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Species limits in *Cannomois virgata* complex (RESTIONACEAE)

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ABSTRACT

The variation in the nut morphology, floral and inflorescence morphology, culm morphology and culm anatomy of the *Cannomois virgata* complex are described. It is shown that this variation is best expressed by recognising three main clusters: the NW-Swartberg, Caledon-Langeberg and Coastal. The existence of these clusters was largely influenced by the size of the nuts, bracts, perianths and hollow cavity to culm diameter ratio. These traits were congruent with the overall morphometric variation, shown by the results of the phenetic analysis. The clusters correspond to three species proposed under the operational definition, which recognises species from differentiated clusters in phenetic space whose distinctness was assumed to be the manifestation of underlying fixed and qualitative differences following speciation. These units were considered appropriate as terminals for phylogenetic reconstruction. Empirical comparison of six prevailing species concepts was made by taking advantage of a common operational exigency i.e., the use of phenotypically irreducible clusters of individuals as first order estimates of species. Also, diagnostic characters were found in each of the clusters indicating the existence of a species complex, rather than a single taxon. I therefore propose that the name *Cannomois virgata* (Rottb.) Steud. be restricted to the individuals of the Coastal group from which the type was collected. A new species, *Cannomois grandis* Mujaju, is proposed for the plants belonging to the Caledon-Langeberg group, owing to the giant form exhibited by these plants which are 2 to 3.5 metres tall. The name, *Cannomois saundersii* Mujaju, was proposed for the NW-Swartberg, in recognition of Mr. Saunders, a seed collector. The distribution of the species were related to the cladogram, suggesting that speciation may have been sympatric for all taxa or somewhat allopatric as shown by the NW-Swartberg taxon which has an overall northern inland distribution within the Cape Floral Region in comparison with the other two.

1. INTRODUCTION

Restionaceae is a plant family of the Southern Hemisphere, comprising evergreen, rush-like xerophytes with erect photosynthetic culms, and leaves which are generally reduced to sheaths. The family is made up of some 400 species in about 40 genera, occurring on the poor sandy soils of the winter-rainfall regions of the SW and S portions of the Cape Province, South Africa, and of S and SW Australia (Linder, 1985a). A few outliers are found further north in Africa, Madagascar, Indo-China and Chile. Although members of the Restionaceae are found in every continent of Southern Hemisphere, it is only in the south-western Cape, southern Africa, where they dominate vegetation types to such an extent that they are used in physiognomic descriptions of the landscape (Taylor, 1978; Kruger and Taylor, 1979; Campbell, 1985). All the 19 genera belonging to the African Restionaceae are present in the south-western Cape, and contribute 4 - 5 % of the total flora of the region (Linder, 1985a), referred to as the Cape Floristic Region (Goldblatt, 1978). This region is generally known for its rich and highly endemic flora i.e., with more than 8000 species known from a mountainous region of 1000 km long and about 200 km wide (Goldblatt, 1978), and an estimated 75 % level of endemism (Bond and Goldblatt, 1984). Since, the family is such of great floristic and ecological importance within the region, a taxonomic knowledge of the members of Restionaceae is therefore of great importance to ecologists and land-managers. The need for taxonomic work has been echoed by Kruger (1981) who remarked that the identification of the Restionaceae was difficult due to inadequate taxonomy.

Many previous taxonomic studies were focused on elucidating the ordinal relationships of the Restionaceae and its allied families (Dahlgren and Clifford, 1982; Dahlgren and Rasmussen, 1983, Dahlgren *et al.*, 1985; Johnson and Briggs, 1981; Rudall and Linder, 1988). Linder (1984) dealt with the generic classification of the African Restionaceae. Recently, several studies have been done on the species level of classification (Linder, 1986; Linder and Vlok, 1991) but there are still many alpha-taxonomic problems. Research at species level has been directed at locating 'key characters' for identifying specimens (Linder, 1990), but with no indication on how extensive the morphological variation within and between species may be. An understanding of the patterns of variation within and between populations of the same species might provide great insight into the evolution of the Cape Flora. The Cape flora,

situated in a complex mosaic of mountains, coastal plains and deep valleys is ideal for studying patterns of evolutionary diversification in plants. However, this has been made difficult because patterns of differentiation between populations have seldom been documented in the Cape taxa (cf. Balfour and Linder, 1990; Johnson, 1994; Johnson and Linder, 1995). In addition, the knowledge of the extent and distribution of variation within and between populations can be used as a foundation on which to base conservation decisions.

