AN INVESTIGATION INTO THE EVOLUTION OF ANNUALNESS IN THE GENERA *KARROOCHLOA* AND *SCHISMUS* (DANTHONIDEAE: POACEAE)

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ABSTRACT

Despite the considerable work conducted on this subject, the relationships between the genera within the tribe Danthonideae (Poaceae) remain poorly understood (Tomlinson 1985, Conert 1986). In the Danthonideae the annual life history has evolved in only five of the currently recognised genera. Two of these genera that contain annual species, *Karroochloa* Conert and Türpe and *Schismus* Beauv., are regarded as very closely related (Conert 1986), but this has not been confirmed by cladistic analysis. This study sought to investigate the evolution of the annual life history in this clade, necessitating the construction of a phylogeny.

The results of the cladistic analysis do not support the monophyly of *Karroochloa* plus *Schismus*, and indicate that *Karroochloa* is more closely related to the genus *Rytidosperma*. The genus *Schismus* was found to display a sister group relationship to *Tribolium*, which also contains both annual and perennial species. Annualness was found to have evolved four times and reversed twice within this clade.

No clear correlation was established between the evolution of the annual life history and ploidy levels, although the annuals in this clade are generally diploid. Whether the species are widespread, locally common or rare was also found to be unrelated to their life history. The annual species are confined mostly to the arid Succulent Karroo, and it is postulated that climatic constraints may have been the primary forces driving the evolution of annualness in this clade.

The annual species *S. barbatus* is the exception in this clade and is thought to have undergone additional adaptations that have facilitated it becoming widespread in southern and northern Africa and the middle east. The unusual distribution of this species is examined, and some hypotheses regarding its causation are forwarded.

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1. INTRODUCTION

The relationships between the genera in the grass sub-family Arundinoideae are highly unresolved and unstable, chiefly because most genera are plesiomorphic for many characters. Consequently Arundinoid taxonomy is in a state of disarray (Conert 1980, Campbell 1985, Watson 1990, Davis and Soreng 1993). The tribe Danthonieae is considered to contain the core genera of the Arundinoideae and is comprised of a loose group of taxa with a phenetic resemblance to *Danthonia* sensu stricto (Tomlinson 1985, Renvoize 1980, Campbell 1985). Despite considerable study, the phylogenetic and taxonomic relationships within the Danthonideae remain obscure (Tomlinson 1985, Conert 1986).

The Danthonideae are usually perennial (Conert 1986, Campbell 1985) and do not show any physiological adaptations as a group to specific environments (Renvoize 1980). One of the most intriguing patterns seen in the Danthonideae is the evolution of the annual life history in species of *Karroochloa, Schismus, Tribolium, Ehrhartia* and *Pentaschistis*. These genera have all had their origin in Africa (Linder, pers. comm.). The appearance of the annual life history in only these African Danthonideae presents an interesting situation which requires explanation. Very little work has been conducted on elucidating the forces driving the evolution and selective advantage of the annual life history in grasses other than those important for cereal domestication (Tainton 1984).

In this study, the relationship between two of these African Danthonid genera containing annual species, *Karroochloa* and *Schismus*, will be investigated. These two genera each have 50% of their species being annuals, and have been regarded as closely related on the basis of leaf anatomy and habit (De Wet 1956, Conert and Türpe 1969, Conert 1971, Tomlinson 1985).

A major obstacle to understanding their relationships is that neither *Karroochloa* nor *Schismus* have any easily recognised autapomorphies and are plesiomorphous for most characters. In addition, they are superficially very similar. Their exact position in relation to each other and to other closely related Danthonid genera has not previously been established by cladistic methods.

In order to investigate the evolution of the annual life history in this segment of the Danthonid phylogeny, an evolutionary hypotheses is required. The aims of this study are therefore to reconstruct the phylogeny within this clade, in order that the evolution of annualness and its geographical distribution can be examined.

2. METHODS

2.1 Justification for the use of primarily morphological characters:

In a comparative anatomical study of *Danthonia* sensu lato, Tomlinson (1985) examined the leaf anatomy of *Karroochloa* and *Schismus* and established that the features which these two genera share are found elsewhere in the Danthonieae. She conceded that leaf anatomical data from *Schismus* and *Karroochloa* were inconclusive, but generally supported the close relationship between these genera suggested by Conert and Türpe (1969, 1974) and Conert (1971). Nevertheless, leaf anatomy was investigated here, albeit briefly, but was found to be uninformative.

Tomlinson (1985) also found that lodicule morphology is variable in both *Karroochloa* and *Schismus* and is thus of no value in determining their interrelationships. The variation in epidermal microhair types in the Danthonideae has also been shown to be as great within species as it is between them (Klak 1993), and consequently these were not investigated here.

Classification in the Danthonideae is still based largely on characters of the spikelet and lemma morphology, which provides the most distinctive characters of this group, although it is acknowledged that this has undoubtedly been subject to much parallel evolution and convergence (Clayton 1981, Kellogg and Campbell, 1986, Clayton and Renvoize 1986). In the absence of informative anatomical and other types of data, the characters examined in this study were largely morphological.

2.2 Specimens used and methods:

Herbarium material from BOL, NBG and STE (abbreviations follow Holmgren et al. 1990) was examined, and four to five typical specimens were selected from each of the species of *Karroochloa*, and from *S. barbatus*, *S.inermis* and *S. scaberrimus*. The species *S. pleuropogon* and *S. arabicus* were unfortunately not available for investigation. Specimens were selected from as wide a geographical range as possible in order to include most of the major geographical variation, but a typical specimen from the respective localities was chosen to avoid intrapopulational variation. Aberrant specimens and potential hybrids were avoided.

The condition of the specimen, the presence of a caryopsis and the state of maturity of the florets and leaf blades were additional criteria considered during the selection procedure. Species of *Karroochloa* and *Schismus* studied, voucher specimens used and their localities are listed in Table 1.

Floret morphology was investigated from spikelets that were rehydrated by boiling in water with a wetting agent for half a minute. These were then dissected out in water under a Zeiss Stemi SV6 dissecting microscope. The spikelet glumes and the entire second floret were mounted on a microscope slide in glycerine to which a crystal of fuschin had been added. The whole mounts were then sealed using nail varnish, which ensures that they last for approximately six months.

The slides were later examined under both a Zeiss Stemi SV6 dissecting microscope and a Zeiss Standard 25 microscope, both of which were fitted with a graticule and a *camera lucida*. Drawings of the floral parts were made and compared in order to detect differences between the species, and to easily ascertain what is typical of the respective species. The procedures followed to obtain measurements of floral parts is shown in Appendix I for both *Schismus* and *Karroochloa*.

Material from all specimens that was to be used for leaf anatomy sections was first rehydrated by boiling as above before being fixed for at least twenty four hours in FAA prior to sections being cut. Only mature, fully-extended leaves were used; flag leaves were avoided. Transverse sections were only cut from the centimetre of tissue midway along the leaf blade length with a hand held razor blade.

Sections were stained for half an hour in safranin-alcian blue prior to being taken through an alcohol dehydration series to xylene and mounted on a microscope slide in canada balsam (Johansen 1940). The slides were left to dry in a cool oven for at least one month before being examined under a Zeiss Axioscope microscope.

An idea of what is typical of the anatomy for the respective species was gained by examining numerous abaxial epidermal scrapes and transverse leaf sections prepared with a microtome by Dr R.P. Ellis. These were examined under a Zeiss Axioscope microscope using both normal transmission optics and differential interference contrast optics.

Data were collected from mature caryopses which were not hydrated. Unfortunately, not all specimens had caryopses, with the annual species having many more specimens with caryopses than the perennials. In some specimens the caryopses were shrivelled or only half-formed at the time of collection and these were not used. The colour was similarly distorted by the developmental stage and little reliance was thus placed on this attribute. Caryopses were examined in petri-dishes under a Zeiss Stemi SV6 microscope with a *camera lucida*. The hilum was examined using incident lighting but the embryo was viewed from the opposite facet using below-stage lighting. Measurements were taken with the side of the caryopsis to be measured held horizontal by Prestik (by Bostick).

TABLE 1: Voucher specimens examined in this study and their locations, with abbreviations used for each specimen (Code).

CODE	SPECIES	SPECIMEN	HERBARIUM	LOCALITY	GRID
KC1	*Karroochloa curva*	Schlecter STE10899	STE	Port Nolloth	
KC2	*Karroochloa curva*	Esterhuysen 6736	BOL	Humansdorp	3321CC
KC3	*Karroochloa curva*	Mauve, V Wyk & Pare 4	STE	Muiskraal	3225CA
KC4	*Karroochloa curva*	Cleghorn 3156	STE	Somerset East	3420BB
KC5	*Karroochloa curva*	Du Toit 2000	STE	Bredasdorp	
KS1	*Karroochloa schismoides*	Pillans 18262	BOL	Namaqualand	
KS2	*Karroochloa schismoides*	Williamson 3004	BOL	Holgate Gorge	3017BA
KS3	*Karroochloa schismoides*	Le Roux & Lloyd 657	STE	Springbok	2917DB
KS4	*Karroochloa schismoides*	Crook 1006a	BOL	Springbok	3320BC
KP1	*Karroochloa purpurea*	Ellis 2470	STE	Sutherland	
KP2	*Karroochloa prupurea*	Bolus 520	BOL	Graaf-Reniet	3319BC
KP3	*Karroochloa purpurea*	Ellis 2475	STE	Worcester	3027CA
KP4	*Karroochloa purpurea*	Linder 4838	BOL	Barkly East	3320CB
KP5	*Karroochloa purpurea*	Barker 33	STE	Montague	
KT1	*Karroochloa tenella*	Compton 2882	BOL	Laingsburg	
KT2	*Karroochloa tenella*	Adamson 1806	BOL	Commando Dunes	3118DA
KT3	*Karroochloa tenella*	Linder 4271	BOL	Van Rhynsdorp	
KT4	*Karroochloa tenella*	Schlelpe 8148	BOL	Calvinia	
SS1	*Schismus scaberrimus*	Rodin 1480	NBG	Namaqualand	3119DB
SS2	*Schismus scaberrimus*	Taylor 2767	NBG	Calvinia	3220DA
SS3	*Schismus scaberrimus*	Cloete & Haselau 132	STE	Calvinia	3220DA
SS4	*Schismus scaberrimus*	Cloete & Haselau 225	STE	Roggeveld Escarpment	2917BA
SB1	*Schismus barbatus*	Crook 2245	NBG	Port Nolloth	
SB2	*Schismus barbatus*	Pillans 1727	BOL	Hex River Valley	3220BC
SB3	*Schismus barbatus*	Linder 4996	BOL	Karroo	
SB4	*Schismus barbatus*	Oliver 172	STE	Worcester	
SI1	*Schismus inermis*	Esterhuysen 23297	BOL	Bredasdorp	3325DC
SI2	*Schismus inermis*	Ellis 2563	STE	Port Elizabeth	3420CB
SI3	*Schismus inermis*	Ellis 2536	STE	Bredasdorp	3422AA
SI4	*Schismus inermis*	Parsons 514	STE	Mossel Bay	3420CB
SI5	*Schismus inermis*	Du Toit 1937	STE	Bredasdorp	3318CD
TL	*Tribolium longifolium*	Linder 5022	BOL	S.W. Cape	
C	*Chaetobromus spp.*	Verboom			

TABLE 2: Characters from *Karroochloa* and *Schismus* investigated for the phenetic analyses. Specimen codes are as in Table 1.

1 -Lower glume length
2 -Upper glume length/ Lower glume length
3 -Glume to spikelet g<s (0); g≥s (1); g>>s (2)
4 -Upper glume awn: absent (0); present (1)
5 -Length of upper glume awn
6 -Number of veins in upper glume
7 -Number of veins in lower glume
8 -Florets per spikelet
9 -Lemma length
10-Ratio of lemma length/lemma width
11-Ratio of mucro length/awn + column length
12-Ratio of column length/lemma length
13-lemma lobe length
14-Lemma lobe width
15-Ratio of lemmalobe length/lemmalobe width
16-Ratio of lemmalobe length/lemma length
17-Ratio of mucro length/lemma length
18-Upper row of transverse lemma hairs: present (1); absent (0)
19-Lower row of transverse lemma hairs: present (1); absent (0)
20-Diagonal row of lemma hair tufts: present (1); absent (0)
21-Lemma margin: entirely hairy (1); not entrirely hairy (0)
22-Middle of lemma: hairy (1); glabrous (0)
23-Length of upper lemma hairs
24-Length of lower lemma hairs
25-Shape of lemma hair tips: clavate (0); pointed (1)
26-Ratio of upper lemma hair length/column length
27-Ratio of upper lemma hair length/lemma lobe length
28-Lemma lobe veins: apical (1); shorter (0)
29-Palea length
30-Ratio of palea length/palea wiidth
31-Ratio of palea length/lemma length
32-Ratio of palea length/lemma + column length
33-Ratio of palea length/column length
34-Internal palea hairs: present (1); absent (0)
35-External palea hairs: present (1); absent (0)
36-Caryopsis surface: shiny (1); dull (0)
37-Caryopsis colour: yellow (1); cream (2)
38-Caryopsis length
39-Caryopsis length/width
40-Embryo length/caryopsis length
41-Hilum length/caryopsis length
42-Anther length
43-Life history: annual (1); perennial (0)
44-Callus length
45-Ratio of rachilla segment length/callus length
46-Leaf indumentum: hairy (1); glabrous (0)
47-Awn: simple (0); geniculate (0)
48-Palea shape: spoon (0); paddle (1); linear (2)
49-Caryopsis shape: linear (0); obovate (1); semi-triangular (2)

TABLE 3: **Data collected from *Karroochloa* and *Schismus* for phenetic analysis, attribute number is as in Table 2, whilst specimen number is as in Table 1. Missing or non-applicable data are represented by 999.**

