesta) with cross- to dumbbell-shaped silica bodies (rounded in C. pilosa).

Lodicule Morphology.--Lodicules cuneate or with a distinct apical lobe; hairy, with 2-3 celled microhairs in C. hapalotricha; hairy, without microhairs in C. pilosa and C. modesta; glabrous, with microhairs in C. pungens; glabrous, without microhairs in C. archboldii.

Schismus

Leaf Cross-section.--Adaxial furrows wide, open; adaxial ribs present, similar, and rounded over all VBs (lacking over third order VBs in S. scaberrimus). Midrib lacking

(present in S. barbatus). VBs round to elliptical. OBS complete (incomplete below in S. scaberrimus); cells equal to or smaller than parenchyma cells, inconspicuous. IBS unevenly thickened (evenly thickened in S. scaberrimus). Metaxylem vessels smaller than or equal to OBS cells. Phloem not divided. Adaxial sclerenchyma present as strands over all VBs in S. inermis, absent over third order VBs in S. arabicus and S. scaberrimus, and absent altogether in S. barbatus; abaxial sclerenchyma present, or absent under third order VBs, as strands (T or anchor in S. scaberrimus). BS extensions absent. Colorless cells absent. Mesophyll not radiate. Upper epidermal cells unspecialized; hypodermic prickle hairs absent. Bulliform cells absent (apparently present as simple fan-shaped groups in S. scaberrimus).

Conert and Türpe (1974) note no bulliform cells in S. scaberrimus, though they do occur in S. pleuropogon, which was not included in the present study. Available material of S. scaberrimus was poorly preserved, and consequently the leaf cross-sections are not entirely clear; nevertheless, bulliform groups appear to be present.

Leaf Abaxial Epidermis.--Microhairs present (none seen in S. inermis). Intercostal long-cells with parallel walls, undulations generally U-shaped. Costal short cells in long

rows, with cross- to dumbbell-shaped silica bodies (mainly paired, with rounded silica bodies in S. inermis).

Lodicule Morphology.--Lodicules cuneate, hairy, with 2-celled microhairs (glabrous or hairy, without microhairs in S. arabicus).

DISCUSSION

Danthonia has been subdivided by various authors because of obvious heterogeneity in morphological and anatomical features (e.g., DeWet, 1954, 1956; Zotov, 1963; Conert, 1971). However, the data presented here reveal that extensive variation in leaf anatomy and lodicule morphology remains within the segregate genera. Three of the taxa investigated are distinct anatomically, as well as morphologically. They are clearly isolated in the Danthonieae:

Centropodia

Members of this genus have the outer bundle sheath complete, with the cells very large and conspicuous, radiate parenchyma, and bulliform cells with the central cell much enlarged. The abaxial leaf surface is deeply grooved, with the grooves overarched by prickles. This combination of characters is not found elsewhere in the study group. The genus also differs from the rest of the Danthonia complex in morphological characters, such as its 5-11 nerved glumes,

and its very small chromosomes (DeWet, 1954, 1956; Conert, 1962; Wright, 1984).

Dregeochloa

Leaf anatomy of this genus is distinctive, especially in its deeply grooved lower surface and bulliform cells which occupy over half the depth of the leaf. Morphologically it is equally distinctive, particularly in the form of the mature caryopsis. Ellis (1977) and Conert (1966, 1971) have expressed the opinion that this genus occupies an isolated position in the Danthonieae.

Pseudopentameris

Like Dregeochloa and Asthenatherum, Pseudopentameris has large and distinct outer bundle sheath cells. Additionally, the lower epidermal cells are larger than those of the upper epidermis and often inflated, a condition not found elsewhere in this study group. Its morphology is also distinctive, especially the structure of the caryopsis and the stigmatic hairs which are decurrent and join over the top of the ovary (DeWet, 1954, 1956; Conert, 1971).

The remaining taxa in the study group show more similarities to one another than to any other taxa. Nevertheless, their interrelationships are not clear based on either anatomy or overall morphology.

Chionochloa

This genus is relatively uniform in leaf anatomy. Zotov (1963) found similar uniformity in morphological characteristics. He noted that the variation which occurs is clinal in nature, rendering it difficult to separate the genus into species groups, or even to discover features differentiating species with 2n = 36 from those with 2n = 42. Anatomical variation which occurs is not necessarily paralleled by morphological differences. For example, C. bromoides and C. beddiei, both coastal New Zealand rock-dwelling species and morphologically very similar, differ in primary VB shape, adaxial sclerenchyma shape, the type of intercostal long cell wall undulations, and in the presence or absence of microhairs on the lodicules. These differences suggest the possibility of convergent evolution in these two species.

Cortaderia

Anatomical data strongly support the inclusion of C. archboldii, a distinctive New Guinean member of this genus, in Section Bifida (Connor and Edgar, 1974). Despite its unusual appearance (fig. 8), it shows marked similarities to C. hapalotricha and C. pungens, the other representatives of this section, in features of the outer bundle sheath and extensions, presence of bulliform cells, undivided phloem, and the arrangement of the costal short cells in long rows rather than pairs.

Chionochloa and Cortaderia show a number of anatomical similarities, as pointed out by Zotov (1963) and Conert (1971). For instance, the overall outline of the leaf and the shape of the ribs are similar, and broadly papillate upper epidermal cells are found in all Chionochloa and some Cortaderia. However, Cortaderia differs substantially in many other features. The bundle sheath extensions are more strongly developed in Cortaderia, and in some species the OBS is also thickened, a feature not found in Chionochloa. The silica bodies are nearly always cross- to dumbbell-shaped in Cortaderia, and rounded in Chionochloa. Thus, the two genera appear distinct and not particularly closely related. This conclusion is supported by Wright (1984), who found no evidence of cladistic relationship between these genera.