The genus *Cannomois* within the family Restionaceae exhibits an array of species whose species limits have not been explored. The genus is very distinct, characterised by bony bracts and woody shiny black nuts that are flattened on one side. It is highly variable, thereby making the delimitation of the species extremely difficult and species limits almost impossible to define. Linder (1984, 1985a) acknowledged this complexity and noted three 'taxa' which he could not formally name. In this respect, the species *Cannomois virgata* is a typical representative of the genus; i.e., it is highly variable and may contain several segregates. The species *Cannomois virgata* (Rottb.) Steud. is endemic to the Cape Floristic Region of South Africa. It is a widespread species, ubiquitous in the mountains of the Cape Floristic Region, extending from Uitenhage to Nieuwoudtville. In drier areas it grows along streams and in seepage, whereas in wetter areas it extends onto the open mountainside. Altitudinally, it ranges from near sea level to 1800 m (Linder 1985a).

Cannomois virgata varies in growth habit, with the height of some plants ranging between 2 - 3 m whereas others are below 1.5 m. Other varying features include bracts, culms, nuts and perianths. Masters (1869) on close examination of the specimens confirmed the variability of *Cannomois virgata* in size, luxuriance of inflorescence and the shape of bracts. Similarly, Linder (1985a) noticed variability in habit for the plants growing in the mountains, on dry north-facing slopes and on wetter south-facing slopes. In the Swartberg Mountains and the dry north-facing slopes of the Outeniqua Mountains *Cannomois virgata* grows into a 2 - 3 m tall, bamboo-like plant, whereas on the wetter south-facing slopes of the coastal ranges it grows about 1 m tall. Pillans (1928) also noticed variation in the female perianth shape, which he used to subdivide some of the *Cannomois* species, but did not subdivide *C. virgata*. According to Van der Walt (1985) species showing continuous morphological variations probably indicate that they are still actively speciating.

Cannomois virgata was first described in 1772 by Rottboell as *Restio virgatus*. His description was based on the male plant. *Restio virgatus* was distinguished by its branching culms and panicled inflorescence. The history of *Cannomois virgata* (Table 1) reflects a period of instability due to inadequate sampling (leading to inadequate diagnostic features) and integradation among taxa in most characters. However, Pillans (1928) had a much better description of the species and established *Cannomois virgata* (Rottb.) Steud. as the species name. Linder (1985a) retained the same name *Cannomois virgata* (Rottb.) Steud. as Pillans in his description.

Table 1. History of *Cannomois virgata* complex.

	Specific names of different type specimens within the complex				
Author	**virgatus**	**scopa**	**elegans**	**cephalotes**	**Robustus**
Rottboell, 1772:	*Restio*				
Thunberg, 1788:		*Restio*			
Poiret, 1804:			*Restio*		
Persoon, 1807:			*Elegia paniculata*		
Thunberg, 1811:	*Restio*	*Restio*			
Desvaux, 1828:				*Cannomois*	
Kunth, 1841:	*Thamnochortus*			*Cannomois*	*Thamnochortus*
Steudel, 1855:	*Cannomois*				
Masters, 1878:	*Cannomois*				
Masters, 1897:				*Cannomois*	
Pillans, 1928:	*Cannomois*				
Linder, 1985a:	*Cannomois*				

Both Pillans (1928) and Linder (1985a) relied heavily on features of the female inflorescence, female flowers and culm morphology in their keys; with no indication on how extensive the morphological variation may be within and between species. Consequently when delineating *Cannomois virgata* from the rest of the species within the genus they only used one character, i.e., culms much branched, regardless of the presence of variation in other characters. This use

of a single character, led Linder (1985a) to key a large population of a plant on the Great Swartberg which is morphologically intermediate between *C. virgata* and *C. scirpoides* and probably of hybrid origin, under *C. virgata*. The plant also occupies an intermediate habitat - slightly damp to dry sandy plateaux, and can be separated from *C. virgata* by the petals, which are only a third as long as the nut, instead of being at least half as long as the nut. However, Linder (1985a) observed the variability of the species and attempted to locate any characters which could consistently separate all the forms, but without success. He acknowledged that *C. virgata* is a species complex of probably three distinct species. This, however, remains subjective, unless tested. Andersson (1994), acknowledged the problems of classifying morphologically variable species below the species level.