	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	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49
KC1	4.44	0.66	1	1	0.13	3	5	4	1.28	1.03	3.62	1.17	1.34	0.66	2.27	1.05	2.83	1	0	0	1	1	1.29	0.23	1	0.95	0.98	1	2.44	3.67	1.91	0.68	1.63	1	0	1	1	0.68	999	0.41	0.41	1.84	0	0.41	0.85	0	0	2	1
KC2	4.63	1.06	1	1	0.25	3	3	4	1.28	1.03	4.25	1.22	1.16	0.56	2.47	0.91	3.32	1	1	0	1	1	1.19	0.56	1	0.78	1.03	1	2.78	4.71	2.17	0.98	1.76	1	1	999	999	999	999	999	999	1.44	0	0.03	2.67	0	0	2	999
KC3	4.12	0.9	1	1	0.25	3	7	4	1.2	1.03	3.62	0.94	1.25	0.34	3.68	1.04	3.02	1	0	0	1	1	0.2	0.89	1	0.18	0.18	1	2.22	3.98	1.85	0.95	1.98	1	1	1	1	0.86	999	0.51	0.42	999	0	0.41	0.85	0	0	2	1
KC4	4.31	0.96	1	1	0.19	5	3	4	1.28	2.29	2.94	1.02	1.25	0.16	2.23	0.98	2.3	0	1	0	1	1	1.11	0.5	1	0.85	0.89	1	2.53	4.52	1.98	0.98	1.93	1	1	999	999	999	999	999	999	1.52	0	0.06	0.38	0	0	2	999
KC5	3.62	0.85	1	0	0	5	5	4	1.12	0.78	3.38	1.34	1.34	0.41	2.03	1.2	3.02	0	1	0	1	1	1.16	0.67	1	0.77	0.87	1	2.25	3.57	2.01	0.86	1.5	1	1	999	999	999	999	999	999	1.48	0	0.33	1.33	0	0	2	999
KS1	4.94	0.98	1	1	0.44	3	5	3	1.48	1.48	4.31	0.97	1.25	1	2.66	0.84	2.91	1	0	0	1	1	0.98	0.16	1	0.69	0.75	1	2.47	3.58	1.67	0.85	1.72	1	1	1	1	0.84	0.57	0.57	0.24	999	1	0.43	1.07	0	0	2	1
KS2	3.69	0.94	1	1	0.19	3	5	3	1.28	1.52	2.69	0.93	1.09	0.16	2.66	0.86	2.1	1	0	0	1	1	0.69	0.21	1	0.58	0.63	1	2	4	1.56	0.81	1.88	1	1	1	1	1.12	0.36	0.17	0.2	1.08	1	0.37	1.03	0	0	2	0
KS3	5.56	0.96	1	1	0.25	3	5	4	1.4	1.13	4.31	1.39	1.28	0.5	1.94	0.91	3.06	1	0	0	1	1	1.19	0.11	1	0.61	0.93	1	2.63	3.91	1.88	0.79	1.36	1	0	1	1	1.02	0.47	0.5	0.29	1.24	1	0.36	1.29	0	0	2	1
KS4	6.25	0.93	1	1	0.63	3	5	3	1.76	1.42	7	1.49	1.63	0.91	2.91	0.93	3.96	1	0	0	0	0	1.13	0	1	0.43	0.69	1	3.03	4.39	1.72	0.69	1.15	1	0	1	1	1.04	0.31	0.44	0.37	1.66	1	0.44	1.11	0	0	2	0
KP1	6	0.99	1	1	0	9	9	5	1.36	0.81	5.66	1.79	2.19	999	2.61	1.61	4.32	1	0	1	1	0	2.14	1.25	1	0.86	0.96	0	3.59	3.49	2.64	0.94	1.47	0	1	999	999	999	999	999	999	2.44	0	0.7	0.57	1	0	1	999
KP2	5.5	1.02	1	0	0	9	5	5	1.48	0.8	4.12	1.22	1.47	999	1.27	0.99	2.78	1	0	1	0	0	1.75	0.71	1	0.87	1.19	0	2.89	2.66	1.82	0.82	1.49	0	1	1	1	0.96	0.58	0.58	0.38	1.66	0	0.47	0.6	1	0	2	1
KP3	6.56	1	1	1	0	5	5	6	1.56	0.96	4.76	1.12	1.53	999	1.66	0.96	3.04	1	0	1	0	0	1.66	0.97	1	0.96	1.1	0	3.22	4.47	2.06	0.97	1.84	1	1	999	999	999	99	999	999	2	0	0.67	0.25	1	0	2	999
KP4	6	1	1	0	0	5	7	5	1.48	1	5.25	1.48	1.47	999	2.13	0.99	3.55	1	0	1	0	0	1.74	0.79	1	0.79	1.18	0	3.03	3.22	2.06	0.83	1.38	0	1	1	1	0.98	0.55	0.57	0.47	1.8	0	0.62	0.39	1	0	1	1
KP5	7.36	1.05	1	1	0	5	7	4	1.48	0.97	4.81	1.52	2.19	999	3.04	1.48	3.25	1	0	1	0	0	2.17	1.16	1	0.96	0.99	0	3.56	3.91	2.41	0.96	1.56	0	1	999	999	999	999	999	999	2.04	0	0.67	0.25	1	0	2	999
KT1	5.94	1.04	2	0	0	5	7	4	1.16	0.91	4.75	2.04	1.16	999	1.97	1	4.09	1	0	1	0	0	1.12	0.45	1	0.47	0.97	0	2.47	3.92	2.13	0.7	1.04	0	0	1	1	0.94	0.45	0.36	0.36	1.76	1	0.54	0.74	1	0	2	1
KT2	6.62	1.01	1	1	0	5	7	4	1.2	1.03	5.31	2.29	1.03	999	1.75	0.86	4.43	1	0	1	0	0	1.13	1.15	1	0.41	1.1	0	2.47	4.66	2.06	0.83	0.9	0	0	1	1	1.06	0.5	0.46	0.41	2.06	1	0.48	0.5	1	0	2	2
KT3	6.06	0.96	2	1	0.69	5	7	4	1.32	1	6.94	1.99	1.56	999	2.56	1.18	5.26	1	0	1	0	0	1.43	0.7	1	0.54	0.92	0	2.5	3.79	1.89	0.83	0.96	0	0	1	1	0.88	999	0.5	0.43	2.04	1	0.19	3.11	1	0	1	999
KT4	6.19	1.06	2	1	0.69	5	7	5	1.2	0.91	5.31	2.03	1.16	999	1.76	0.87	4.43	1	0	1	0	0	0.86	0.71	1	0.36	0.76	0	2.26	3.17	1.9	0.83	0.93	0	0	999	999	999	999	999	999	1.64	1	0.52	0.67	1	0	1	999
SS1	4.7	1.15	0	1	0.5	7	7	5	2.8	1.56	1.15	999	0.3	999	0.75	0.41	0.41	0	0	0	0	1	0.71	0.36	0	999	2.37	0	3.3	3	1.18	999	999	1	0	1	1	1	0.7	0.7	0.26	0.8	0	0.25	2	0	1	1	999
SS2	4.5	1	0	1	0.25	7	7	4	2.5	1.47	0.07	999	0.05	999	0.2	0.03	0.03	0	0	0	0	1	0.56	0.31	1	999	11.2	0	2.8	2.8	1.12	999	999	0	0	1	0	0.7	0.57	0.74	0.54	1.81	0	0.25	2.4	0	1	0	999
SS3	4.75	0.94	0	1	0.19	5	7	4	2.59	1.76	0.06	999	0.01	999	999	999	0.03	0	0	0	0	1	0.31	0.73	1	999	31	0	3.44	3.25	1.28	999	999	0	0	999	999	999	999	999	999	1.44	0	0.25	3.04	0	1	1	999
SS4	5.37	1.03	0	1	0.25	7	7	5	2.6	1.44	0.86	999	0.01	999	999	999	0.33	0	0	0	0	1	0.64	0.76	1	999	64	0	2.81	2.9	1.06	999	999	0	0	999	999	999	999	999	999	1.28	0	0.33	1.24	0	1	1	999
SB1	5.2	1.04	0	1	0.25	7	7	6	1.36	1.17	0.05	999	0.25	999	0.83	0.19	0.04	0	0	0	0	1	0.79	0.41	0	999	3.16	0	1.95	2.79	1.44	999	999	1	0	1	1	0.8	999	0.43	0.4	0.5	1	999	999	1	1	0	2
SB2	3.4	0.94	0	0	0	5	7	6	2.65	1.77	0.05	999	0.05	999	0.25	0.02	0.02	0	0	0	0	1	0.52	0.25	0	999	10.4	0	2.8	3.11	1.06	999	999	1	0	999	1	0.74	0.66	999	0.36	1.1	1	0.2	2	0	1	0	2
SB3	4.1	0.94	0	0	0	7	7	6	1.8	1.71	0	999	0.08	999	0.53	0.04	0	0	0	0	0	0	0.71	0.29	0	999	8.86	0	1.8	2.77	1	999	999	0	0	1	1	0.94	0.66	0.66	0.43	0.5	1	0.2	1.75	0	1	0	1
SB4	3.91	0.86	0	1	0.19	5	5	5	1.76	1.63	0.03	999	0.19	999	0.73	0.09	0.02	0	0	0	1	1	0.75	0.44	0	999	4.69	0	2.09	2.79	1.19	999	999	0	0	1	1	0.76	0.82	0.66	0.29	0.36	1	0.25	1.66	1	1	0	2
SI1	4.69	1.07	0	1	0.06	5	5	6	2.46	1.72	0.26	999	0.31	0.13	1.11	0.13	0.15	0	0	0	1	1	0.67	0.47	1	999	2.81	1	2.81	3.09	1.13	999	999	1	1	999	999	999	999	999	999	0.7	0	0.3	1.07	0	1	1	999
SI2	3.62	0.93	0	0	0	5	5	4	2.04	1.42	0.34	999	0.34	0	0.92	0.17	0.17	0	0	0	1	1	0.84	0.37	1	999	2.47	1	2.22	2.74	1.09	999	999	1	1	999	1	0.92	0.59	0.28	0.28	0.44	0	0.36	1.22	0	1	1	1
SI3	3.44	0.9	0	1	0.06	5	5	3	2.16	2.36	0.13	999	0.13	0.03	1	0.06	0.06	1	0	0	1	1	0.86	0.34	1	999	7.54	1	2.5	3.79	1.16	999	999	1	1	1	1	0.9	0.82	999	0.31	999	0	0.64	1	0	1	1	1
SI4	4.63	0.98	0	0	0	5	5	4	2.4	2.07	0.37	999	0.34	0	1.21	0.14	0.16	0	0	0	1	1	0.87	0.2	1	999	2.85	1	2.69	3.32	1.12	999	999	1	1	1	1	1.1	0.56	0.42	0.35	1.44	0	0.44	1.23	0	1	1	1
SI5	4.38	0.92	0	1	0.13	5	4	5	1.86	1.75	0.13	999	0.13	0.06	0.66	0.06	0.06	0	0	0	1	1	0.87	0.26	1	999	6.69	1	2.72	3.49	1.62	999	999	1	1	1	1	1.06	0.59	0.41	0.33	0.56	0	0.32	1	0	1	1	1
TL1	4.69	1.23	1	1	1.36	5	5	12	4.16	2.06	0.31	999	999	999	999	999	0.07	0	0	0	1	0	0.79	999	1	999	999	0	3.95	5.03	0.86	999	999	0	0	0	999	999	999	999	999	1.96	0	0.19	1.16	0	1	2	999
C1	12.5	1.12	2	1	1.36	5	9	999	3.48	1.53	9.31	1.06	1.79	4.69	2.37	0.51	2.68	0	1	0	0	0	906	0.53	1	999	999	0	4.53	4.67	1.3	0.83	1.21	0	0	0	0	3.36	0.21	999	0.43	4.6	0	0.48	3.25	0	0	2	0

TABLE 4: Characters used for cladistic analysis and their coding. Measurements are given in millimeters.

0. Annual/perennial: annual (0); perennial (1).
1. Leaf indumentum: absent (0); present (1).
2. Inflorescences: terminal (0); axillary (1).
3. Inflorescences: open (0); contracted (1).
4. Dispersal unit: floret (0); inflorescence (1).
5. Spikelet arrangement: spikelets distichously arranged (0); spikelets not distinchously arranged (1).
6. Spikelets per inflorescence: 5-20 (0); 20-50 (1); 50-100 (2) [additive].
7. Spikelet length: 2.5-2.9 (0); 3-5 (1); 5-6 (2); 7-10 (3); 10-20 (4) [additive].
8. Flowers per spikelet: 2 (0); 3-4 (1); 5-6 (2) [additive].
9. Glumes rel spikelet: longer (0); as long (1); shorter (2) [additive].
10. Glume apex: acute (0); acuminate (1); long-acuminate (2) [additive].
11. Glume bristles: present (0); absent (1).
12. Glume prickles: present (0); absent (1).
13. Glume macrohairs: stiff (0); inflated (1).
14. Callus: villous (0); glabrous (1).
15. Lemma: acute (0); lobed (1).
16. Lemma hairs: scattered (0); two lateral tufts (1); three tufts (2); two lateral rows (3) [additive] [deactivated].
17. Scattered lemma hairs: absent (0); present (1).
18. Lateral lemma hair tufts: absent (0); present (1).
19. Upper lemma hair row: absent (0); present (1).
20. Lower lemma hair tufts: absent (0); v-shaped (1).
21. Lemma hairs: penicillate (0); broadly clavate (1).
22. Lemma macrohairs: absent (0); present (1).
23. Lemma apex: acute (0); acuminate (1); long-acuminate (2) [additive].
24. Lemma lobe veins: shorter (0); apical (1).
25. awn; simple (0); geniculate (1).
26. Setae: lobe apex (0); lobe sinus (1).
27. Palea apex: wide (0); narrow (1).
28. Palea Indumentum: absent (0); present (1).
29. Palea margins: glabrous (0); villous (1).
30. Lodicule bristles: absent (0); present (1).
31. Anther length: 0.5-0.8 (0); 0.8-1.9 (1); 2-2.5 (2); 2.5-3 (3) [additive].
32. Caryopsis surface: dull (0); shiny (1).

TABLE 5: Data matrix from *Karroochloa, Schismus* and a selection of *Danthonid* species submitted for analysis to Hennig86 (Farris 1988) to produce Figure 9. Character numbers and states are given in Table 2.

```
                          0    5    10   15   20   25   30
                          ↓    ↓    ↓    ↓    ↓    ↓    ↓
Pentaschistus curvifolia  1000012400011-010100000-01111?120
Pentaschistus rodwayi     1000011210110-010110000-110010020
Rytidosperma laeve        1100011420011-013001000-1101001*0
Rytidosperma linkii       1*00011420110-013111000-1101111*0
Rytidosperma carphoides   1100010310110-013011000-1101111*0
Danthonia pallida         1000011420011-010100000-110111130
Karroochloa purpurea      1100011210011-013001100-010001121
Karroochloa tenella       0100011210011-013001100-010000011
Tribolium acutiflorum     1011011222010010200001010--000100
Tribolium alternans       1101000222101010010001000--111110
Tribolium brachystachyum  1101000122201010010001000--111120
Tribolium ciliare         0001010001001010101000000--110000
Tribolium echinatum       0101012100200010101000010--101010
Tribolium hispidum        1101012101100010101000000--220010
Tribolium obliterum       1001012121011010101000010--00*110
Tribolium obtusifolium    1001012111000010101000010--000110
Tribolium uniolae         1001000322111010011001000--101130
Tribolium utriculosum     0101011110201110010001000--111110
Tribolium pusilla         0101111210201010010001120--101010
Karroochloa curva         1100011210110-010101000-110111?11
Karroochloa shismoides    0100011210110-010101000-110111?11
Schismus barbatus         0000010122110-010100010-0001*0101
Schismus arabicus         0000010022110-010100000-100110101
Schismus inermis          1000011222010-010100000-1001111*1
Schismus scaberrimus      1000011222110-011010000-000100111
Schismus pleuropogon      110101-121010-111010000-100100100
Monostachya nivicola      100001021*010-011010000-110101110
```

2.3 Data analysis

Phenetic analysis

Characters that were examined for phenetic analysis are listed in Table 2, while the data set is shown in Table 3. Two sets of analyses were preformed; firstly on the whole data set and secondly on each genus separately, as the phenetic approach used produces superior results at the infrageneric level (G.A. Verboom, pers.comm.). For the infrageneric analyses, characters which varied between these two genera but not within them were omitted. Characters present in only one species were included in all of these phenetic analyses.

Morphological, anatomical and caryopsis data were analyses using NTSYS (Version 1.80, Rohlf 1993). Data were standardized by column, similarity intervals were computed and Manhattan distances calculated by rows. The UPGMA distance algorithm was used to cluster the most similar specimens together to produce the phenograms.

Cladistic Analysis

As the exact sister-group relationships of these genera are unclear, a database representing all species of *Tribolium* was included, as well as "placeholders" for most other major Danthonid lineages. Data was obtained from a comprehensive database being developed by H. P. Linder, and entered into a combined matrix (Table 5). The characters investigated, as well as which of these were deactivated in the final analysis are shown in Table 4.

These data were handled using DADA (written by Kevin Nixon), and analysed using the *ie option of hennig86 (Version 1.5, Farris 1988). Successive weighting (Carpenter 1988) was used to locate a single minimal length tree.

2.4 Distributions

Distribution patterns and ploidy levels were investigated from the literature (Conert and Türpe 1969, 1974, Conert 1971,1986, Gibbs-Russell et al. 1990, Chippindall 1955, Clayton and Renvoize 1986, Spies et al. 1988) in order to ascertain whether any correlation exists between these factors and the evolution of the annual life history. Altitudinal gradients and habitat preferences were noted. Whether the species in the Danthonid genera containing annual forms are widespread or rare in their respective habitats, as well as their ploidy level, is given in Table 6.

Distribution maps were obtained for all species in *Karroochloa* and *Schismus*, and these are presented in Figures 1-4. The distribution of the genera and the relevance of these distributions to the evolution of the annual habit was considered. In addition, the striking distribution pattern seen in the annual species of the genus *Schismus* were examined (Figure 5), and some hypotheses regarding its origin are subsequently proposed.