Conert (1961) suggested a relationship between Cortaderia and Merxmuellera. This relationship is not strongly supported by the anatomical data presented here. Differences exist in sclerenchyma and bundle sheath extension development, as well as in costal short cell arrangement and silica body shape. However, Merxmuellera is extremely variable anatomically and further study is clearly required before any conclusions can be reached.

Danthonia s. str.

The North American and European species of this genus are uniform anatomically as well as morphologically, as pointed out by De Wet (1954). West Indian and South American species tend to possess anatomical specializations, notably the division of the phloem and the paired arrangement of the costal short cells in some species, which are not found in other Danthonia s. str. Perhaps the most interesting finding is the distinction between D. domingensis and D. shrevei, which were combined as subspecies by Conert (1975a). These two species show many anatomical differences, including the shape and the presence of hairs on the lodicules. Clearly, closer study is needed. However, in spite of the variation within Danthonia s. str., no clear-cut divisions are possible. Wright (1984) found that all these species appeared to form a monophyletic group.

Danthonia cachemyriana and D. exilis

These two species have not been formally removed from Danthonia, though morphological differences (notably the tufted arrangement of the lemma hairs) as well as anatomical features such as the complete absence of bundle sheath extensions, sclerenchyma shape, and lodicule morphology, indicate a closer relationship to other taxa such as Karroochloa. Wright (1984) found evidence that these two

species may represent sister groups of Karroochloa, and this possibility deserves further investigation.

Karroochloa and Schismus

Leaf anatomical data presented here are inconclusive, but generally support the suggested close relationship between these two genera (Conert and Türpe, 1969, 1974). Both genera lack colorless cells, bundle sheath extensions, and, in some species, bulliform cells; Karroochloa and S. scaberrimus have the inner bundle sheath cell walls evenly thickened. The two genera differ primarily in sclerenchyma development. The features they share, however, are found elsewhere in the study group. Lodicule morphology is variable in both genera, and is not helpful in resolving the problem.

Merxmuellera

The anatomy of this genus is extremely variable, but no clear-cut patterns are as yet detectable. One aberrant species is M. guillarmodae. Conert (1975b) suggested that this species is most closely related to M. macowanii or to M. stricta. Although neither hypothesis is strongly supported by the anatomical data presented here, a relationship with M. stricta appears more plausible.

Wright (1984) indicated that the genus appears to be polyphyletic. More extensive investigations of these species are in progress in an effort to clarify their

relationships to each other and to other taxa within the Danthonieae.

Monachather

Morphologically, this monotypic genus is distinctive and apparently isolated (Vickery, 1956); anatomically it is unusual in this study group in having bulliform cells in fan-shaped groups but with the center cell enlarged. This feature also occurs in Centropodia. Monachather also has the inner bundle sheath evenly thickened, a feature which is relatively uncommon. However, in most respects it is similar to species of Rytidosperma. Based on all available evidence, Monachather warrants generic status, but its closest relationships appear to lie with Rytidosperma.

Erythranthera, Plinthanthesis, and Pyrrhanthera

The anatomical data provide little support for the separation (Zotov, 1963; Blake, 1972) of these genera from Rytidosperma. However, cross-section preparations of several species were marginal or inadequate due to poor preservation of the leaf material, and further investigation is clearly needed. Lodicules in these genera are glabrous, a condition rare in Rytidosperma.

Monostachya

Leaf anatomy of this monotypic genus is similar to that of Rytidosperma. In the presence of paired costal short

cells with rounded silica bodies it resembles R. virescens, R. glabrum, and R. pallide.

Rytidosperma

The Australian species of this genus are uniform in leaf anatomy and lodicule morphology, which is consistent with the observation that these species hybridize readily and appear to form a polyploid complex (Brock and Brown, 1961; Wright, 1984). The New Zealand species such as R. corinum, R. clavatum, and R. setifolium, and the South American species R. glabrum and R. virescens, show greater differences in anatomy.

Rytidosperma appears to be distinct from Danthonia s. str. both on morphological and anatomical grounds (Wright, 1984). Though leaf anatomy in these taxa is similar, lodicule morphology is distinctive for each genus. Lodicules in Rytidosperma are hairy except in rare cases and have microhairs, while in Danthonia s. str. they are almost exclusively glabrous and lack microhairs.

This study points out the broad similarities present in the anatomy of this group of grasses. Renvoize (1982) found that anatomical features were not reliable in delimiting tribal groups within the Arundinoideae, and suggested that characters which could be used in delimiting such subgroups would have to be morphological. However, the variation in anatomical features which does occur in the Danthonieae is

not necessarily correlated with morphological differences. This fact is the major source of difficulty in the development of an internally consistent taxonomic system for the group. The evolutionary history of the Danthonieae must have involved extensive convergences and parallelisms which have obscured its pattern. Distinguishing characteristics may exist which would enable us to decipher the evolutionary relationships among these species, but are not yet recognized, just as the characteristics now used to separate the Poeae and the Eragrosteae were known long before they were considered significant. Further studies of these taxa are underway, and it is hoped that they will lead to breakthroughs in the systematics of this fascinating group.

LITERATURE CITED

Blake, S. T. 1972. Plinthanthesis and Danthonia and a review of the Australian species of Leptochloa (Gramineae). Contr. Queensland Herb. 14:1-19.

Brock, R. D., and J. A. M. Brown. 1961. Cytotaxonomy of Australian Danthonia. Austr. J. Bot. 9:62-91.

Conert, H. J. 1961. Die Systematik und Anatomie der Arundineae. J. Cramer, Wienheim.

_____. 1962. Über die Gramineen-Gattung Asthenatherum Nevski. Senckenberg. Biol. 43:239-266

_____. 1966. Dregeochloa, eine neue Gattung der Gramineen (Gramineae, Arundinoideae, Danthonieae). Senckenberg. Biol. 47:335-343.

_____. 1971. The genus Danthonia in Africa. Mitt. Bot. Staatssamml. Munch. 10:299-308.

_____. 1975a. Über Danthonia domingensis Hackel & Pilger. (Poaceae: Arundinoideae: Danthonieae) Senckenberg. Biol. 56:293-313.