The aim of the project is to investigate the variation in the *C. virgata* complex, and to test the hypothesis that there are at least three distinct entities within this complex. If three species are acknowledged, then to establish whether they are distinct morphologically, and also whether they can be separated ecologically. A combination of ordination, clustering, and cladistic techniques were explored to fully elucidate these relationships.

2.1. Data sampling

The morphological data were obtained from literature and observations of dried material from herbaria. All collections of *Cannomois virgata* from the following herbaria: BOL, NBG and PRE (abbreviations follow Holmgren *et al.*, 1990) were examined (Appendix 1).

The data were supplemented by field observations. Seven populations of the *Cannomois virgata* complex representing the full ecological and morphological range of the groups, were sampled. Each sample population is represented by a single voucher specimen deposited at the Bolus Herbarium, University of Cape Town, South Africa (Table 2.1).

Table 2.1. Sample population localities, with number of plants sampled (n).

Pop. number	Locality	Geographic co-ordinates	n	Voucher no.	Code used in Phenetics
1	Kirstenbosch Botanical Garden	33° 59' S 18° 26' E	4	Mujaju 1	Muj1-CP
2	Du Toit Kloof Pass	33° 42' 34 S 19° 04' 18 E	2	Mujaju 2	Muj2-DT
3	Ceres mountains	33° 23' 40 S 19° 17' 14 E	2	Mujaju 3	Muj3-CM
4	Ceres mountains after Witzenberg Pass	33° 14' 10 S 19° 18' 03 E	2	Mujaju 4	Muj4-CM
5	Bainskloof Pass near road	33° 35' 02 S 19° 07' 58 E	10	Mujaju 6	Muj6-BP
6	Bainskloof Pass near Bainskloof lodge	33° 37' 06 S 19° 06' 06 E	6	Mujaju 7	Muj7-BL
7	Bainskloof Pass about 7 km from Wellington, by the streamside.	33° 38' 39 S 19° 05' 24 E	3	Mujaju 8	Muj8-B

Fifty-five herbarium specimens (Table 2.2) and 29 plants from the field (Table 2.1) representing the known range of variation within the *C. virgata* complex were selected for detailed investigation and phenetic analysis. Herbarium specimens not included in the investigation were either immature specimens or made up of male plants only or that they have been collected before 1900. Specimens collected before 1900 and those made up of male plants lacked most useful features like nuts and female inflorescence. Distribution of all specimens as well as their ecology were taken from the notes on herbarium sheets corresponding to 55 specimens.

Table 2.2. Specimens examined

Code used in Phenetics	Name of collector	Coll. no.	Locality	Area	Herbarium
Poc-S209	Pocock, M. A.	S209	Swartberg, bottom of narrow kloofs	Swartberg Mts.	PRE
Marl-3161	Marloth, R. L.	3161	Seven Weeks Poort, Swartebergen	Swartberg Mts.	PRE
Gold-3814	Goldblatt, P.	3814	Cape Province - Witteberg	Witberg Mts.	BOL
Ester-30721a	Esterhuysen, E.	30721a	Cape Province - Calvinia district, Lokenberg.	Hantam	BOL
Ester-?	Esterhuysen, E.	?	Cape Province - Calvinia district.	Olifants River Mts.	BOL
Ester-25967a	Esterhuysen, E.	25967a	Cape Province - Ladysmith, Anysberg	Anysberg Mts.	BOL
Brus-5392	Brusse, F.	5392	Cape Province - Worcester, Ceres. Southern end of Witsenberg range	Ceres Mts.	BOL
Lind-3332	Linder, H. P.	3332	Cape Province - Clanwilliam	Olifants River Mts.	BOL
Powrie-87	Powrie, E.	87	Cape Province - Calvinia district, Oorlog's Kloof	Hantam	BOL
Comp-3146	Compton, R.H.	3146	Tweedside, Laingsburg Div.	Witberg Mts.	BOL
Magu-1779	Maguire, B.	1779	Top of Gydo Pass, Ceres	Ceres Mts.	BOL
M. R. L.-6660	Marloth, R. L.	6660	Swartberg Pass, Outshoorn Div.	Swartberg Mts.	BOL
Comp-4887	Compton, R.H.	4887	South Western Region - Rosendal, Ceres Div.	Ceres Mts.	BOL
Bolus-9662	Bolus, H.	9662	Ceres, Mitchell's Pass	Ceres Mts.	BOL
Ester-24778	Esterhuysen, E.	24778	Cape- Laingsburg, Sewen Weeks Poort	Swartberg Mts.	BOL
Ester-13017	Esterhuysen, E.	13017	Cape Province; Clanwilliam Div.; west end of Elands' Kloof above Citrusdal near stream	Olifants River Mts.	BOL
Ester-7877	Esterhuysen, E.	7877	South Western Region, Clanwilliam Div., Cederberg Mts., Welbedagt cave	Cederberg	BOL
Lind-5500	Linder, H. P.	5500	S. Cape- Ladysmith, Sewe Weeks Poortberg	Swartberg	BOL
Taylor-3549	Taylor, H. C.	3549	Heidelberg	Langeberg Mts.	PRE
Kerf-5738	Kerfoot, O.	5738	Stellenbosch c.p. - Dwarsberg in a sheltered gorge below Victoria Peak	Caledon	PRE