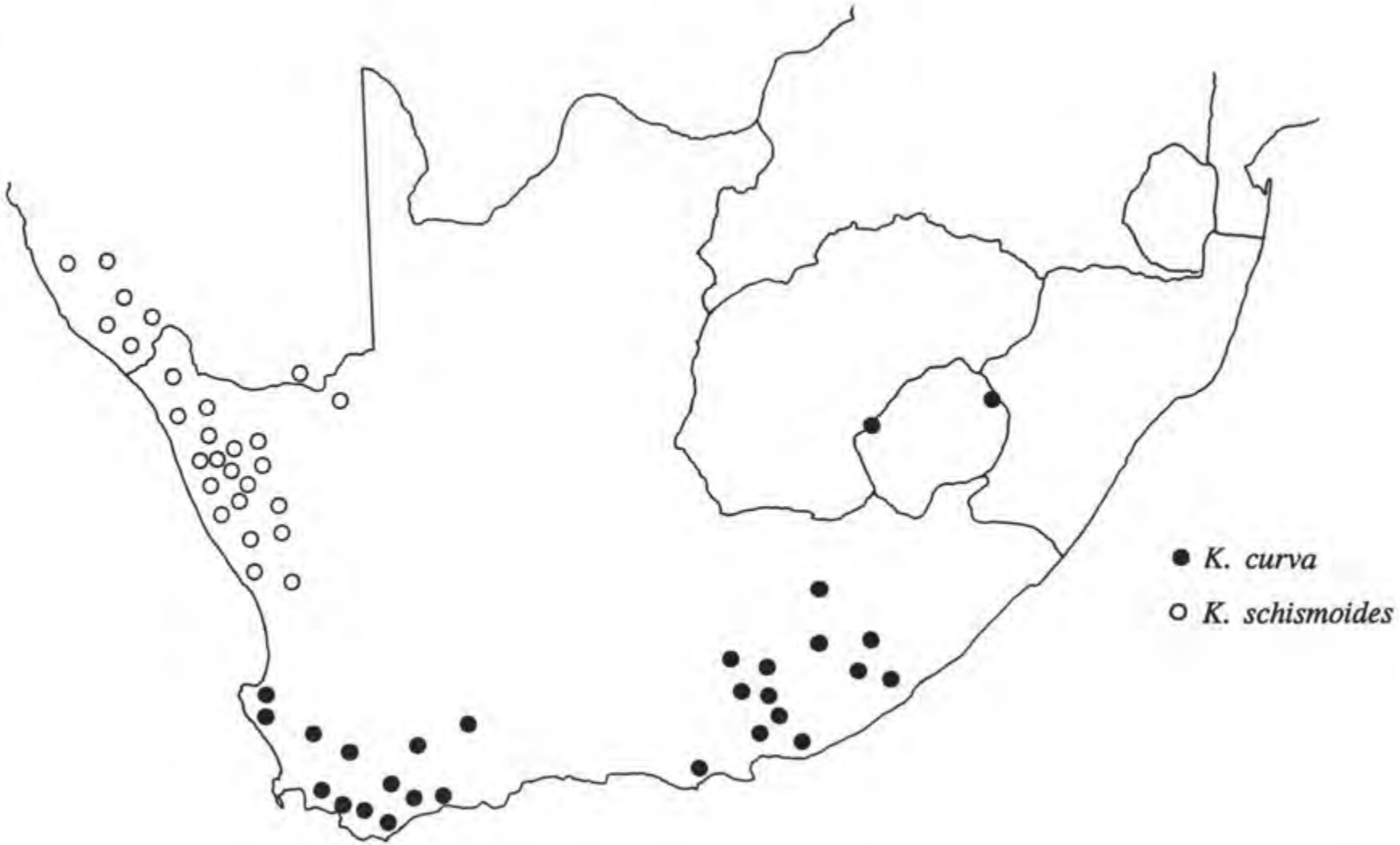


FIGURE 1: **Distribution of the perennial species *K. curva* and the annual species *K. schismoides*, assimilating data from Conert and Tűrpe (1969) and Gibbs-Russell et al. (1990).**

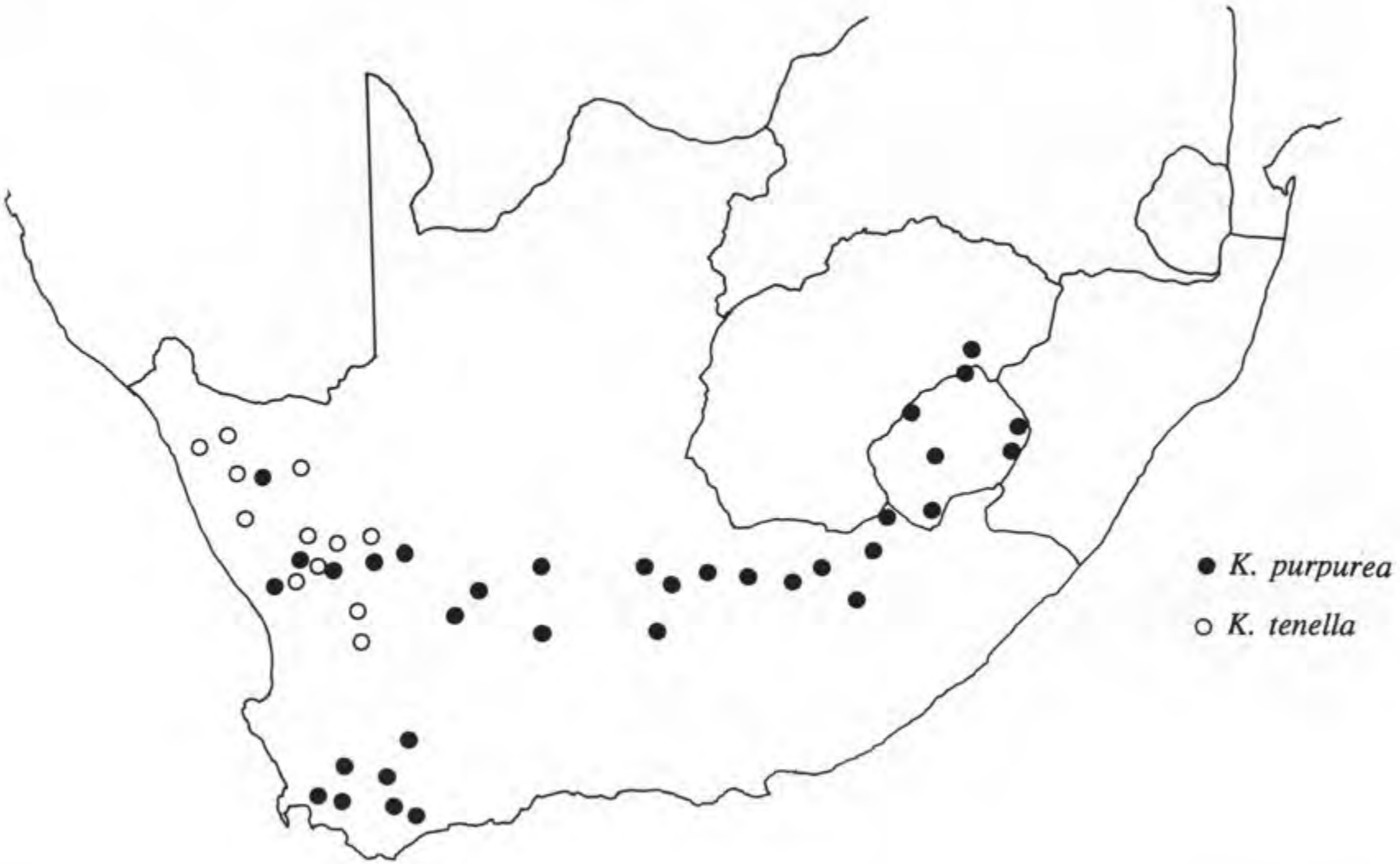


FIGURE 2: **Distribution of the perennial species *K. purpurea* and the annual species *K. tenella*, assimilating data from Conert and Türpe (1969) and Gibbs-Russell et. al. (1990).**

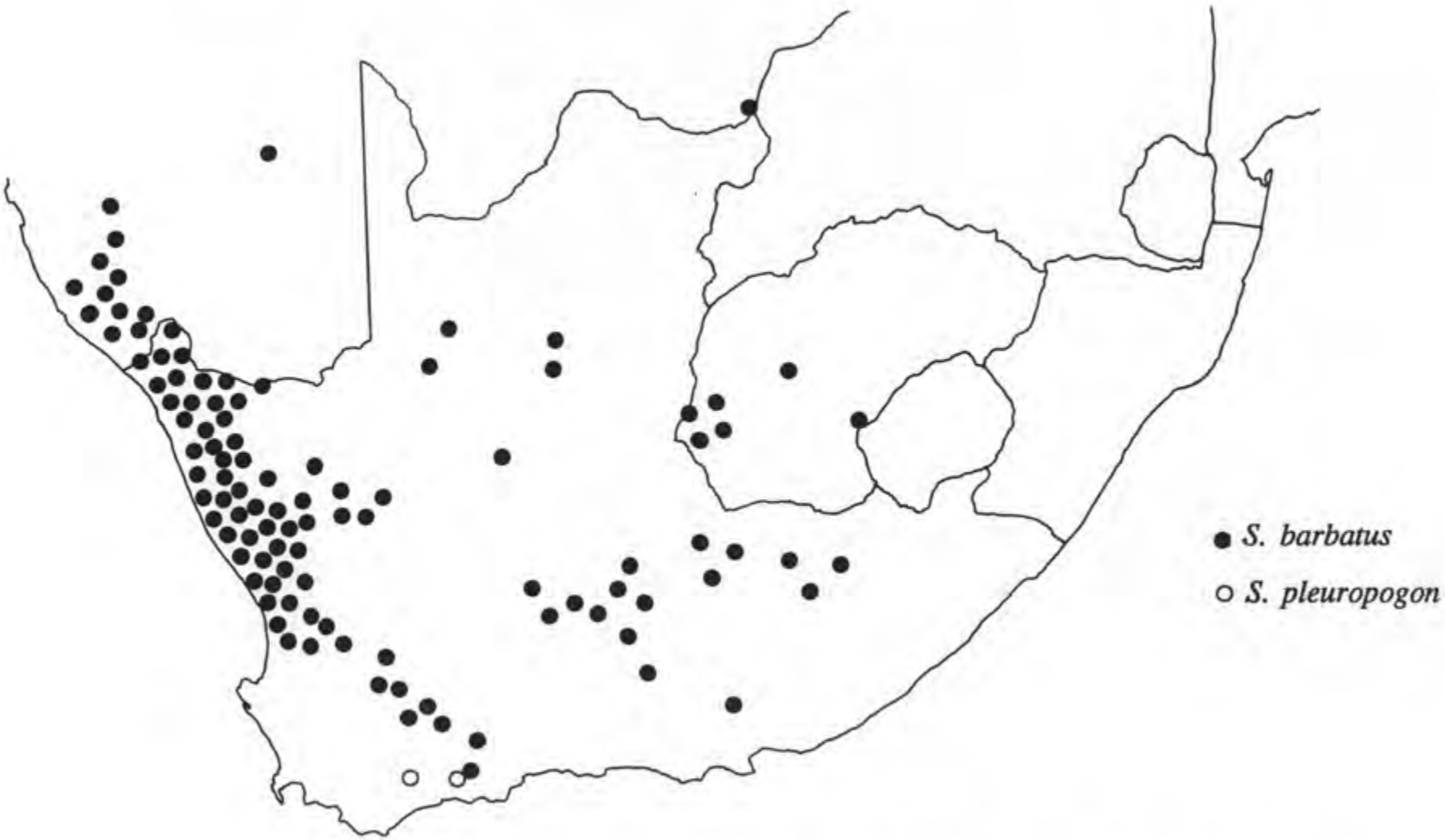


FIGURE 3: **Southern African distribution of the annual species *S. barbatus*, and the rare perennial species *S. pleuropogon*, assimilating data taken from Conert and Türpe (1974) and Gibbs-Russell et al. (1990).**

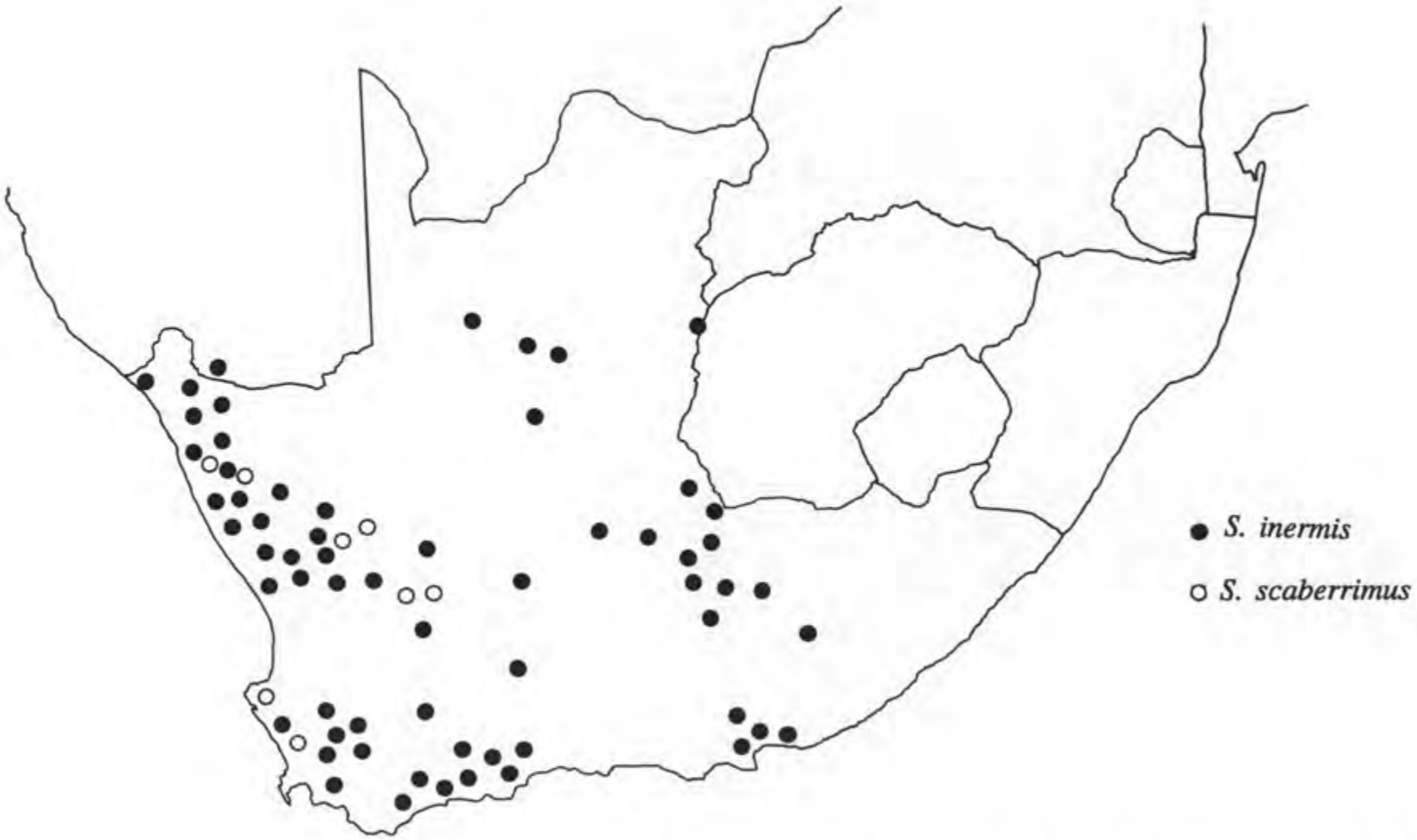


FIGURE 4: **Distribution of the perennial species *S. inermis* and *S. scaberrimus*. Note that further investigation is required of the habitat discernments of these two species, and the distributions here may be subject to alteration.**