_____. 1975b. Merxmuellera guillarmodae Conert n. sp. (Gramineae: Arundinoideae). Senckenberg. Biol. 56:145-152.

_____, and A. M. Türpe. 1969. Karroochloa, eine neue Gattung der Gramineen. Senckenberg. Biol. 50:289-318.

_____, and _____. 1974. Revision der Gattung Schismus (Poaceae: Arundinoideae: Danthonieae). Abh. Senckenberg. Naturforsch. Ges. 532:1-81.

Connor, H. E., and E. Edgar. 1974. Names and types in Cortaderia Stapf (Gramineae). Taxon 23:595-605.

Cronquist, A. 1978. The Evolution and Classification of Flowering Plants. Allen Press, New York.

De Wet, J. M. J. 1954. The genus Danthonia in grass phylogeny. Amer. J. Bot. 41:204-211.

_____. 1956. Leaf anatomy and phylogeny in the tribe Danthonieae. Amer. J. Bot. 43:175-182.

_____. 1960. Leaf anatomy and morphology in South African species of Danthonia. Bothalia 7:303-310.

Ellis, R. P. 1976. A procedure for standardizing comparative leaf anatomy in the Poaceae. I. The leaf blade as viewed in transverse section. Bothalia 12:65-109.

_____. 1977. Leaf anatomy of the South African Danthonieae (Poaceae). I. The genus Dregeochloa. Bothalia 12:209-213.

_____. 1979. A procedure for standardizing comparative leaf anatomy in the Poaceae. II. The epidermis as seen in surface view. Bothalia 12:641-671.

Johansen, D. E. 1940. Plant Microtechnique. McGraw-Hill, New York.

Metcalfe, C. R. 1960. Anatomy of the Monocotyledons. I. Gramineae. Clarendon Press, Oxford.

_____. 1979. Purposes of systematic anatomy. Pp. 12-13 in Metcalfe, C. R., and L. Chalk, 1979. Anatomy of the Dicotyledons, 2nd ed. Clarendon Press, Oxford.

Renvoize, S. A. 1982. The subfamily Arundinoideae and its position in relation to a general classification of the Gramineae. Kew Bull. 36:85-102.

Schmid, R., and M. D. Turner. 1977. Contrad 70, an effective softener of herbarium material for anatomical study. Taxon 26:551-552.

Tateoka, T. 1964. Notes on some grasses XVII. Metcalfia, a primitive genus of the tribe Aveneae. Bot. Mag. (Tokyo) 77(909):69-72.

Vickery, J. W. 1956. A revision of the Australian species of Danthonia DC. Contrib. New South Wales Nat. Herb. 2:249-325.

Wright, K. L. Tomlinson. 1984. Studies in the Danthonieae (Poaceae). Part I. Systematic relataionships in Danthonia s. lat. (Danthonieae: Poaceae). PhD dissertation, Univ. of Oklahoma.

Zotov, V. D. 1963. Synopsis of the grass subfamily Arundinoideae in New Zealand. New Zealand J. Bot. 1:78136.

Footnote

The author is grateful to S. J. Carlquist for his invaluable assistance with the photography and for many fruitful discussions; and to D. L. Kama for preparation of the plates. In addition, I thank J. R. Estes, R. J. Tyrl, G. Uno, G. Schnell, and S. C. Barber for many helpful comments on the manuscript. This work was supported in part by a National Science Foundation Graduate Fellowship, and forms part of a doctoral dissertation submitted to the University of Oklahoma.

Rancho Santa Ana Botanic Garden, Claremont, CA 91711.

Table 1. Genera examined.

Centropodia Reichb.	*Merxmuellera* Conert
(= *Asthenatherum* Nevski)	*Monachather* Steud.
Chionochloa Zotov	*Monostachya* Merrill
Cortaderia Stapf	*Plinthanthesis* Steud.
Danthonia Lam. & DC.	*Pseudopentameris* Conert
Dregeochloa Conert	*Pyrranthera* Zotov
Erythranthera Zotov	*Rytidosperma* Steud.
Karroochloa Conert & Türpe	*Schismus* Beauv.