Burg-2392	Burgers, C. J.	2392	S. W. Cape - Villiersdorp Wild Flower Garden along small Klofie at base of mountain	Caledon	PRE
Joffe-939B	Joffe, H.	939B	Cape Prov.- Prince Albert, Swartberg Pass on road to 'Die Hel'	Swartberg	PRE
Tredg-432	Tredgold, E.	432	Langeberg, Cogmanskloof.	Langeberg	PRE
G.K.T&St-3328	G.K.Theron and Studente	3328	Kaap, Caledon district, Riviersonderendberge	Caledon	PRE
Ester-9664	Esterhuysen, E.	9664	South Western Region - Paarl Div., Wemmershoek Mts., Winterberg.	Caledon	BOL
Linder-6124	Linder	6124	Oudtshoorn district, Kammanassie, W. end. low ridge extending S. from main peaks	Swartberg	BOL
Rodin-3288	Rodin, R. J.	3288	Stellenbosch Div., Jonkershoek	Caledon	BOL
Linder-4139	Linder	4139	Mosselbay, Cloetesberg, South slopes above Bergkloof	South Coast	BOL
Marl-2352	Marloth, R. L.	2352	North of Seven Weeks Poort	Swartberg	BOL
Scharf-1224	Scharf, H. T.	1224	Cape Region - Uitenhage district	South Coast	PRE
Acocks-21657	Acocks, J.P.H.	21657	Cape - Knysna district	South Coast	PRE
Horn-2404	Horn, D. H. S.	2404	Cape - Uniondale district, Prince Alfreds' Pass	South Coast	PRE
Rogers-4237	Rogers, F. A.	4237	Mosel Bay C. F.	South Coast	PRE
Noel-RU10445	Noel, A. R. A.	RU 10445	Cape - Uitenhage district, Elands' Rivier Berg	South Coast	PRE
Comp-12904	Compton, R. H.	12904	Voetpadsberg, Worcester		NBG
Ester-37374	Esterhuysen, E.	37374	Montagu, Towsberg	Towsberg	NBG
Morris218	Morris	218	Swartberg Pass, Oudtshoorn-Prince Albert	Swartberg	NBG
Comp-16115	Compton, R. H.	16115	Ceres C. P., Ertjiesland Kloof	Ceres Mountains	NBG
Straus-46	Strauss, M. E.	46	Oudtshoorn	Swartberg	NBG
Greun-8	Van Greuning, J. V.	8	Oudtshoorn	Swartberg	NBG
Reid1390	Reid, C.	1390	Ceres district	Ceres Mountains	NBG
Taylor5137	Taylor, H. C.	5137	Clanwilliam	Cederberg	NBG
Andrag276	Andrag, R. H.	276	Wupperthal, Heuningvlei, Cederberg sand	Cederberg	NBG
Thomp-165	Thompson, M.	165	Elandskloof south, Ceres	Ceres Mountains	NBG
Rour-1076	Rourke, J. P.	1076	Clanwilliam C. P., Heuningvlei	Cederberg	NBG
Phill-?	Phillips, E. P.		Worcester		NBG