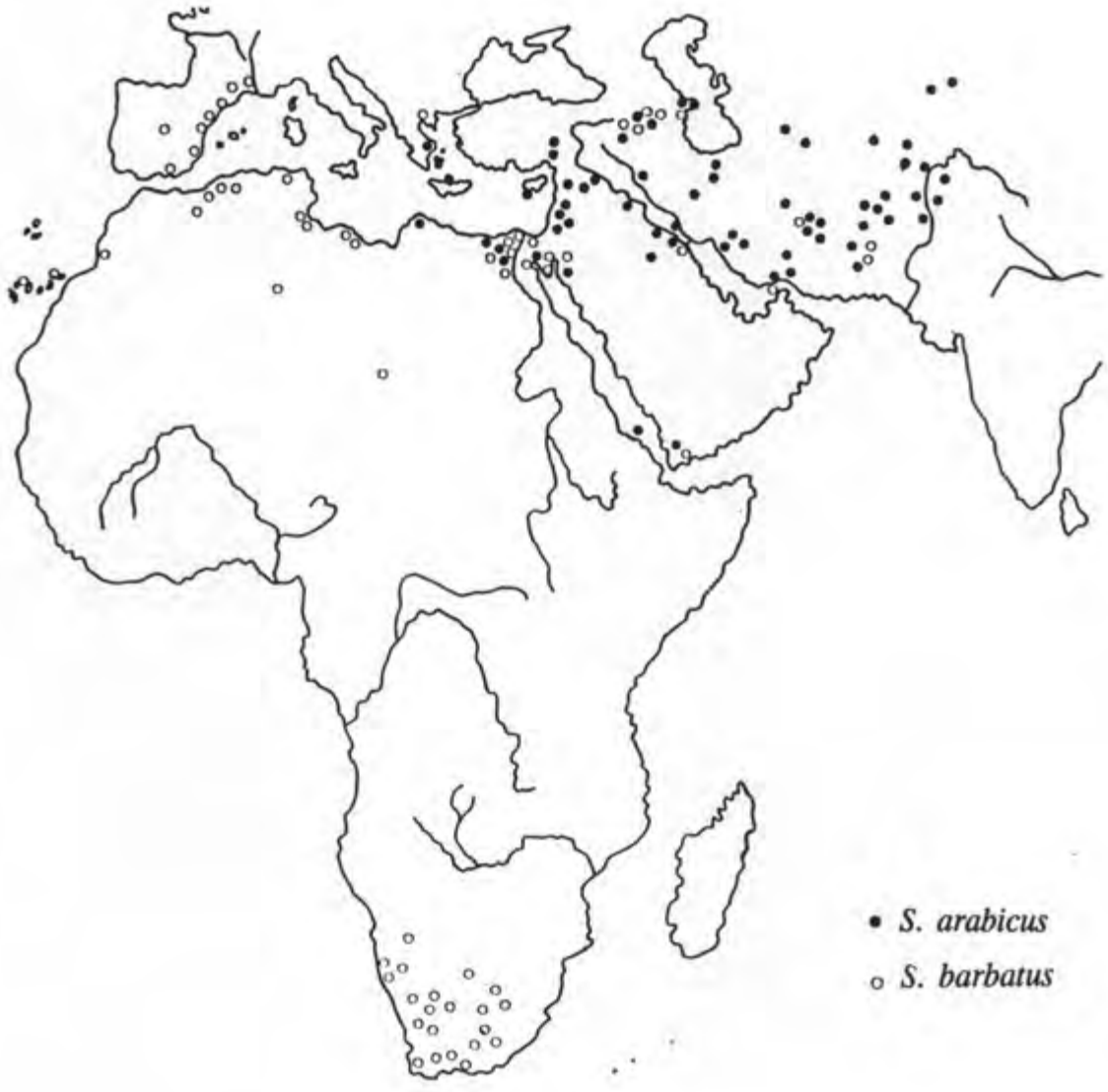


FIGURE 5: Distribution of the annual species of *Schismus* in southern and northern Africa and the middle east, taken from Conert (1986).

Table 6: Species investigated, their ploidy levels, life history and abundance {Data from H.P. Linder, Gibbs-Russell et al. (1990)}.

SCHISMUS			
SPECIES	**PLOIDY LEVEL**	**LIFE HISTORY**	**RARE OR COMMON**
Schismus barbatus	2n - 6n	Annual	Common
Schismus arabicus	2n	Annual	Common
Schismus scaberrimus	8n - 12n	Perennial	Locally Common
Schismus inermis	2n - 6n	Perennial	Common
KARROOCHLOA			
SPECIES	**PLOIDY LEVEL**	**LIFE HISTORY**	**RARE OR COMMON**
Karroochloa curva	2n	Perennial	Common
Karroochloa schismoides	4n	Annual	Common
Karroochloa purpurea	4n	Perennial	Common
Karroochloa tenella	2n - 4n	Annual	Common
TRIBOLIUM			
SPECIES	**PLOIDY LEVEL**	**LIFE HISTORY**	**RARE OR COMMON**
Tribolium acutiflorum	4n	Perennial	Rare
Tribolium obliterum	4n - 6n	Perennial	Common
Tribolium obtusifolium	?	Perennial	Rare
Tribolium hispidum	2n - 6n	Weakly Perennial	Common
Tribolium brachystachyum	4n	Perennial	Common
Tribolium alternans	?	Perennial	Rare
Tribolium uniolae	4n - 6n	Perennial	Common
Tribolium ciliare	2n	Annual	Rare
Tribolium uticulosum	2n	Annual	Common
Tribolium echinatum	2n	Annual	Common
Tribolium pusilla	2n	Annual	Locally common

3. RESULTS

3.1 Phenetic Analysis

The phenograms produced by analyses of both genera together and *Schismus* and *Karroochloa* separately are presented in Figures 6-8. The results of the phenetic analyses indicate that the species in these two genera are distinct entities and are thus suitable operational taxonomic units (OTU's) for cladistic analysis.

3.2 Cladistic Analysis

When data for *S. pleuropogon* was analysed in Hennig 86 with data from *Karroochloa, Schismus* and *Tribolium*, it upset the generic groupings (results not shown). Due to the suspicion that this taxon is of hybrid origin, Wagner's (1980) proposition to exclude hybrids from phylogenetic analysis was applied, and data from *S. pleuropogon* was deactivated.

The subsequent cladistic analysis resulted in a single tree with a length of 264 steps (Figure 9). The tree has a consistency index (CI) of 62 and a retention index (RI) of 85 (with uninformative characters removed). This tree groups the species of the respective genera together, and showed *Schismus* to have a sister group relationship to *Tribolium*, not to *Karroochloa*, which grouped closer to *Rytidosperma*.

The evolution of the annual life history is indicated on Figure 10 by thickened black lines.

FIGURE 6: **Phenogram generated using NTSYS (Rohlf 1993) for the genera *Karroochloa* and *Schismus*. Branch labels are as indicated in Table 1.**

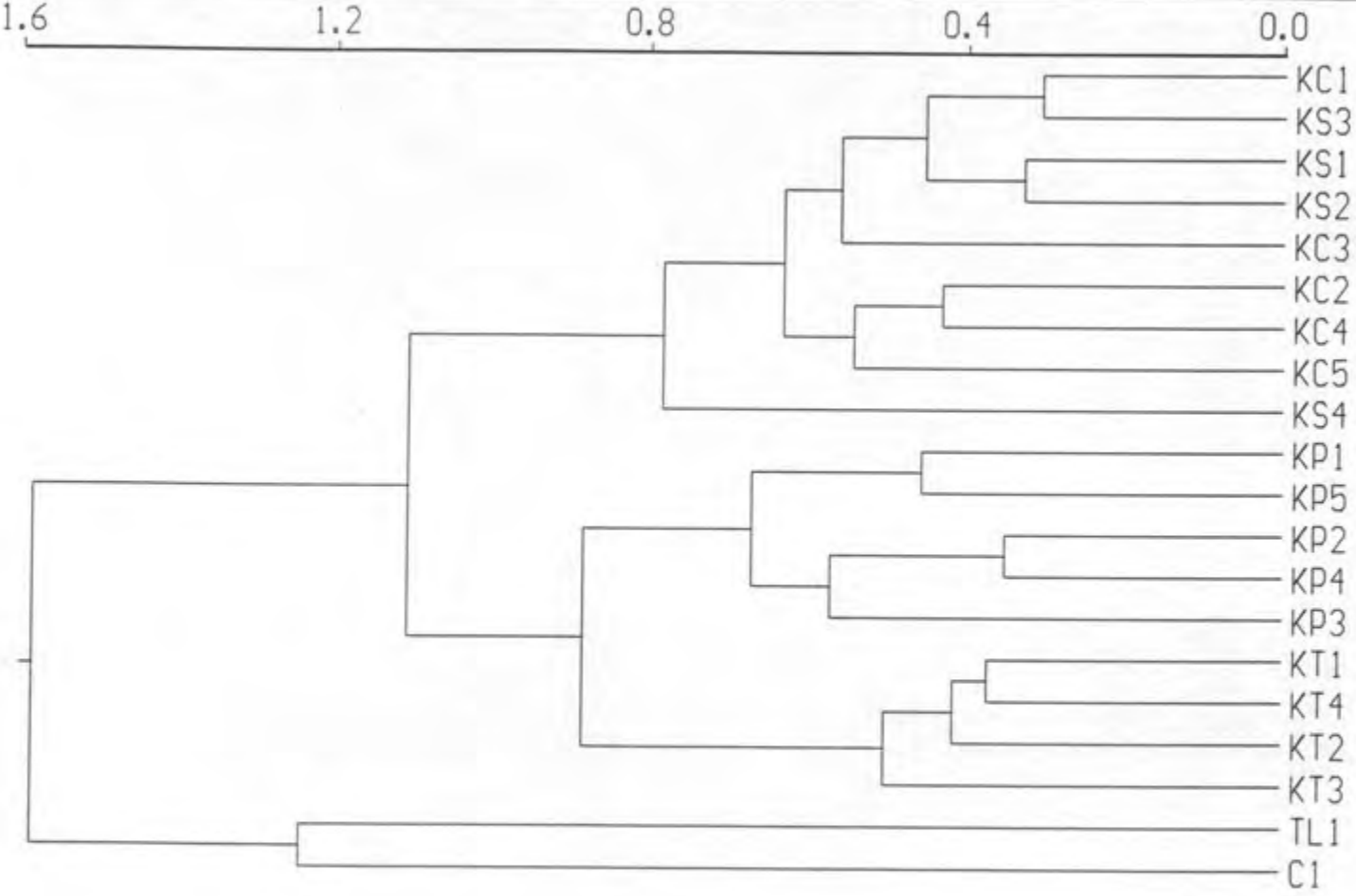


FIGURE 7: **Phenogram generated using NTSYS (Rohlf 1993) for the genus *Karroochloa*. Branch labels are as indicated in Table 1.**

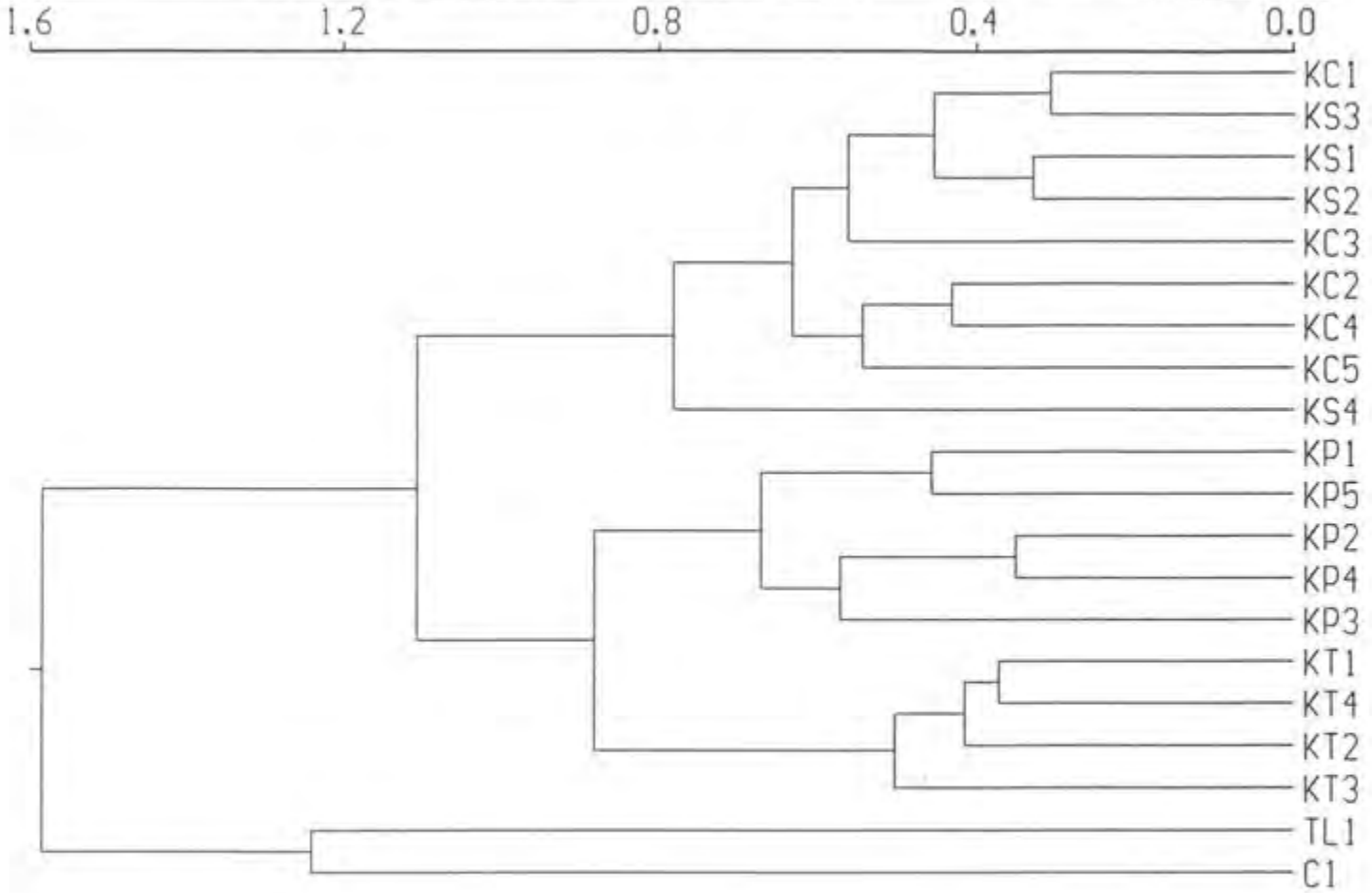
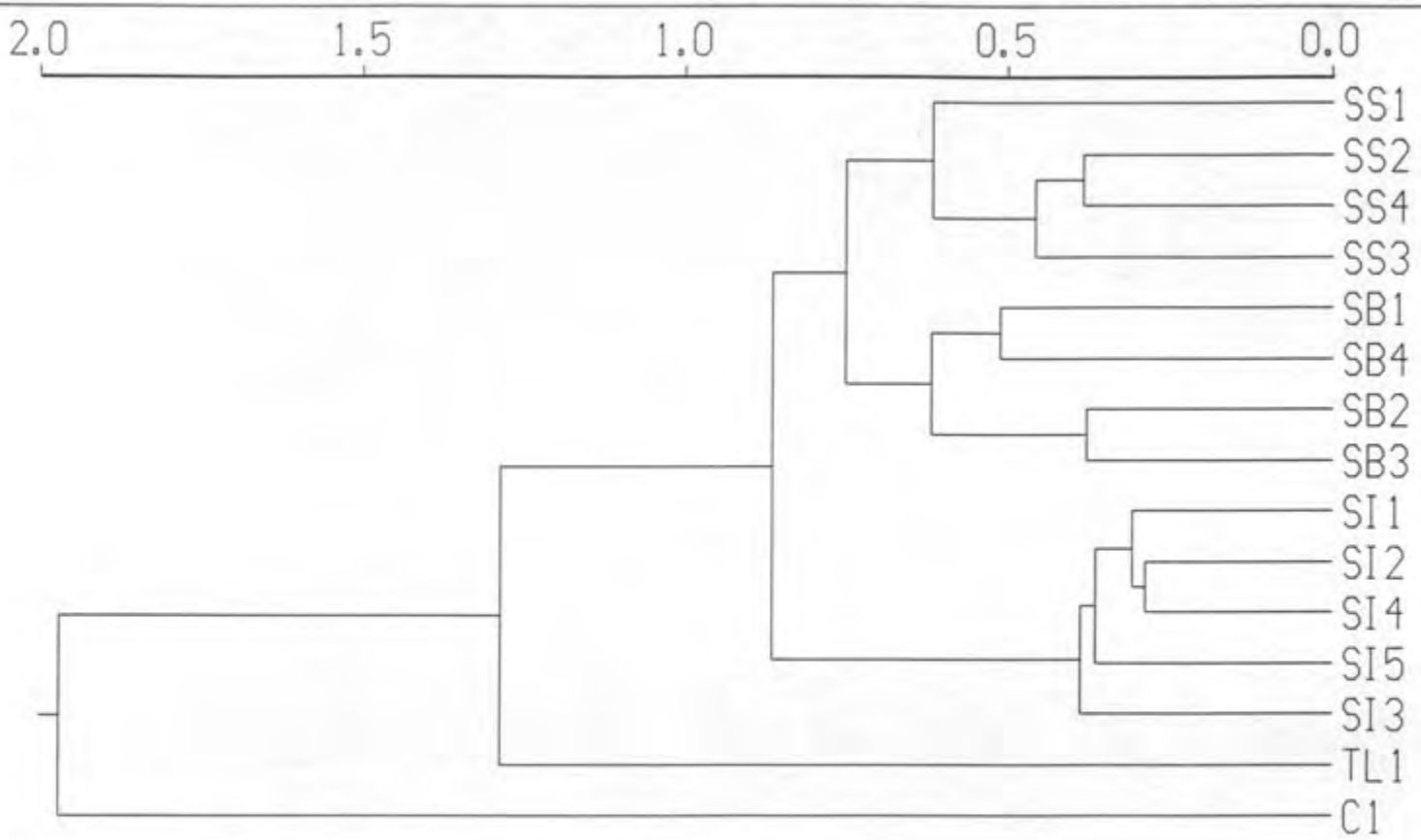


FIGURE 8: Phenogram generated using NTSYS (Rohlf 1993) for the genus *Schismus*, branch labels are as indicated in Table 1.