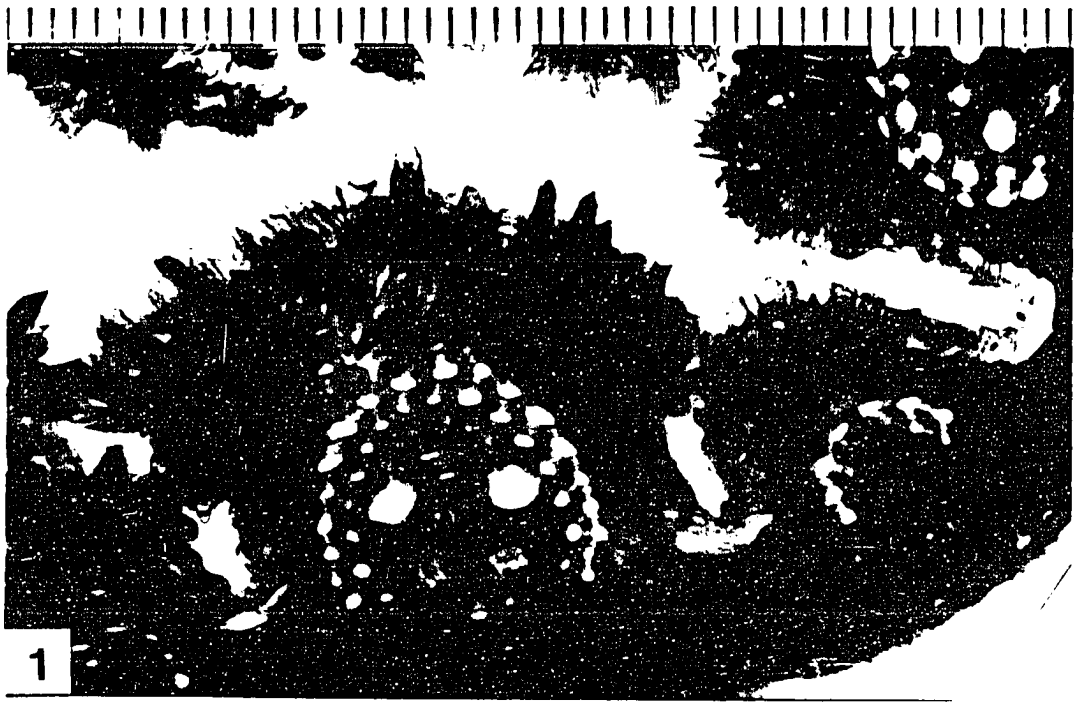
FIGURES

Fig. 1-2.--Fig. 1. *Merxmuellera davyi*, leaf XS. Hypodermic prickle hairs and phloem evenly divided into two groups of conductive strands.--Fig. 2. *Monachather paradoxus*, leaf XS. Bulliform cell groups with center cell enlarged. (Scale: 1 division = 10 μm.)

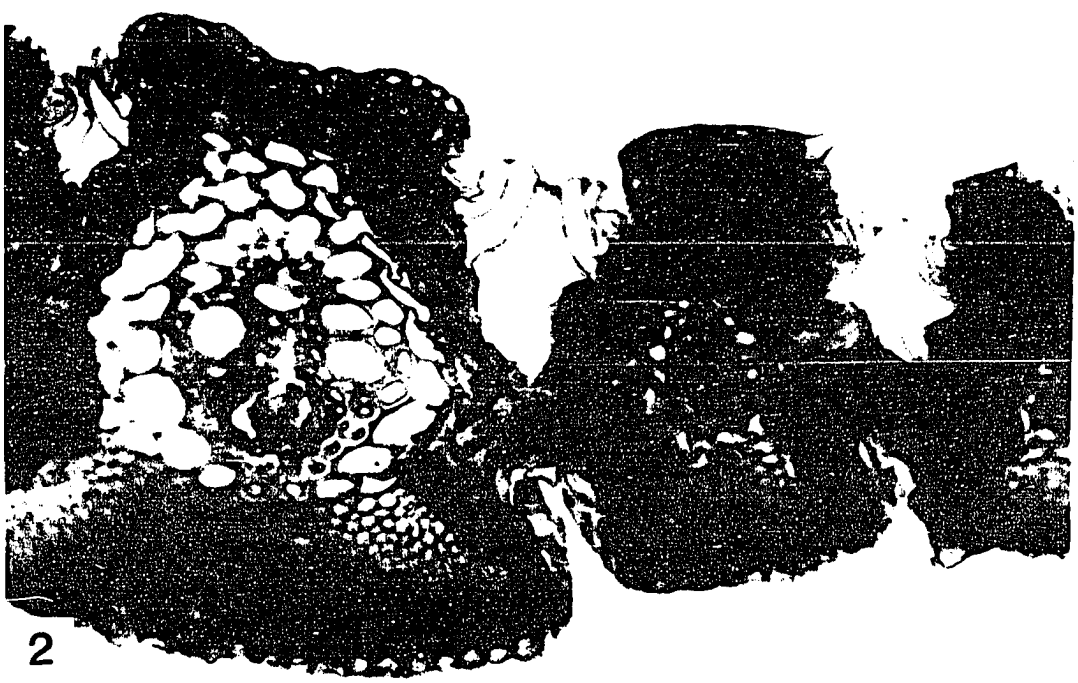
Fig. 3-4.--Fig. 3. *Merxmuellera papposa*, leaf XS. Massive ribs and extensive development of colorless cells.--Fig. 4. *Cortaderia pungens*, leaf XS. Broadly papillate upper epidermal cells. (Scale: 1 division = 10 μm.)

Fig. 5-6.--Fig. 5. *Merxmuellera davyi*, lower epidermis. W-shaped undulations of intercostal long cell walls.--Fig. 6. *Rytidosperma nigricans*, lodicule. Apically lingulate shape and multicellular microhair (right). (Scales: 1 division = 10 μm.)

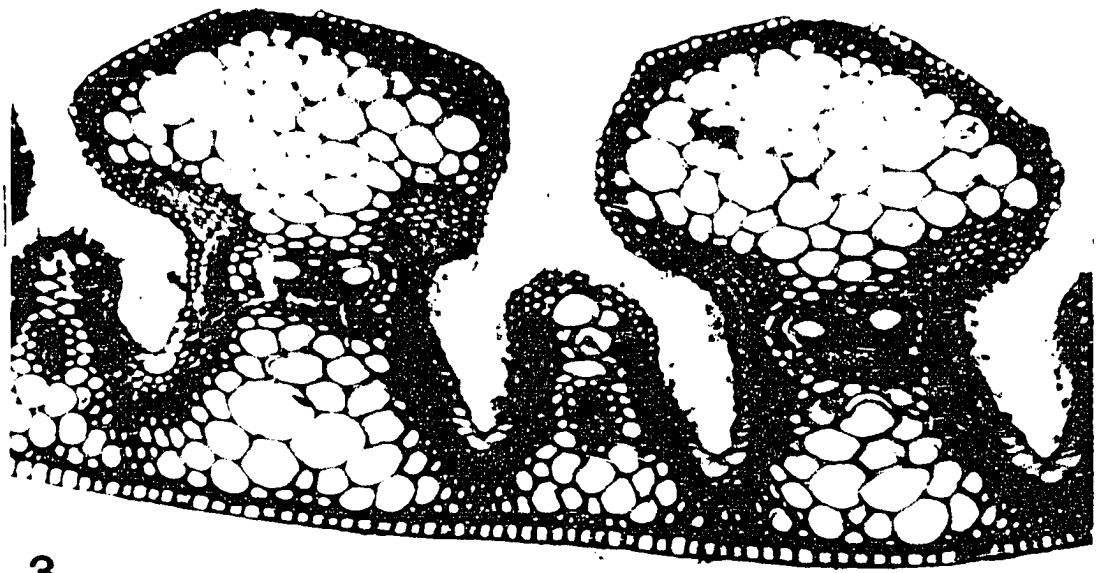
Fig. 7-8.--Fig. 7. *Cortaderia sp.*, leaf XS. Phloem irregularly divided.--Fig. 8. *Cortaderia archboldii*, leaf XS. Fingerlike upper epidermal cells. (Scale: 1 division = 10 μm.)