Kerf-5760	Kerfoot, O.	K5760	Stellenbosch	Caledon	NBG
Vos1351	De Vos, M. P.	1351	Caledon, Klenimand	Caledon	NBG
Comp-13067	Compton, R. H.	13067	Cape Peninsula, Grootkof	Cape Peninsula	NBG
PhMw-2074	Phillip and Merwe	2074	Stellenbosch, Jonkershoek, Swartboskloof	Caledon	NBG
Muir-2339	Muir, J.	2339	Mossel Bay	South Coast	NBG
Comp-23108	Compton, R. H.	23108	Mossel Bay	South Coast	NBG
Fellin-1287	Fellingham	1287	SW Cape, Du Toit's Kloof	Du Toit's Kloof mts	NBG
Bohn-8431	Bohnen	8431	S. Kaap, Riversdal, Gracias Pass	Langeberg	NBG
McDon-2035	McDonald, D. J.	2035	Langeberg, Garcias Forest Reserve	Langeberg	NBG

2.2. Preparation and examination of study material

2.2.1. **Morphology**

All the specimens were examined for morphological characters. A specimen count contains a range of variation. The final characters (Table 2.3) were selected and quantified from mature specimens only, for detecting meaningful comparison between the segregates. An attempt was made to search for vegetative characters that can be used to diagnose sterile, female or male specimens.

Detailed measurements were taken from various features using either a 30-cm ruler or under a Leica MS5 dissecting microscope using a graticule fitted in an eyepiece. A graticule was used where a 30-cm ruler was inapplicable, especially for small metric characters involving width and diameter dimensions of organs, and elaiosome lengths. Where an organ was curving like in some spathe, a soft thread was used to mark the width and then superimposed onto a ruler to read the measurement. All useful morphological characters were based on the nut morphology, inflorescence and floral morphology and culm morphology.

Table 2.3. List of characters used in phenetic analysis

Number	Character	Code used in phenetic analysis
1	Nut length	Nut-L
2	Nut width	Nut-W
3	Petal length	Petal-L
4	Petal width of the outer segment	Petal-W1
5	Petal width of the inner segment	Petal-W2
6	Spikelet length	Spike-L
7	Spikelet width	Spike-W
8	Bract length	Bract-L
9	Bract width	Bract-W
10	Spathe length	Spath-L
11	Elaiosome length	Elaios-L
12	Culm diameter at apex	Culm-D
13	Branch tip diameter	BrT-D
14	Branch base diameter	BrB-D
15	Ratio of nut width to length	RNW-L
16	Ratio of petal length to nut length	RPL-NL
17	Ratio of spikelet width to length	RSkW-L
18	Ratio of bract width to length	RBW-L
19	Ratio of branch tip diameter to base diameter	RTD-BD
20	Ratio of hollow cavity diameter to culm diameter	RHol-CD
21	Ratio of spathe length to spikelet length	RSh-SkL
22	Ratio of elaiosome length to nut length	REl-NutL

2.2.1.1. Nut morphology

The nut morphology of *Cannomois virgata* individuals varies considerably with some having stout nuts and some narrow nuts. Nut dimensions measured include length and width, and the ratio of width to length. The width to length ratios were used to define the shape of nuts of each of the segregates. Elaiosome length was also measured relative to the length of the nut for individual specimens.

2.2.1.2. Inflorescence and floral morphology

Previous treatments of the genus *Cannomois* reveal that floral characters are very informative yet most of these characters have not been used to explore species limits in the *Cannomois virgata* complex. Spikelets from the apex of the inflorescence were removed from the dried material and heated for about 30 minutes in distilled water with a drop of detergent to aid reconstitution of the floral parts. Each spikelet was dissected under a Leica MS5 dissecting microscope to remove the bracts for measurements. Other measured organs include the spathes, petals and the spikelets. For the bracts, spathes and spikelets measurements were taken for width, length, and the width to length ratios. The ratios were useful in defining the shapes of the respective organs. The petals are divided into the inner and outer segments (whorls). Both segments are equal in length per individual specimen considered but showing degrees of variations relative to nut length between specimens. Similarly, the petal segments also show variation in width among specimens. Therefore, for the petals, measurements were taken for the length and width of both the inner and outer segments. Also, the petal length to nut length ratios were noted as they have been used in literature as one of the diagnostic characters between the species of *Cannomois*.