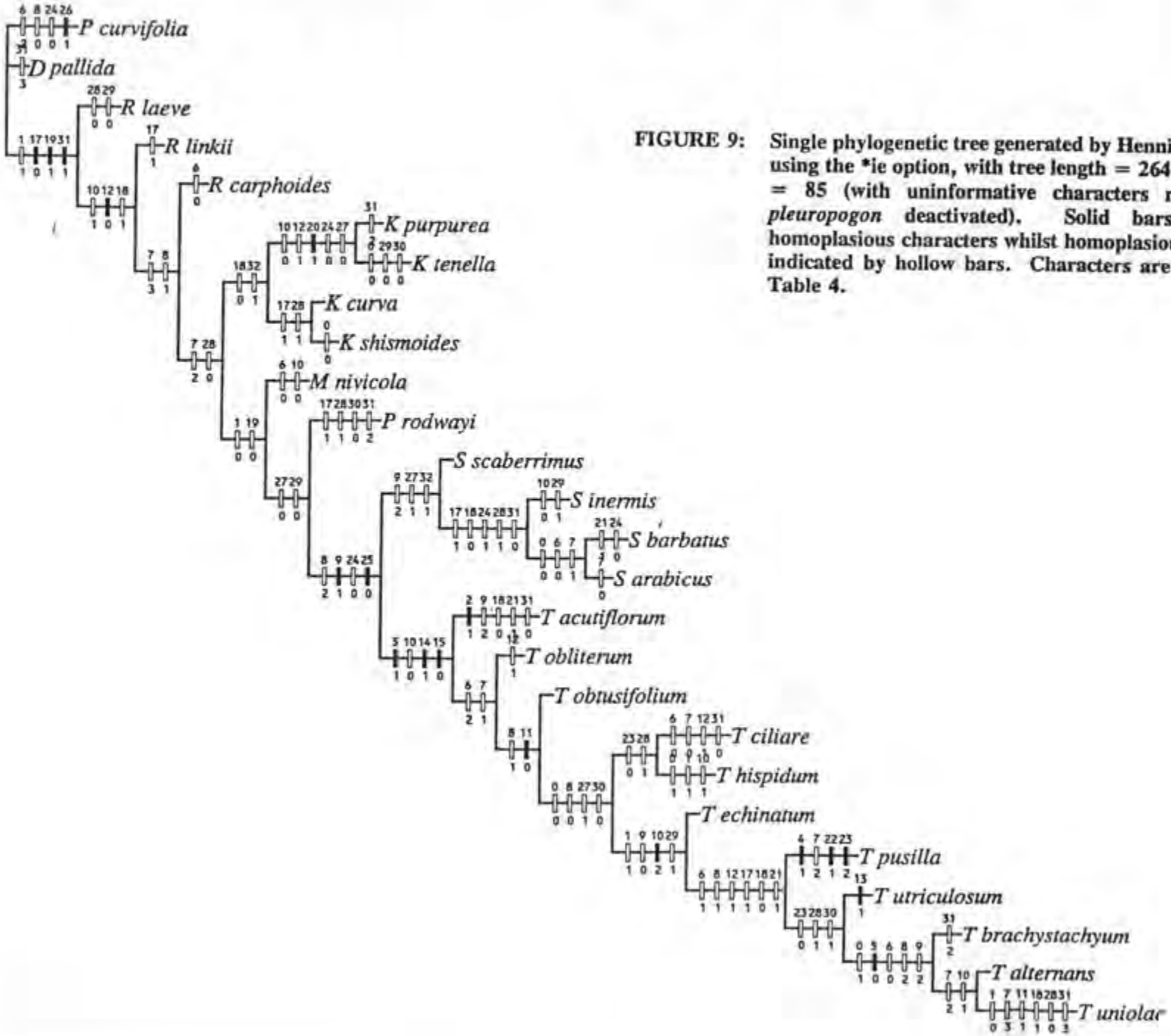


FIGURE 9: **Single phylogenetic tree generated by Hennig86 (Farris 1988) using the *ie option, with tree length = 264, CI = 62 and RI = 85 (with uninformative characters removed and *S. pleuropogon* deactivated). Solid bars indicate non-homoplasious characters whilst homoplasious characters are indicated by hollow bars. Characters are numbered as in Table 4.**

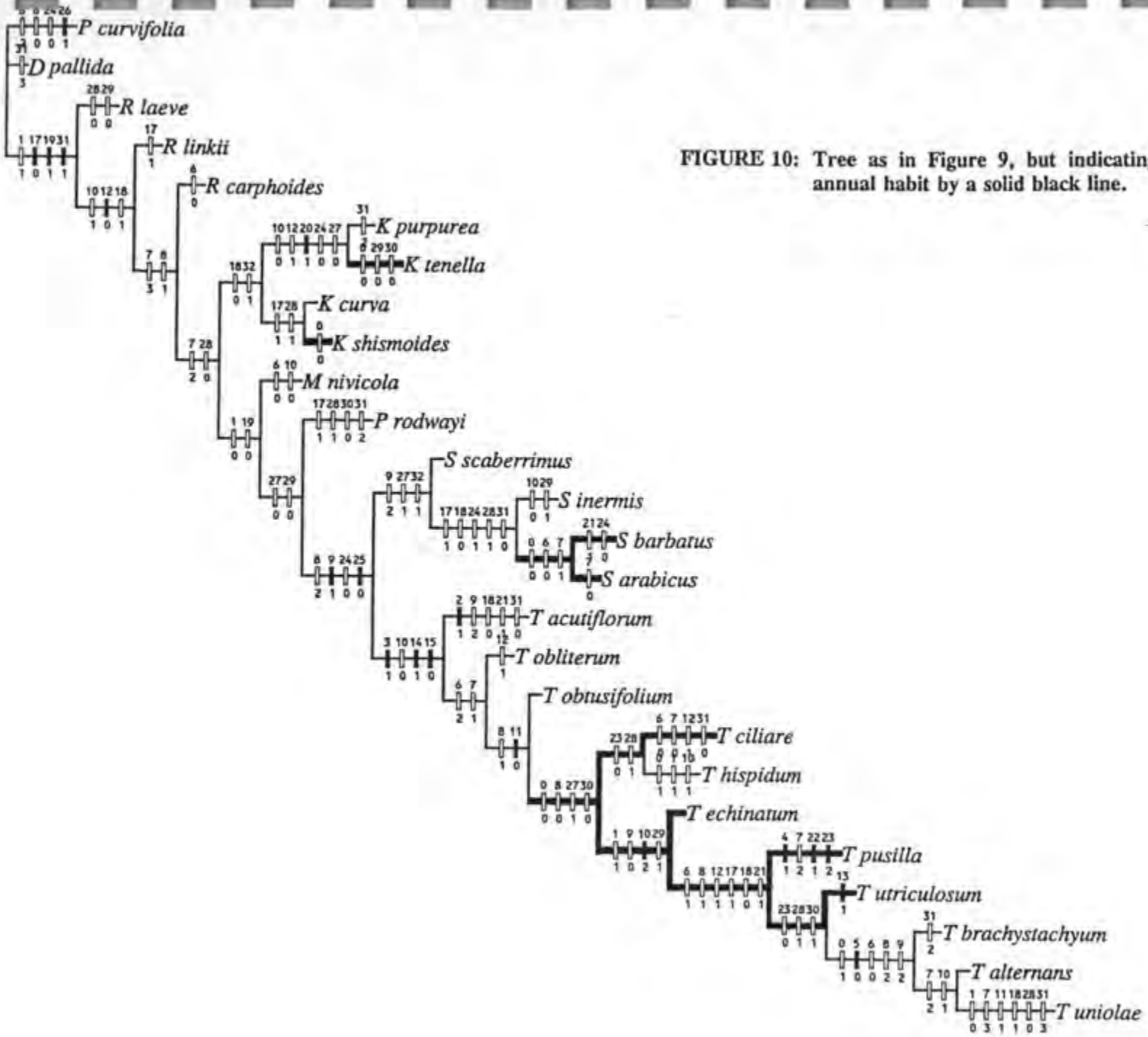


FIGURE 10: Tree as in Figure 9, but indicating the evolution of the annual habit by a solid black line.

4. DISCUSSION

4.1 Species recognition

Four species of *Karroochloa* are recognised (Conert and Türpe 1969,1971, Gibbs-Russell et al. 1990), while *Schismus* contains four distinct species and one taxon of hybrid origin, *S.pleuropogon*, which is addressed in Appendix 2. Diagrams of the species of *Karroochloa* and *Schismus* are displayed in Appendix 3.

The phenetic analyses performed in this study demonstrate that the species of both *Schismus* and *Karroochloa* are clearly discernable, with the exception of *K. curva* and *K. schismoides*, which were slightly intermingled (Figures 6-8). These two species were found to be difficult to separate using floral morphology, but could be separated on leaf anatomical characters.
There was no intermingling of the two genera, as they display many vastly different characters (Figure 6). The lack of autapomorphies supporting the grouping of the species into these two genera is clearly visible on the cladogram (Figure 9).

4.2 Putative Sister group relationships and characters supporting these

A sister group relationship between *Karroochloa* and *Schismus*, based primarily on the work of Conert and Türpe (1969 and 1974) and Conert (1971), is tentatively assumed by many authors in the literature (cf Kellogg and Campbell 1986). However, only two putative synapomorphies that group *Schismus* to *Karroochloa* have been identified. The only rigorous synapomorphy is that these two genera both posess a shiny caryopsis. Conert and Türpe (1974) reported that *Karroochloa* and *Schismus* share the character of bicarinate chartaceous prophylls, the keels of which are excurrent to form stiff pilose awns. However, this character appears only to be present in the annual species, and could reasonably be ascribed to parallel evolution (Linder, pers. comm.).

Significantly, the results of this analysis do not support the monophyly of *Schismus* plus *Karroochloa*. *Schismus* displays a sister group relationship to *Tribolium*, whilst *Karroochloa* groups closer to the members of the genus *Rytidosperma*. Renvoize (1980) recently sunk the genus *Karroochloa* into *Rytidosperma*, a large and diverse genus of southern Danthonids which was originally segregated from *Danthonia* by Zotov (1963) as *Notodanthonia*, but is now known by the earlier valid name *Rytidosperma*.

Recent molecular analyses using a grass-specific insert in the *rpo*C2 gene in the chloroplast genome suggested a sister-group relationship of *Karroochloa* to *Rytidosperma* (Barker et al. in prep.). The results of the cladistic analysis conducted here support the placement of *Karroochloa* nearer to *Rytidosperma* than to *Schismus*.

The sister group relationship between *Schismus* and *Tribolium* is supported by two non-homoplasious characters. The first of these is the presence of the simple awn type (character 25 on Figure 9); which may or may not be a good character, as there is no convincing basis for assuming a single evolution of the simple awn type in a common ancestor.

The second non-homoplasious character linking these two genera is that, in both, the spikelets are as long as, or longer than, the glumes (character 9 on Figure 9). Whilst the glumes usually exceed all the florets in the Danthonideae (Conert 1986), this character is surely dependant to some extent on the number of florets in the spikelet (Renvoize 1985).

In addition, several species of *Tribolium* have the lemma hair tips clavate shape (Renvoize 1985, Visser and Spies 1994) as is found in *S. barbatus* and occasionally in *S. scaberrimus*, which facilitates the grouping of these two genera on the cladogram (character 21 on Figure 9). The placement of *Tribolium acutiflorum*, *T. obtusifolium* and *T. obliterum* nearer to *Schismus* on the cladogram is reinforced by the absence of bristles on the glumes (character 11 on Figure 9).

In general, *Schismus* has many character states in common with many of the perennial species of *Tribolium*, but few in common with the *Tribolium* annuals (Figure 9). The exact topology of the respective *Tribolium* species in relation to *Schismus* will probably be subject to some alteration as more data accumulates, but the results of this analysis nevertheless support the monophyly of *Schismus* plus *Tribolium*, while contradicting the hypothesis of a sister-group relationship between *Karroochloa* and *Schismus*.

4.3 Distribution Patterns

The two perennial species of *Karroochloa, K. curva* and *K. purpurea*, are widespread throughout the southern Cape and occur in mountainous regions as far north as Lesotho (Figures 1 and 2). The annuals *K.tenella* and *K.schismoides* are largely restricted to the Nama-Karroo and Succulent Karroo where they are locally common and occur sympatrically (Figures 1 and 2). It is pertinant to note that the annual *Tribolium* species are also confined mostly to the Succulent Karroo, but occasionally occur slightly further north and south, extending into the Nama-Karroo and Fynbos Biomes.

Schismus displays a very peculiar disjunct distribution, with the genus undoubtedly being centered in southern Africa, as are the related genera *Karroochloa* and *Tribolium*, with the *Schismus* perennials, *S. inermis, S. pleuropogon* and *S. scaberrimus*, being endemic to South Africa (Figures 3 and 4). *S. inermis* is supposedly more common and displays a wider distribution than *S. scaberrimus*, which is supposedly rare, occurring only in the Succulent Karroo and adjacent areas of the western Karroo. However, these distributions are currently being critically examined. *S. pleuropogon* is rare and restricted to the Swellendam district.

Schismus extends its range into the Mediterranean region via two annual species, *S. barbatus* and *S. arabicus*. The species *S. barbatus* is widespread throughout southern Africa in addition to occurring in the western and northern Sahara, in the mountains of the central Sahara and the western Mediterranean (Conert and Türpe 1974, as shown in Figure 5), and in Australia and Argentina, where it has presumably been introduced (Nicora 1968).

In contrast, *S. arabicus* does not occur in southern Africa and has its centre of distribution in south west Asia, with its range extending westwards as far as Greece in the north and Cyrenaica in the south (Conert and Türpe 1974).

4.4 Ploidy levels

In herbaceous plants, the incidence of polyploidy is generally lower in annuals than in perennials (Stebbins 1979, Lewis 1979, Ehrendorfer 1979, De Wet 1979), but in the Poaceae, a somewhat abnormal situation exists where the annuals are usually tetraploid or have higher ploidy levels. In the Danthonoid clade investigated here, the annuals are usually diploid (Table 6), a situation which is somewhat atypical, as diploid annual grasses are rare (Linder, pers. comm.).

The generalised notion that the diploid species of a taxon are usually more limited in their distributions (as in relictual) than their polyploid relatives (Lewis 1979) does not hold true for *Schismus*, and whether the species are common or rare and their ploidy levels are not at all correlated in *Karroochloa*.

It has also been proposed that, in general, polyploids have a greater adaptability and colonizing ability than do diploids (Zeven 1979, Dewey 1979, Lewis 1979). The annual *S. barbatus* is widespread and contains tetraploid

and hexaploid forms in addition to the diploids, and if this theory is applied, it could be stated that the degree of adaptability afforded by polyploidy may have aided the dispersal of *S. barbatus* to the Mediterranean and middle east.