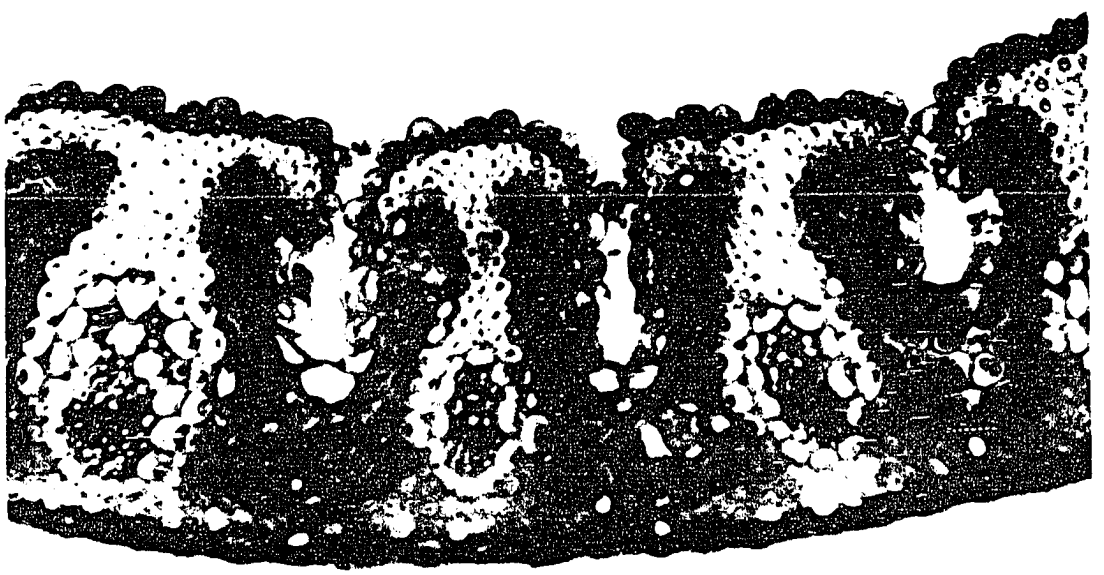
1



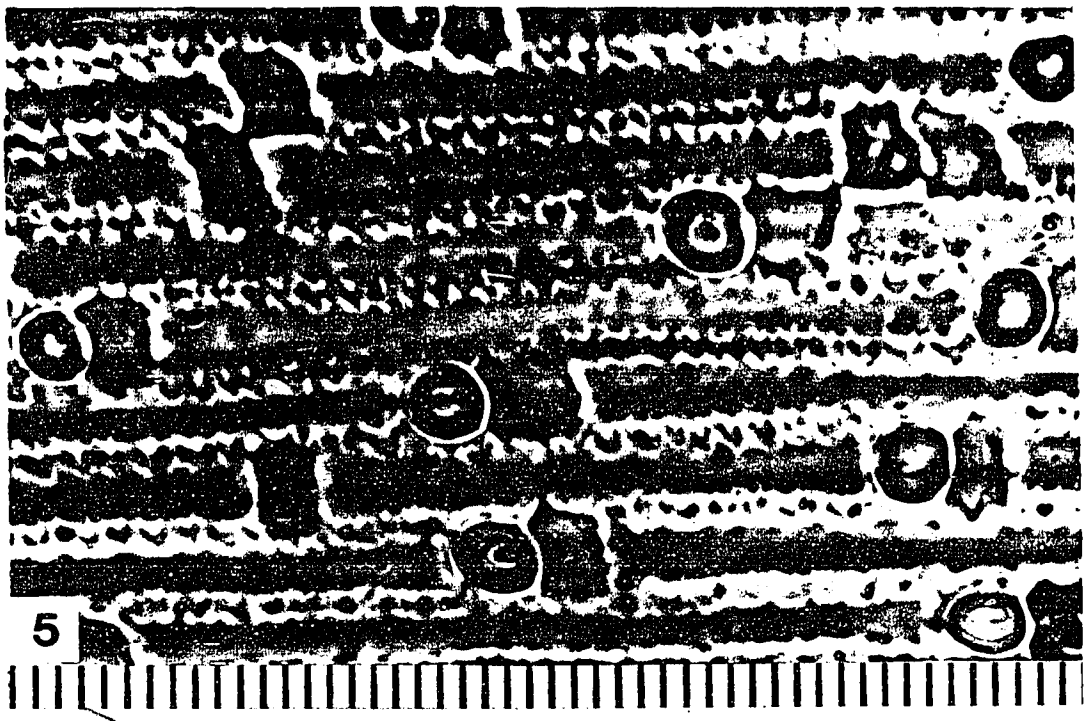
2



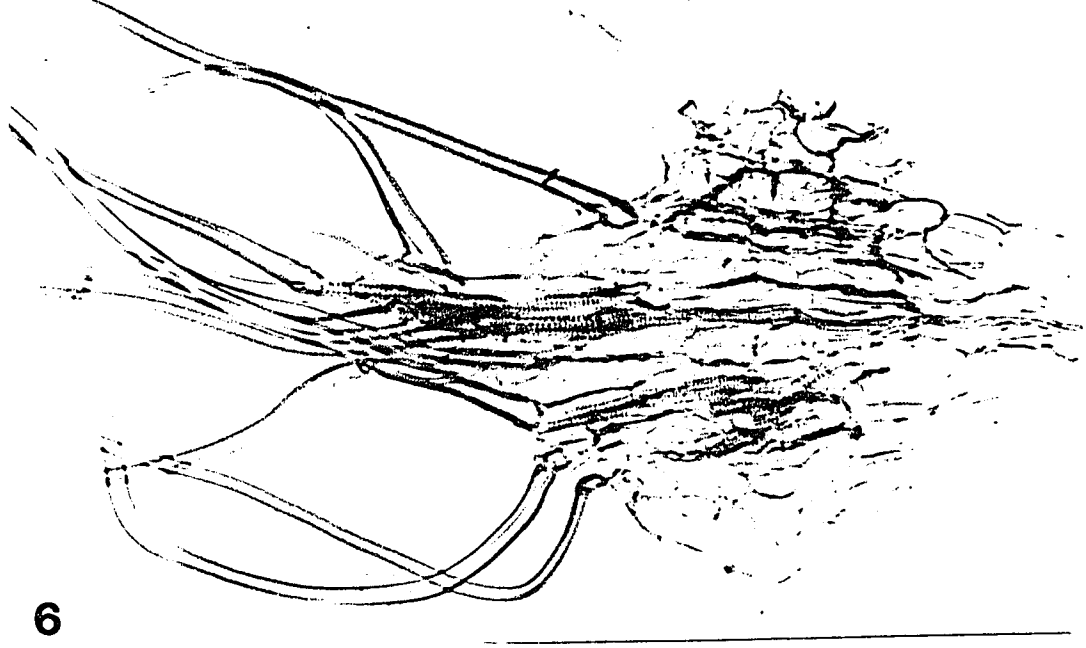
3



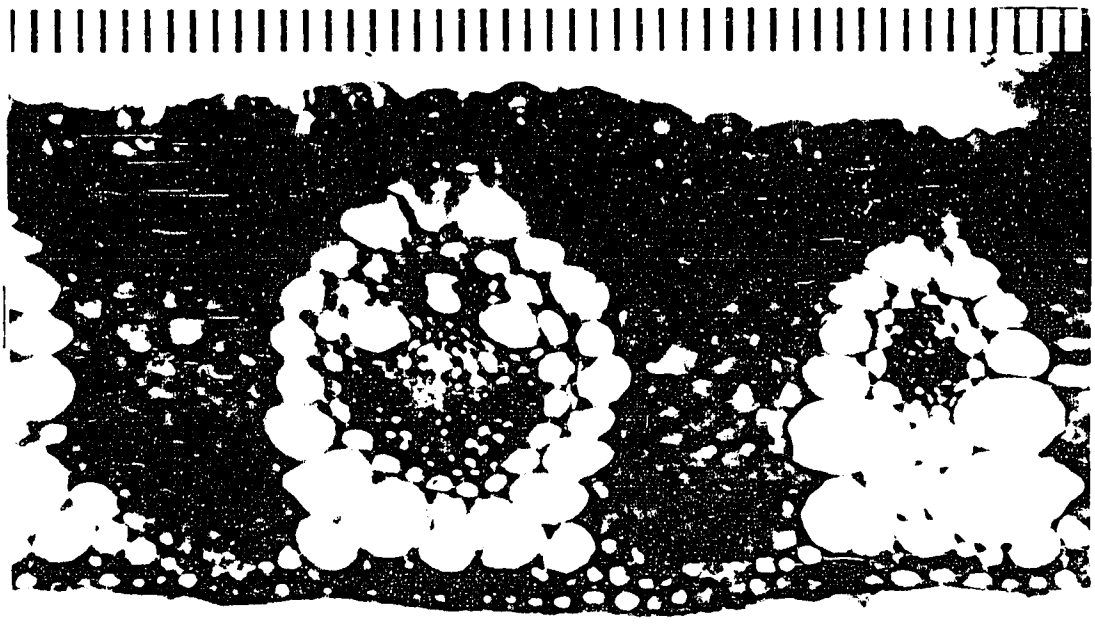
4