However, the perennial *S. scaberrimis* is rare and restricted in distribution, and this species' unusually high ploidy level of 8n - 12n (Table 6) indicates that it may have had a polyploid origin (Stebbins 1982). In addition, *S. inermis* is widespread and also contains forms that are diploid to hexaploid, as encountered in *S. barbatus*, but has also not experienced a major dispersal around the world. Therefore, the above theory is evidently not applicable to *Schismus*; this suggests that the annual habit has probably had more to do with the dispersal of *S. barbatus* than do ploidy levels.

In conclusion, neither ploidy levels, nor whether the species are widespread or rare, shows any correlation to the annual or perennial life history in the genera examined.

4.5 The evolution of annualness on the cladogram

The annual growth habit appears repeatedly in many genera of grasses and is the apomorphic condition. In *Schismus*, the annual life history has arisen once, and occurs only in the sister species *S. barbatus* and *S. arabicus*. In *Karroochloa, K. purpurea* and *K. tenella* show a sister group relationship, as do *K. schismoides* and *K. curva*; this is presumed to be correct, despite the homoplasy introduced by the evolution of the annual life history twice within this genus.

The situation regarding the evolution of the annual life history in *Tribolium* is somewhat more complicated, with the results of the cladistic analysis conducted here showing annualness to have arisen once in *Tribolium* and to have reversed twice (Figure 10). In the cladogram for the entire clade, annualness has thus evolved four times and reversed twice.

From the hypothesis of relationships developed here, it is improbable that the annual life history evolved once in a common ancestor. This would require far more evolutionary events (12 steps on the cladogram) to explain, given the current topology, than the evolution of the annualness more than once, which is accounted for by 6 steps on the cladogram (Figure 10). Thus it is essentially a parsimony argument which states that it is more plausible to assume that annualness evolved independently in these related genera than it is to assume that it arose once in a common ancestor.

Why a large proportion of the species in this clade of the Danthonideae have independently evolved annualness remains enigmatic, but it has undoubtedly been greatly influenced by their habitat.

It is known that climate constitutes a major influence on the evolution of the annual life history. An example of this is the evolution of an extraordinary number of early spring annual grasses in the mediterranean regions of the world, which has been attributed to the ill-adaptation of the grass growth cycle to a cold weather rainy season (Clayton and Renvoize 1986). All three genera occur in the more arid areas of South Africa, with the annual species of *Karroochloa* and *Tribolium* being largely restricted to the Succulent and Nama-Karroo (Figures 1 and 2). The annual *S. barbatus* is considerably more widespread, but nevertheless concentrated in the Succulent Karroo (Figure 3).

In this region, the extreme seasonality and low annual rainfall (generally less than 100mm (Schulze and McGee 1978)) may have strongly influenced the evolution of annualness. Annualness has proven to be an effective strategy ensuring survival in harsh environments, as seasonally unfavourable conditions can be avoided. In extremely arid environments, the seeds can remain dormant for the duration of the dry season. In addition, annual species have a faster genetic turnover, due to the shorter generation times, than perennial species, which may assist the annual species to track and cope with an

extremely harsh environment. Natural selection therefore favours annualness under extremely arid conditions, providing that sufficient soil nutrients are available for rapid growth (Bond, pers. comm.).

Colonizing ability is essential in annuals, with many of these being pioneer species that invade disturbed transient habitats (De Wet 1981). The annual life history is often associated with the evolution of specialized reproductive parts that aid in seed dispersal (Stebbins 1982). A failure to reproduce in annuals could lead to local extinction, thus annualness requires a high degree of reproductive efficiency and accuracy (Clayton and Renvoize 1986).

The Succulent Karroo has no clearly defined rainy season (Schulze and McGee 1979); this has probably forced exceedingly fine adaptation to climate and perception of environmental stimuli in the species occurring there. *Karroochloa* and *Tribolium* annuals have not managed to disperse far into adjacent biomes; this may be as a result of them being unable to escape the strict reproductive constraints exerted on them by their habitat. Strong selection pressures favouring strict reproductive adherence to prevailing climatic conditions has possibly narrowed these annuals' tolerances to such an extent that they have not been able to pre-adapt to succesfully competing under the conditions prevailing in adjacent areas.

Poor seed-set or low colonizing ability is presumably what prevented the perennial species of both *Schismus* and *Karroochloa* from dispersing to become globally widespread in a similar manner to the annual *S. barbatus*, although they can be widespread in southern Africa. The species *S. barbatus* is more likely to be the exception to the rule in this clade, and must have embarked on adaptational pathways that have facilitated it becoming globally widespread (Connor 1981).

The contribution of grazing pressure to the evolution of annual grass forms has received no attention in the literature (Tainton 1984). Grazing pressure exerted by the millions of Springbok and other game that occurred in the arid regions of South Africa in the past may have been significant in selecting for the annual life history.

Linder has observed that in the arid regions near Van Rhynsdorp where these Danthonid grass genera containing annuals occur, large tracts of land can be seen that have recently changed from karroid vegetation, dominated by shrubs with the grass component of the vegetation comprising primarily of perennial grasses, to areas of annual grasslands. This situation is reminiscent of the Sahel region in northern Africa, where a widespread changeover from perennial to annual grassland is occurring (Kernick 1990). This is primarily as a result of extreme overgrazing by domestic livestock, and indicates that the annual life history is well adapted to cope with severe grazing pressure. This may be due to the lowering of the carrying capacity of the veld in the dry months, insuring that less grazers will be around to graze in the wet months, which ensures some sucessful seed set. Indeed, *Karroochloa*, *Tribolium* and *Schismus* can be locally dominant in overgrazed annual habitats which occur in their ranges (Linder, pers. comm.).

4.5 The distribution of *Schismus*

Grasses are thought to be poor natural travellers, with two thirds of grass genera being confined to the continent upon which they evolved (Clayton 1981). However, man has facilitated the dispersal of many species of grasses all over the world via the importation of livestock fodder and cereals. It is conceivable that *S. barbatus* reached the middle east via ancient trade routes, where agricultural disturbance may have provided this annual species with an ideal habitat. The Arabs are known to have visited Southern Africa in the past, as indicated by archaeological evidence from settlements like Zimbabwe

Castle, although the furthest inland that these peoples ventured was the edge of the eastern escarpment (Linder, pers.comm.). It is plausible that they could have imported *S. barbatus* back to Arabia, as its present distribution does reach the eastern escarpment, but it is not particularly abundant there (Figure 3). Even if this hypothesis can be refuted, the suggestion that the distribution of *Schismus* is due to dispersal, is essentially an unfalsifiable hypothesis.

Karroochloa annuals may never have been afforded the opportunity to disperse as *S. barbatus* was, as the ancient trade routes that are hypothesised to have aided the dispersal of *S. barbatus* never reached the Succulent Karroo.

An alternative vicariance explanation is that the ancestral or floristic origin of *Schismus* may have been widespread throughout Africa, with an ancient floristic track that stretched northwards up the west coast of Africa being responsible for the contemporary distribution of this genus.

The Southern African/Mediterranean distribution pattern is not unique to *S. barbatus*, and other species are known to have this extreme disjunct distribution, for example the genus *Centropodia* (Conert 1971). This vicariance hypothesis is reinforced by the occasional collection of specimens of *S. barbatus* slightly north of the equator (Figure 5), but these specimens' only relevance may be to give an indication of the route that *Schismus* took to get to the Mediterranean, or they may have no relevance at all, having reached these areas via the recent intervention of man.

The presence of two distinct species of *Schismus* annuals in north Africa and the middle east suggests that a speciation event occurred there. If Schismus was indeed introduced by ancient traders rather than following a much more ancient floristic track, this speciation event would have occurred extremely rapidly, in less than 10 000 years (De wet 1981). This is probably too short a time period to have allowed for the evolution of a new species, although this

possibility cannot at present be discounted. These two sympatric sister species tend to support the vicariance hypothesis.

In material from the areas where the distribution of these two *Schismus* annuals overlap (Figure 5), the morphological distinctions often become obscured (Conert and Türpe 1974, Conert 1986). This suggests the occurrence of hybridisation that is common between closely related species, or alternatively, the incomplete separation of the two taxa following a speciation event, which may be caused by a lack of, or ineffective, isolating mechanisms.

Although it is tempting to speculate that *S. arabicus* arose from *S. barbatus*, there are complications in trying to explain *S. arabicus's* chromosome complement as arising from that of *S. barbatus*. *S. arabicus* is the sole species of *Schismus* in which all specimens are diploid, so this taxon would presumably have had to have arisen from diploid stock of *S. barbatus*, considering that the polyhaploid origin of new species is deemed unlikely (Stebbins 1979).

Data in the literature does not mention whether ploidy levels in *S. barbatus* are different in southern Africa and the middle east, which could be useful in understanding the putative evolution of another species of *Schismus* in the latter region.

However, there is no evidence at present indicating that *S. arabicus* did not occur in southern Africa in the past and has not gone extinct there, but still managed to remain extant in its northern habitats.

One method of testing these alternate vicariance and dispersal hypotheses may be molecular analyses comparing the Mediterranean and middle eastern forms of *Schismus* with the southern African forms. This may give a preliminary indication of the time period involved between the separation of the northern

and southern African species of *Schismus*, and shed some light on the evolutionary relationships of *S. arabicus* to the rest of the genus.

These hypotheses cannot be confirmed nor refuted by fossil evidence, due to the paucity of the fossil record for grasses, but archaeological evidence may still be forthcoming that will provide some insight into the evolution and distribution of *Schismus*.

5. CONCLUSION

The high degree of similarity in morphology and leaf anatomy between *Karroochloa* and *Schismus* makes the assumption of a close relationship plausible. However, this overall similarity could easily be ascribed to the occurrence of parallel evolution under the constraints of their similar habitats (Clayton 1981), and given their close position as peripheral genera related to *Danthonia*.

The cladogram presented in Figure 9 is merely a hypothesis of relationship between *Karroochloa* and *Schismus*, and undoubtedly the exact topology will be subject to change as additional data accumulates. It is nonetheless not supportive of the evolution of the annual habit once in this clade, nor of the monophyly of *Karroochloa* plus *Schismus*. *Karroochloa* may indeed be more closely related to *Rytidosperma* than to *Schismus*, which is proposed as a putatative sister group to *Tribolium*.

Overall, the pattern observed in these Danthoid grasses is difficult to interpret with respect to life history, habitat and ploidy levels, so that inferences regarding adaptability according to these factors cannot readily explain the distributions seen in these genera. It is more likely that climatic constraints have been the primary selective forces behind the evolution of the annual life history in this clade.

Further research is necessary to understand the evolution of the annual habit in this section of the Danthonideae, with more emphasis being placed on the exact habitat discernments of the respective species and whether differences in ploidy levels exist in the same species in different localities.

The causes of the curious distribution of *Schismus* are undoubtedly very complicated, and the hypotheses proposed to explain this distribution need to be tested. The environmental constraints or other mechanisms whereby the dispersal of the annuals of *Karroochloa* have been constrained relative to those of *Schismus* require further investigation.

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APPENDIX 1

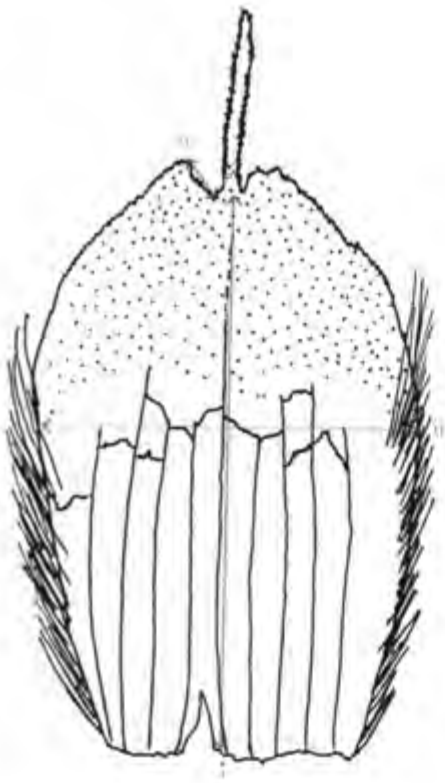
Specifications of how measurements were collected

i) Length of the lemma was measured at the midline from the base to the beginning of the column or awn.

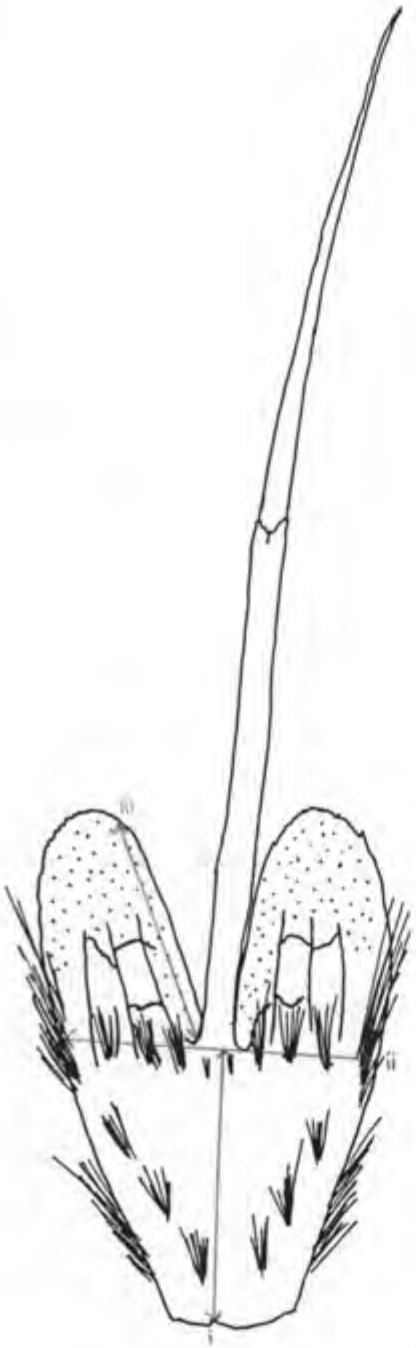
ii) The width of the lemma was measured either at the level of the column or at the anastomization of the veins if no column was present.

iii) Length of the lemma lobes was measured along the margin of the lobe from the base of the column/awn to the beginning of the lemmalobe awn or the tip.

iv) The palea width was measured at the widest point.



Schismus 25



Karroochloa

25

APPENDIX 2

The identity of *Schismus pleuropogon*

S. pleuropogon is known only from two gatherings, one in Swellendam and the other in the Riversdale District. This taxon was unavailable for this study, but Conert and Türpe (1974) produced a exceedingly detailed description of the specimens together with an informative diagram, which were studied in lieu of the specimens.

From Conert and Türpe's (1974) work, it can be seen that *S. pleuropogon* exhibits characters typical of both *Schismus* and *Tribolium* (Figure pleu). The lemma backs are glabrous with only two marginal hair tufts near the base, as seen in some species of *Tribolium*. The lemma lobes are small and fused to 3/4 of their length to the *Tribolium*-type central awn, thus displaying the characters of both genera. The inflorescence is compacted, as in Tribolium, and the caryopsis was described by Conert and Türpe (1974) as being rough (not shiny). The callus was also described as glabrous, a typical *Tribolium* character, but yet this taxon displays enough similarity to *Schismus* to have been identified as a new species of this genus!

This intermediacy in character states, taken together with its interference with the cladistic analysis, suggests that *S. pleuropogon* originated as a hybrid between *Schismus* and *Tribolium* (Linder, pers. comm.). Hybridization in grasses is extremely common and is often associated with the doubling of chromosomes in a sterile hybrid restoring chromosome pairing and fertility creating new species (Campbell 1985).

S. pleuropogon has recently been collected from roadside ditches in the Swellendam district. Due to habitat destruction that is occurring in this region, *S. pleuropogon* may have been displaced from its natural habitat, which is thought to be on heavy soils in that area, which are suitable for agriculture. This may explain why it is rarely collected, even if it was locally common in the past.

APPENDIX 3

Diagrams of the species of *Karroochloa* and *Schismus*

All diagrams of *Schismus* are from Conert and Türpe (1974) whilst those of *Karroochloa* are from Conert and Türpe (1969).

FIGURE IIIa. *Schismus barbatus* (LOEFLING ex LINNAEUS) THELLUNG. Voucher HUTER, PORTA and RIGO 1027. A-B) Plant Habit (x ½);C) Intravaginal shoots of plant in A with prophylls (x ½); D) Spikelet (x 15); E) Lower glume (x 15); F) Upper glume (x 15); G) Lemma (x 15); H) Palea (x 15); I) Tips of lemma hairs (x 100); J) Anthers (x 15); K) Lodicules (x 15); L) Caryopsis (x 15).

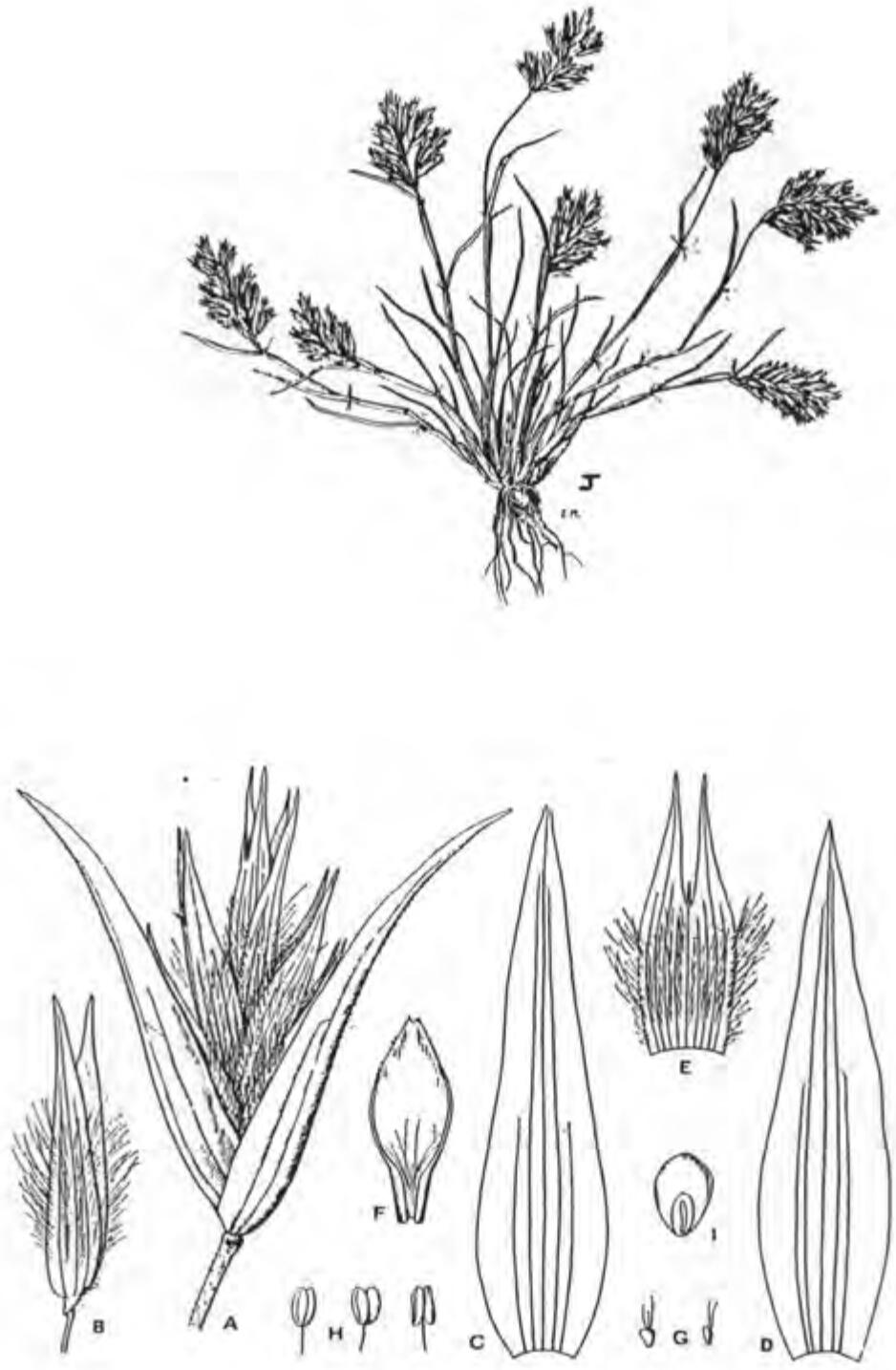


FIGURE IIIb. *Schismus arabicus* NEES. Voucher SHIMPER 391.
A) Spikelet (x 15); B) Floret side view (x 15); C) Lower glume (x 15); D) Upper glume (x 15); E) Lemma (x 15); F) Palea (x 15); G) Lodicules (x 15); H) Anthers (x 15); I) Caryopsis (x 15); J) Habit (x ½).

FIGURE IIIc. *Schismus inermis* (STAPF) C.E. HUBBARD. Voucher TYSON 27.
A_1-B_1) Plant habit (x ½); A) Spikelet (x 15); B) Lower glume (x 15); C) Upper glume (x 15); D) Lemma (x 15); E) Palea (x 15); F) Lodicules (x 15); G) Anthers (x 15); H) Caryopsis (x 15).

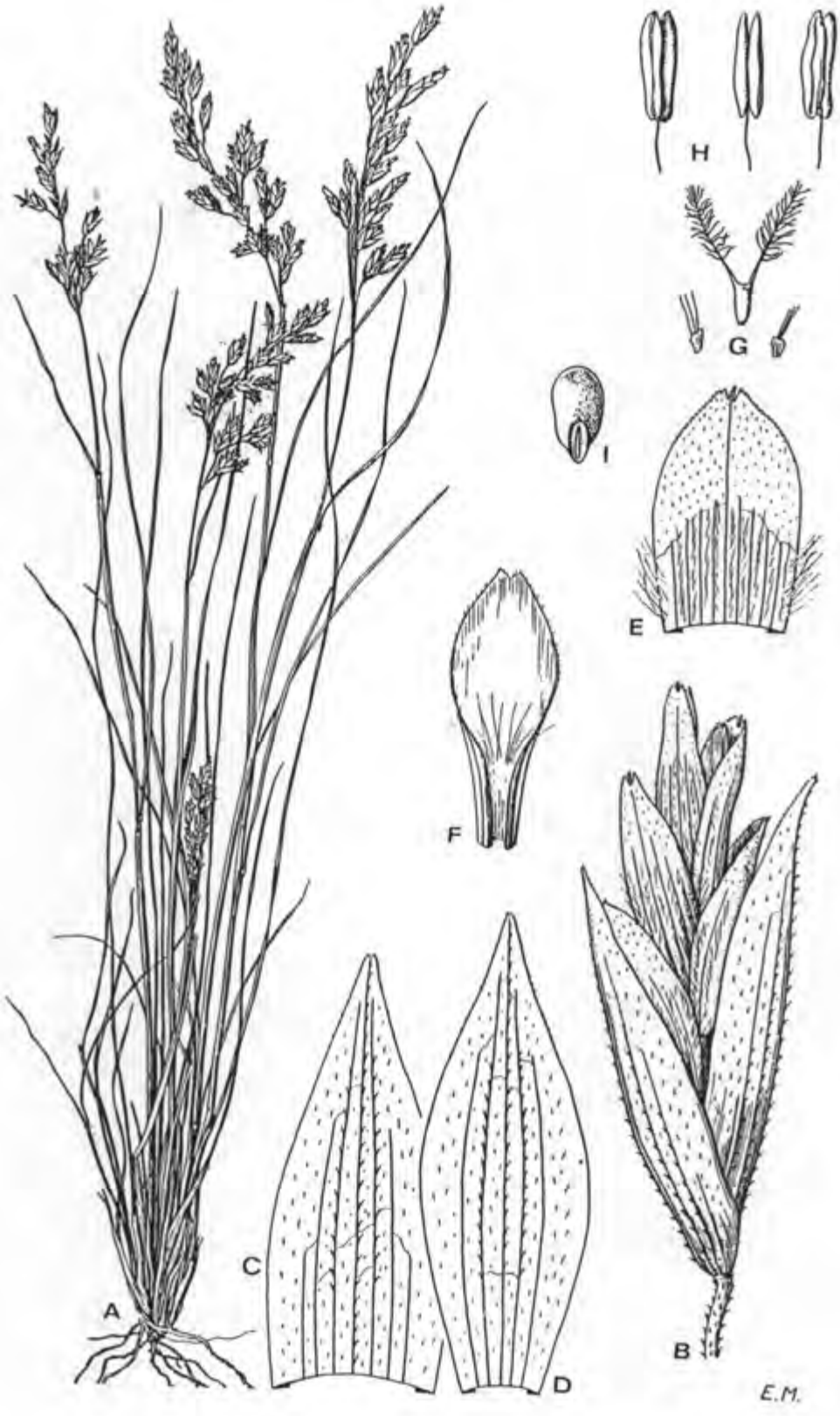


FIGURE IIId. *Schismus scaberrimus* NEES. Voucher BOLUS 13842.
A) Habit (x ½); B) Spikelet (x 15); C) Lower glume (x 15); D) Upper glume (x 15); E) Lemma (x 15); F) Palea (x 15); G) Ovary and lodicules (x 15); H) Anthers (x 15); I) Caryopsis (x 15).

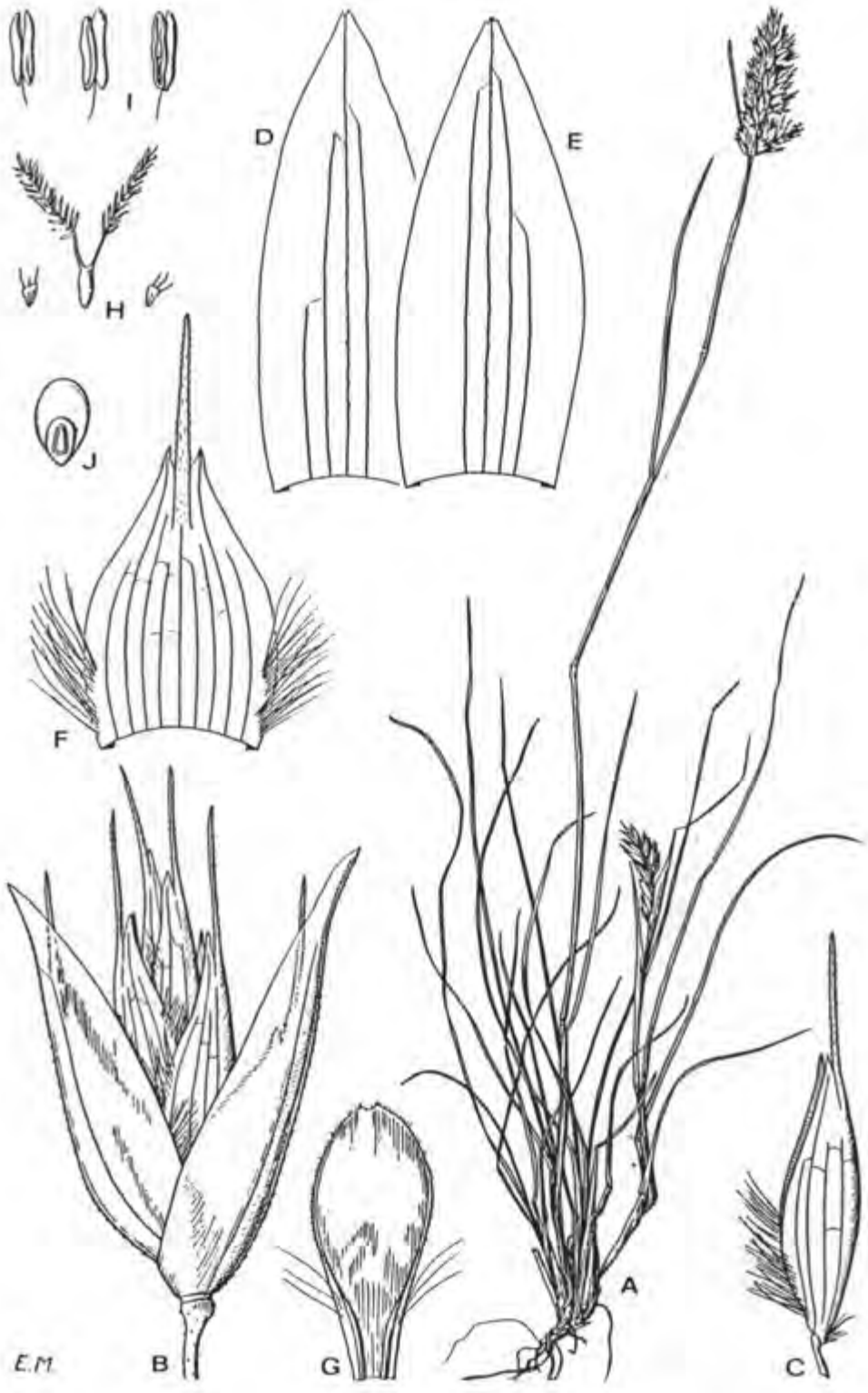


FIGURE IIIe. *Schismus pleuropogon* STAPF. Voucher SCHLECTER 1759.
A) Habit (x ½); B) Spikelet (x 15); C) Side view of lemma (x 15); D) Lower glume (x 15); E) Upper glume (x 15); F) Glume (x 15); G) Palea (x 15); H) Ovary and lodicules (x 15); I) Anthers (x 15); J) Caryopsis (x 15).

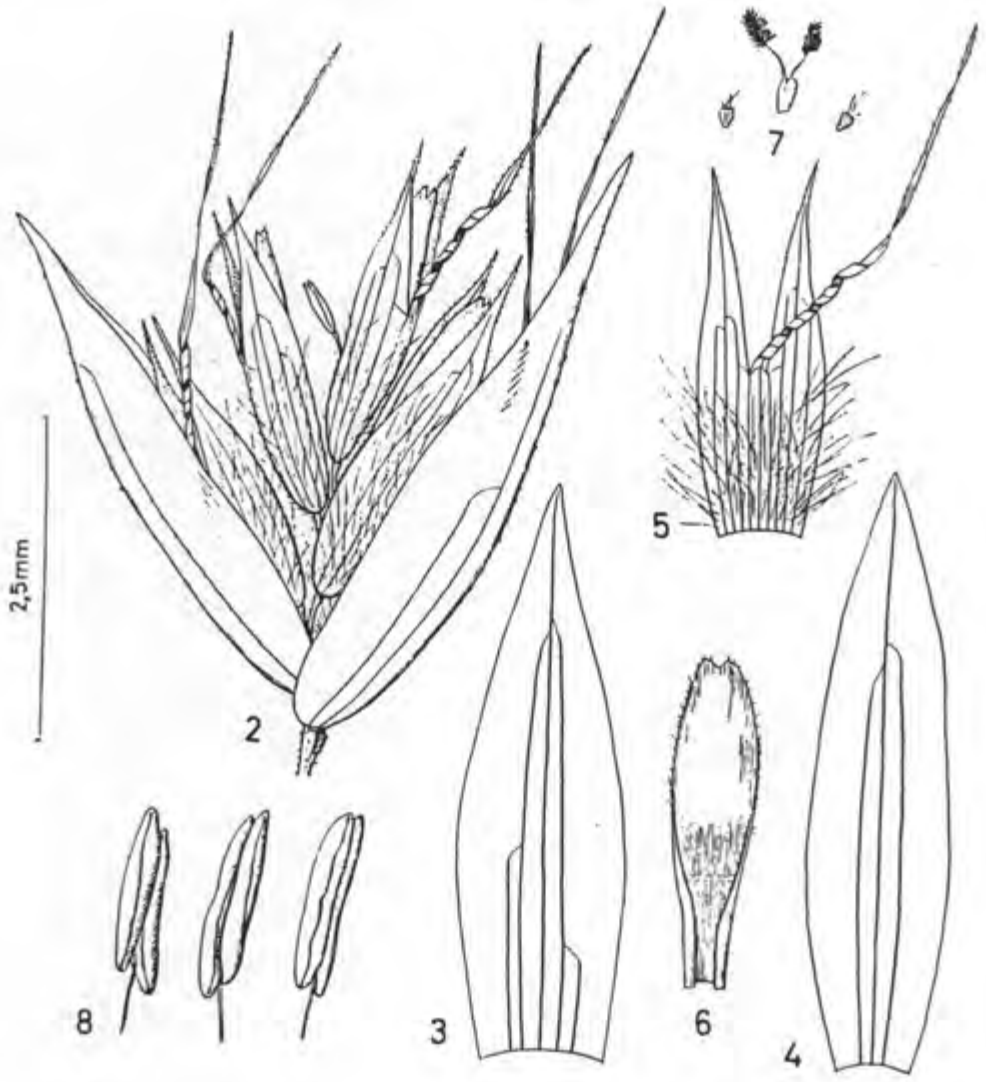


FIGURE IIIf. *Karroochloa curva* (NEES) CONERT and TURPE. Voucher ZEYHER 76.
2) Spikelet; 3) Lower glume; 4) Upper glume; 5) Lemma; 6) Palea; 7) Ovary and Lodicules; 8) Anthers.