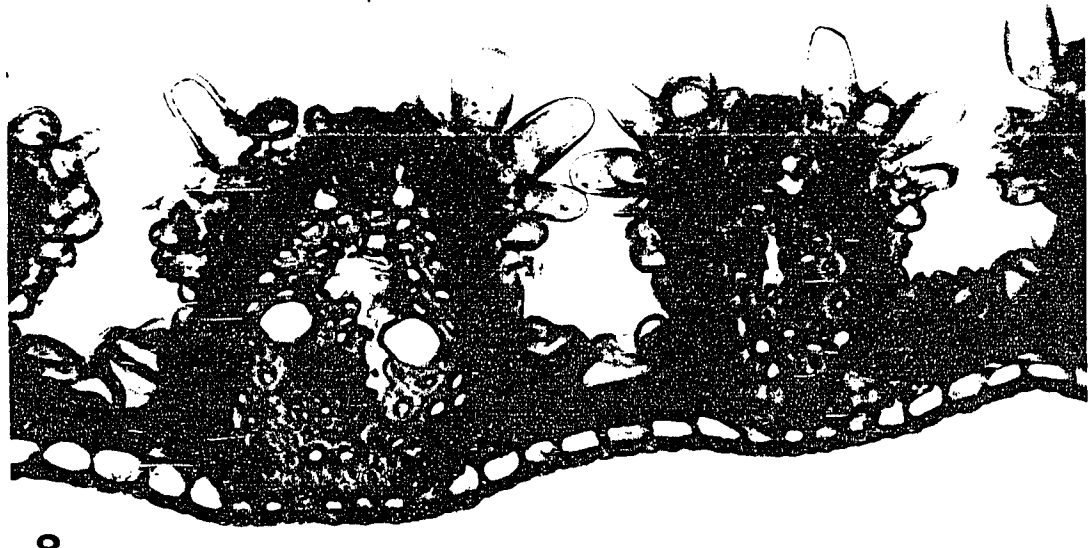
5



6



7



8

STUDIES IN THE DANTHONIEAE (POACEAE)

PART III

ARUNDO, *PHRAGMITES*, AND *DANTHONIA* IN THE SOUTHEASTERN UNITED STATES

ARUNDO L.

1. A. donax L. GIANT REED. Large, coarse, rhizomatous perennials. Culms erect, 2-8 m tall, glabrous; internodes hollow; terete in cross-section, leaves cauline. Sheaths open, terete, longer than internodes, glabrous; auricles absent. Ligules membranous, apex densely ciliate, 1-1.5 mm high. Collars light-colored to inconspicuous on back, often with a wrinkled, dark brown, triangular area at each side, glabrous or with a few long hairs at margins. Blades plane, firm, glabrous, 20-90 cm long X 17-35 mm wide, tapering to a long, fine tip; margins scabrid. Inflorescence a large, elongate-oval panicle, (16-)30-70 cm long X (5-)10-35 cm broad; branches ascending, glabrous to scabrous, up to 20 cm or more long. Spikelets laterally compressed, 10-14 mm long; 2-4 flowered, florets perfect but rarely setting seed; rachilla glabrous. Glumes 2, subequal, lanceolate, apex acuminate; about as long as lemmas, straw-colored to purplish, thinly chartaceous, glabrous, 3-4 nerved, 8-13 mm long. Lemmas mucronate, hyaline to straw-colored, sometimes purple-tinged, chartaceous, lanceolate, apex acuminate, 11-14 mm long, 4-7 nerved, often with evident cross-nerves; pubescent with hairs 6-7 mm long or longer; mucro 1-2 mm long, lateral nerves often also slightly excurrent; callus blunt, pubescent. Paleas about 1/2 as long as lemmas, 2-nerved, hyaline, glabrous or sparsely pubescent below, ciliolate on keels, apex narrow, truncate, erose. Lodicules 2, cuneate. Stamens 3, anthers light brown, 2-2.5 mm long. Caryopses not seen. (2n = ca.

60, 108, 110, ca. 120). Late summer - fall. Roadsides, waste places, moist areas; cp and pied. SE except Del. [Tex, Okla, Mo].

An Old World native, widely introduced in the southern United States. A cultivar with variegated blades has been described as var. versicolor (Miller) Stokes.

PHRAGMITES Adanson

1. P. australis (Cav.) Trin. ex Steud. COMMON REED. Stout, rhizomatous perennials forming large colonies. Culms erect, up to 4.5 m tall, glabrous; internodes hollow, terete in cross-section; leaves cauline. Sheaths open, terete, longer than internodes, glabrous; auricles absent. Ligules a very short membrane crowned with a dense rim of hairs 0.5-7 mm long. Collars glabrous or with a few long hairs at sides, light to dark brown across back, often with dark triangular areas at sides. Blades plane, stiff, glabrous, tapering to a very fine tip, 20-65 cm or more long X 12-36 mm or more wide, deciduous; margins scabrid. Inflorescence a dense, oval to elongate panicle, 12-45 cm long X 5-20 cm broad, branches ascending, up to 20 cm or more long, glabrous to scabrous, often with tufts of long white hairs in axils and below spikelets. Spikelets laterally compressed, (5-)10-15(-17) mm long, (3-)4-8 flowered; lowest floret male or neuter, upper florets bisexual but rarely setting seed; lowest joint of rachilla glabrous, upper joints densely pubescent with silky, silvery hairs 4-6(-10) mm long. Glumes 2, unequal, shorter than lemmas, brown, chartaceous, glabrous; first glume acute, 3-nerved, 1/2-2/3 as long as second, 2.5-5 mm long; second glume acuminate, occasionally mucronulate, 3-5 nerved, about 1/2 as long as first lemma, 4-7 mm long. Lemmas lance-acuminate, brown or purplish brown, chartaceous, 3-nerved, glabrous; lowest lemma 7-12 mm long; upper ones 8-13 mm long, the upper half of lemmas readily breaking off; callus blunt. Paleas 1/3-1/2 as long

as lemmas, fragile, chartaceous, glabrous, 2-nerved. Lodicules 2, tiny; stamens 3, anthers pale, 1-2 mm long. Caryopsis dark brown, 1.8 mm long X 0.5 mm broad. (n = 24, 27, 36, 48). Fall. Brackish and freshwater marshes, wet areas; all prov; SE except Tenn. [ALL]. (P. communis Trin.--F, G, R; P. phragmites (L.) Karst.--S).

Clayton, W. D. 1968. The correct name of the common reed. Taxon 17:168-169.

DANTHONIA DC. Oat Grass

Caespitose perennials. Culms erect to slightly geniculate, glabrous or minutely pubescent below nodes; internodes hollow; terete to triangular or somewhat flattened in cross-section with one side concave; leaves mainly basal. Sheaths open, terete, generally shorter than internodes, glabrous to pubescent; auricles absent. Ligules a dense ring of white hairs. Collars glabrous or pubescent. Blades plane or folded, glabrous to pubescent, midrib not prominent; apex acute; margins scabrid. Inflorescence an open to spike-like panicle with spikelets cleistogamous or chasmogamous, additional cleistogamous spikelets 1-flowered (in basal leaf sheaths) to several-flowered (in axils of upper leaf sheaths); branches 1 per node. Spikelets laterally compressed, several-flowered, florets successively smaller above, disarticulation above the glumes and between the florets; rachilla glabrous. Glumes 2, subequal, generally longer than spikelet column but exceeded by lemma awns; green to purple-tinged, fading straw-colored; papery, (1-)3-5 nerved, glabrous; apex acute; margins often hyaline. Lemmas awned from a bifid apex, rounded on back, 5-9 nerved, nerves obscure; green to purple-tinged, fading straw-colored; papery, pubescent to nearly glabrous; margins with a fringe of hairs; callus blunt, glabrous to pubescent; awn geniculate, the lower part flattened and twisted, generally different in color from the apical portion; side lobes triangular to setaceous. Paleas papery, glabrous, 2-nerved; ciliolate on keels; apex acute to truncate or minutely 2-

lobed, reaching approximately to base of awn. Stamens 3, anthers pale to brown, 2-2.5 mm long in chasmogamous flowers, minute in cleistogamous ones. Lodicules 2, cuneate, well-developed only in chasmogamous flowers. Caryopses obovate, brown, 1.5-2.5 mm long X 1-1.5 mm broad.