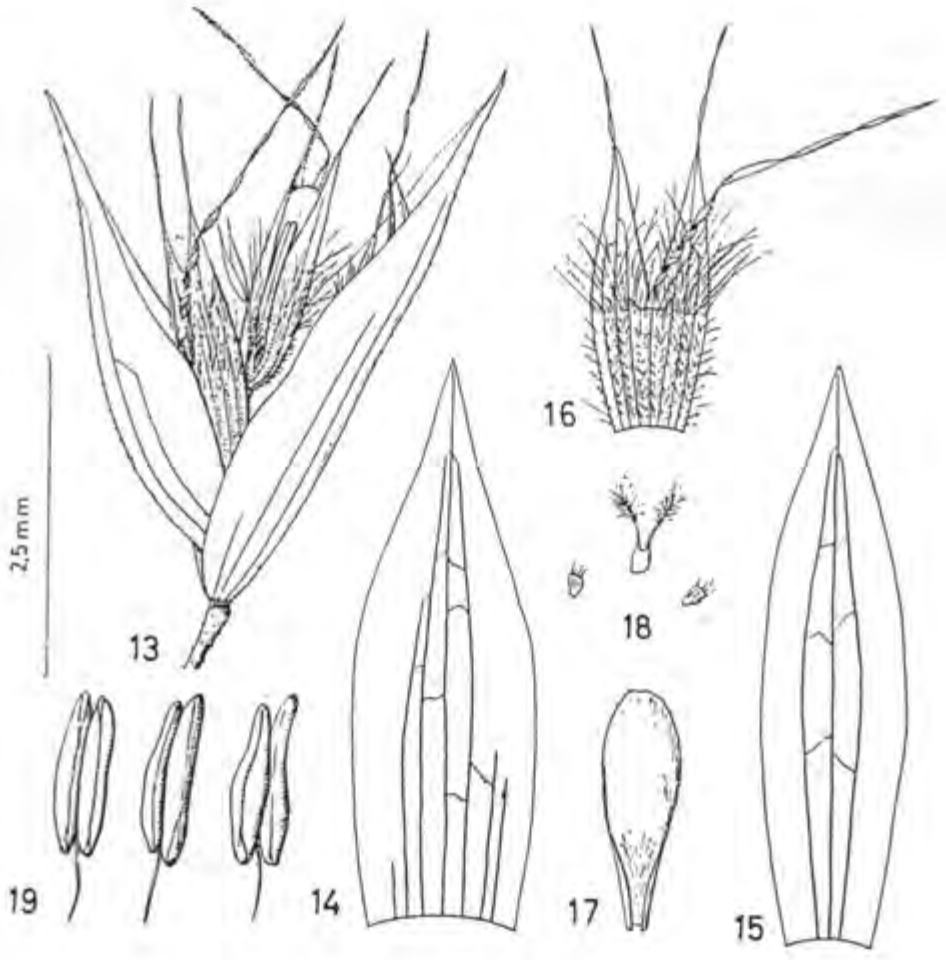


FIGURE IIIg. *Karroochloa schismoides* (STAPF ex CONERT) CONERT and TURPE. Voucher DINTER 6500. 13) Spikelet; 14) Lower glume; 15) Upper glume; 16) Lemma; 17) Palea; 18) Ovary and lodicules; 19) Anthers.

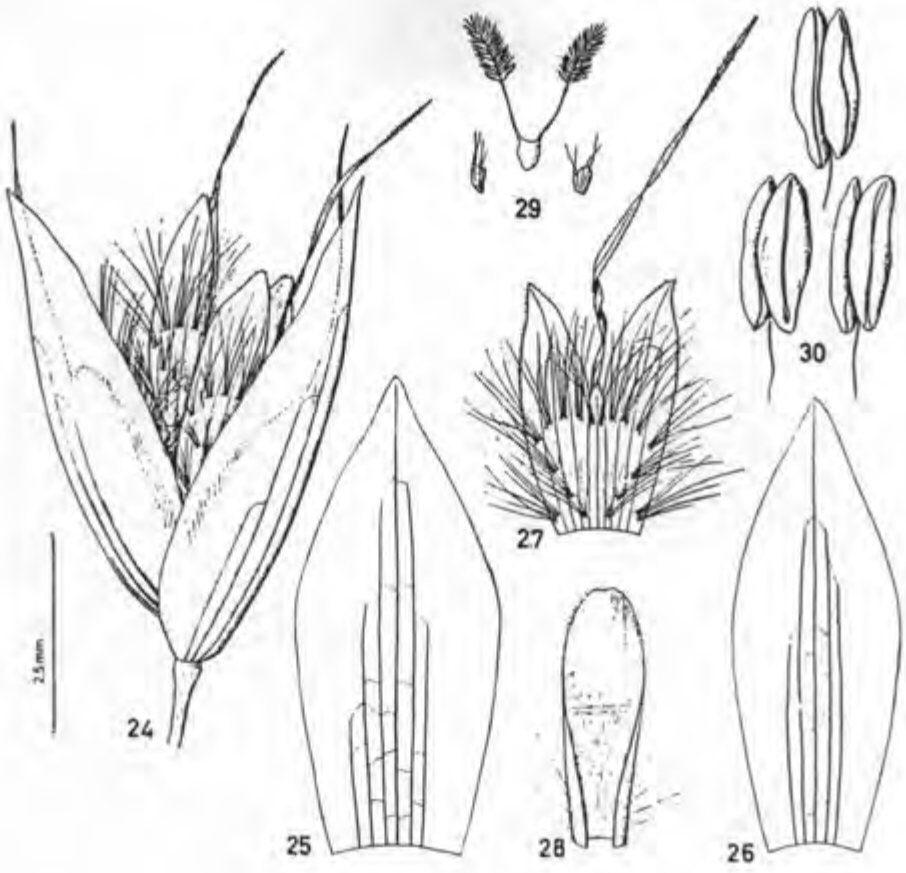


FIGURE IIIh. *Karroochloa purpurea* (LINNAEUS fil.) CONERT and TURPE. Voucher DREGE 673.
24) Spikelet; 25) Lower glume; 26) Upper glume; 27) Lemma; 28) Palea; 29) Ovary and lodicules; 30) Anthers.

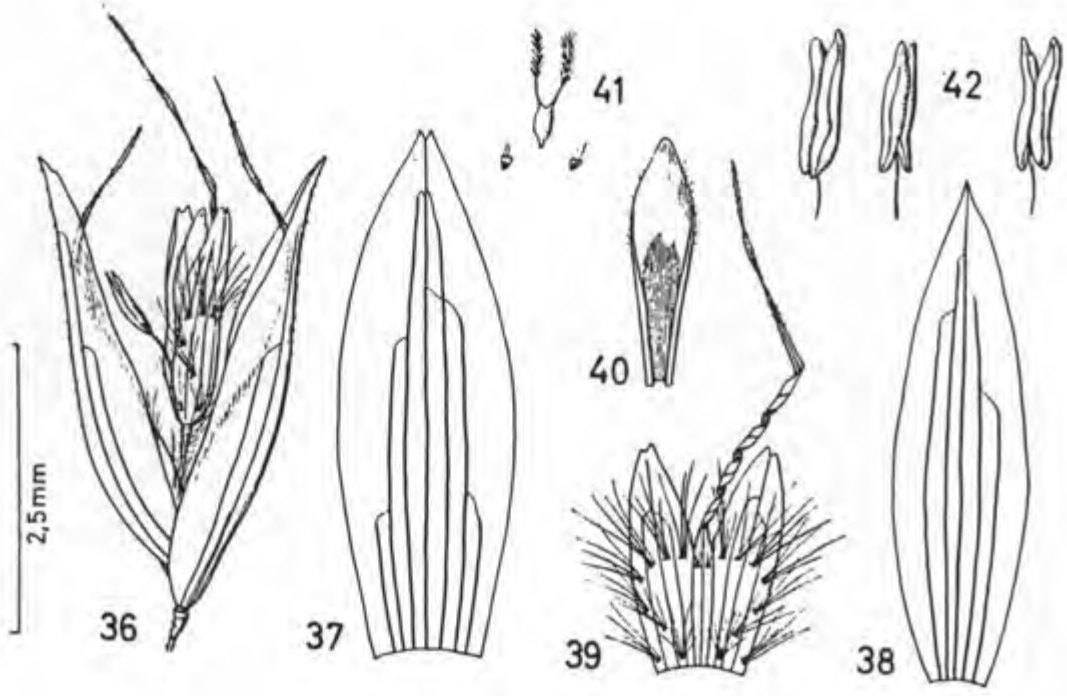
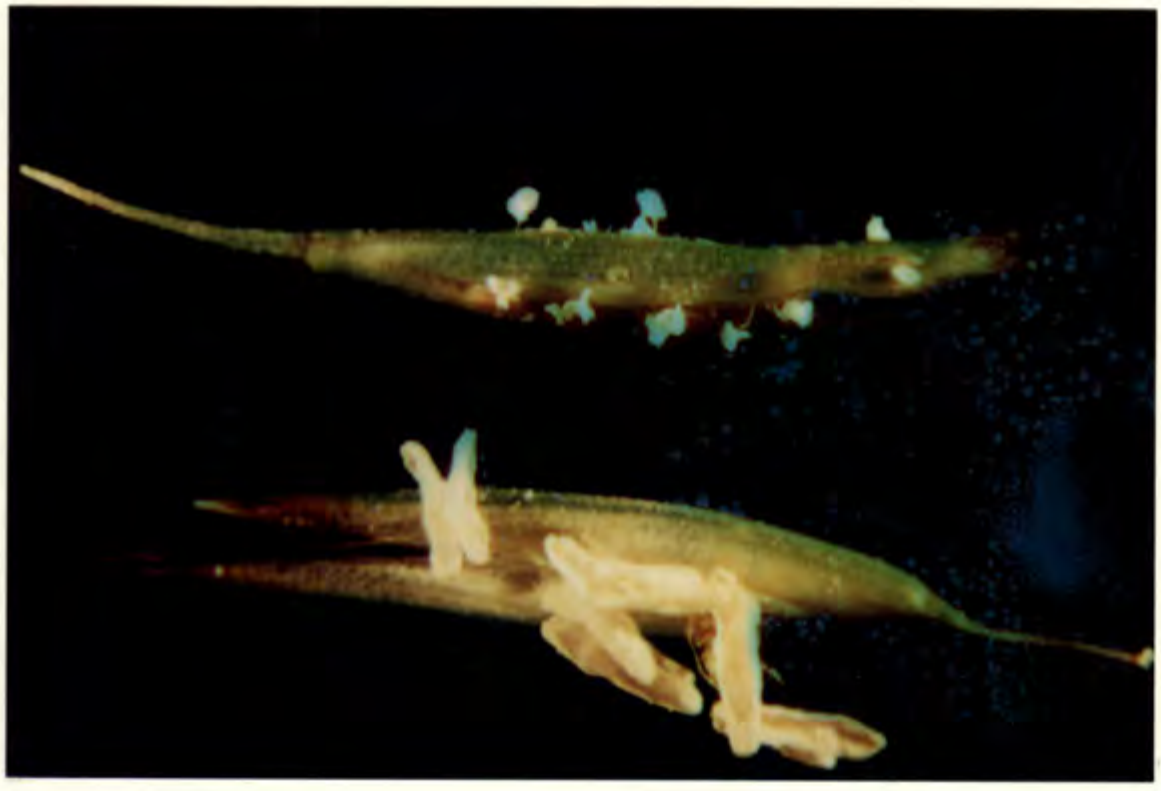


FIGURE IIIi. *Karroochloa tenella* (NEES) CONERT and TURPE. Voucher DREGE 2548.
36) Spikelet; 37) Lower glume; 38) Upper glume; 39) Lemma; 40) Palea; 41) Ovary and Lodicules; 42) Anthers.

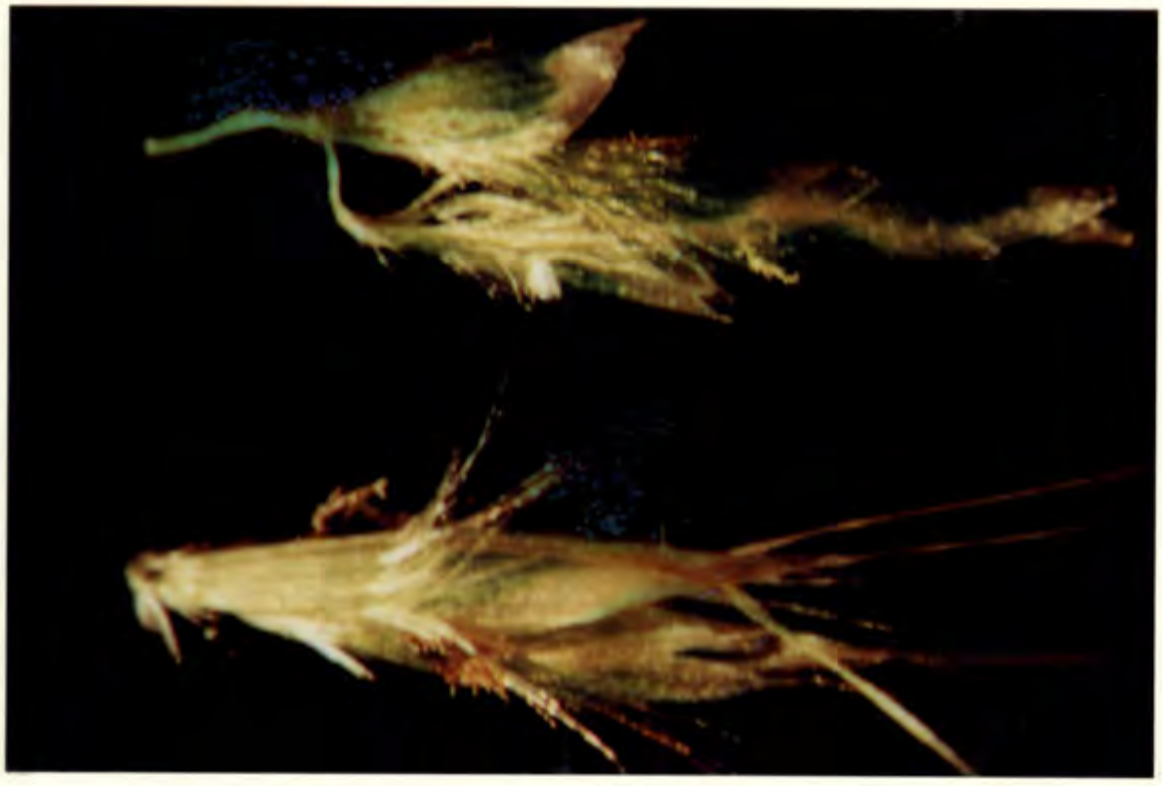
APPENDIX 4

PHOTOGRAPH 1: ***K. schismoides in situ*** **near Van Rhynsdorp, showing the red, sandy soil on which it grows.**

PHOTOGRAPH 2: **Close-up of specimen in Photograph 1.**



PHOTOGRAPH 3: **Spikelets of *S. barbatus* (top) and *K. schismoides* (bottom) at anthesis, showing relative lenghts of glumes and spikelets.**



PHOTOGRAPH 4: **Spikelets of *S. barbatus* (top) and *K. schismoides* (bottom) showing differences in spikelet structure and awns.**

PHOTOGRAPH 5: Young inflorescences of *K. schismoides*.

PHOTOGRAPH 6: *S. barbatus* showing both young inflorescences and inflorescences at anthesis.

PHOTOGRAPH 7: Open inflorescence of *K. schismoides* at anthesis.

PHOTOGRAPH 8: Open inflorescence of *S. barbatus* at anthesis.