1 Glumes 12-18(-20) mm long; hairs on lemma much longer above, upper marginal hairs more than 1.5 mm long.....1. D. sericea

1 Glumes 7-14(-15) mm long; hairs on lemma more or less uniform in length, upper marginal hairs less than 1.5 mm long

2 Lobes of lemma shorter than to slightly longer than basal flattened, twisted, and colored portion of awn, triangular to sub-setaceous; basal leaves usually curly; callus glabrous or with a few hairs at sides.....2. D. spicata

2 Lobes of lemma exceeding basal portion of awn, setaceous; basal leaves straight or curving; callus distinctly hairy.....3. D. compressa

1. D. sericea Nutt. DOWNY O. G. Culms 3-10(-12) dm tall. Most sheaths densely pubescent. Ligules 0.5-3 mm high. Collars densely pubescent on back, with longer hairs at sides. Blades up to 40 cm long X 1.5-3(-4) mm wide, more or less densely long-pubescent below, often minutely hispid-puberulent above. Panicle dense to open, erect or somewhat lax, (4-)6-15 cm long X 2-6 cm broad, with 6-20 or more

spikelets; branches puberulent, with slightly longer hairs in axils and below spikelets, 1-5 cm long, 1-6 spikelets per branch. Spikelets 12-24 mm long including awns, 6-9 flowered. Glumes (11-)13-19 mm long. Lemmas 7-10 mm long including side lobes, silky-pubescent on back especially toward base, upper hairs longer; margins densely fringed, upper hairs more than 1.5 mm long, much longer than basal hairs; side lobes 2-4 mm long, setaceous, exceeding base of awn; callus densely hairy; basal portion of awn golden brown, 2-3 mm long, apical portion 8-15(-19) mm long. (n = 18). Spring and summer. Dry, open woods, waste places, and sandy areas; all prov. SE except WVA. [Tex, Pa, NJ]. (Including D. epilis Scribn.--F, S, G).

Occasional plants are nearly glabrous; these have been segregated as var. epilis (Scribn.) Gleason, but do not appear to be deserving of varietal status.

2. D. spicata (L.) Beauv. POVERTY O. G. Culms 2-8 (-9) dm tall. Sheaths glabrous to sparsely long-pilose, pale to purple at base, often with papilla-based hairs. Ligules 0.2-1 mm high, with longer hairs at sides. Collars sometimes sparsely long-pubescent, especially on margins. Blades 6-20 cm long X 1-2.5 mm wide; glabrous to sparsely long-pubescent on one or both surfaces; basal leaves usually forming a curly tuft. Panicle erect, spike-like to somewhat open, (3-)4-7(-9) cm long X 1-3 cm broad, with 2-15 spikelets; branches appressed to ascending, hispidulous, without longer hairs in the axils, up to 2 cm long, 1-2(-3) spikelets per branch. Spikelets 9-17 mm long including awns,

(4-)6-9 flowered. Glumes (6-)9-15 mm long. Lemmas 3.5-5.5 mm long including side lobes; pilose to nearly glabrous, hairs of relatively uniform length; margins fringed with hairs ca. 1 mm long; side lobes 0.5-1.5 mm long, broadly triangular to subsetaceous, shorter than to slightly exceeding basal portion of awn; callus glabrous or with a few hairs at sides; basal aportion of awn light brown to dark purplish brown, 1-3 mm long, apical portion 3-10 mm long. (2n = 31, 36). Spring - early summer, occasionally later. Dry, open woods, fields, and roadsides, usually on poor soil; all prov. SE. [ALL].

This is an extremely variable species, but the presence of papilla-based hairs at the base of the leaf sheaths is diagnostic. It and the following species appear to intergrade, and occasional plants which appear intermediate are difficult to place. These may represent gene exchange; however, since there appears to be no consistent geographic or ecological pattern, and since the vast majority of specimens can be assigned to one species or the other, this is not considered taxonomically significant.

3. D. compressa. MOUNTAIN O. G. Culms 2.5-7.5(-9) dm tall. Sheaths glabrous to pubescent, often purple. Ligules 0.5-7 mm high. Collars with a distinct tuft of white hairs at sides. Blades 10-30 cm long X 1-3 mm wide; glabrous or occasionally sparsely long-pubescent above. Panicle open or sometimes narrow, 3.5-11 cm long X 1-4 cm broad, with 5-15 spikelets; branches spreading or ascending, hispidulous,

without longer hairs in axils, 1-5 cm long, 1-4(-7) spikelets per branch. Spikelets (10-)12-18 mm long including awns, 4-8 flowered. Glumes 9-13 mm long. Lemmas 5-7 mm long including side lobes, short-pubescent on back to nearly glabrous, hairs of more or less uniform length; margins fringed, upper hairs ca. 1 mm long; side lobes 2-4 mm long, setaceous, exceeding base of awn; callus densely pubescent; basal portion of awn light to dark brown, 1.5-2 mm long, apical portion 5-10 mm long. (n = 18). Spring-summer. Open woods, fields, grassy balds; chiefly mts. SE except Ark, Del, Fla, La. [Ohio, Pa, NJ]. (Including D. alleni Aust--F).

A dominant species on grassy balds and old fields in the mountains.