2.2.1.3. Culm morphology

This character is very important so far in keying out *Cannomois virgata* from the other members of the genus. To explore the species limits, diameter of the main terminal culm was measured at the apex to quantify the thickness of the culm among specimens. Other measurements included the diameters of the branch tips and branch bases, and the ratio of branch tip diameter to base diameter calculated to quantify the fineness of the branch tips. Branch tips were measured from a point about 5 cm from the end using an eyepiece micrometer at magnifications of 1X. Similarly, the branch base and culm diameters were measured using an eyepiece micrometer, whereas sheath length was measured with a 30-cm ruler. Observations of whether the culms were solid or hollow were noted and the hollow cavity diameter to culm diameter measurements taken using a 30-cm measuring ruler. For an individual specimen to be considered hollow, a clear hole through the pith of the stem was observed. Conversely, for a solid specimen no hole was seen, or if seen it was very negligible.

2.2.2. **Anatomy**

2.2.2.1. Culm anatomy

Culm anatomy was investigated by cutting a 2 cm length of internode culm from each species and boiling in water mixed with a drop of detergent for about 45 minutes. Internode culm pieces were softened by boiling. A sledge microcotome was used to cut sections at 25 μm. The sections were stained in a mixture of Safranin and Alcian for 20 minutes, destained in distilled water for about 30 seconds, and then dehydrated through a run of 50 %, 70 %, 80 %, 90 %, 96 % and 100 % ethanol, followed by xylene, for about half a minute per each step. The sections were then mounted on microslides in Canada Balsam, and dried for five days on a hot plate before viewed under a light microscope.

2.3. Data handling

All measurements were recorded in millimetres except for the ratios. Conversion calculations for each measurement with the Leica microscope were made to standardise the data into millimetres. Data were entered directly onto a computerised spreadsheet programme EXCEL version 5.0 and were exported to the NTSYS programme (Rohlf, 1993) for multivariate analysis, and STATISTICA programme (Statsoft, 1995) for univariate analysis.

2.4. Phenetic analysis

Species delimitation in the *C. virgata* complex was investigated using a combination of univariate, bivariate and multivariate analytical methods. This permitted comparison of character variation patterns obtained using the different methods.

Specimens were not pre-selected due to the scarcity of material, except where duplicate specimens were encountered. Where a collection consisted of several specimens, they were treated individually and where there were multiple specimens per sheet, each specimen was measured separately. Therefore, the Operational Taxonomic Units (OTU's) used in the analyses are individual specimens. The specimens are coded using a combination of part of the collector's surname and his/her collector number for herbarium specimens (Table 2.2), and a combination of the collector's name and the plant locality for plants from the field (Table 2.1).

Features such as plant height and culm length were initially considered for the analysis, but were then discarded because they were not recorded in most specimens. Similarly, sheath length was not used in the analysis because the structure was missing in about 75 % of the specimens and plants examined.

2.4.1. **Multivariate analyses**

Both cluster analysis (CA) and ordination methods were performed using the software package NTSYS-pc, version 1.80 (Rohlf, 1993), permitting comparison of groupings revealed by each of the two methods. While clustering methods show a hierachical, categorical structure which is inherently incapable of describing gradients or multiple patterns in data (Crisp and Weston, 1993), ordinations are designed to reveal multiple, continuous, and overlapping patterns of variation (Sneath and Sokal, 1973; Thorpe, 1976, 1983) and are most appropriate under a nonhierarchical model of infraspecific variation (Swofford and Berlocher, 1987). Thus, these two multivariate techniques are also used here to complement each other.

Before multivariate analysis, data were scaled by standardising. Standardisation attempts to ensure that the scaling of individual variables does not affect the outcome of the analysis. It does this by reducing the effect of different scales of measurement in different characters. For example, in this study spikelet length measurements were in excess of 30 mm in all measured individuals whereas all branch tip diameters did not exceed 1.1 mm. The original data matrix of 22 character state rows x 84 OTU's (Appendix 2) was standardised by calculating the standard deviation and mean of each row and expressing each character state as a deviation from the mean in standard deviation units (Sokal and Sneath, 1963). Standardised data were then input into the clustering algorithm and the ordination.

2.4.1.1. Cluster analysis

There are very many coefficients, and they can lead to different results. In this analysis, the Manhattan coefficient was used and its choice is subjectively guided. This coefficient, which is equivalent to the mean character difference of Cain and Harrison (1958), has the advantage of conceptual simplicity.

The formula used to calculate the average Manhattan distance is

$$M_{ij} = 1/n \sum_k |X_{ki} + X_{ki}|$$

where i and j are two objects (OTU's) being compared; k is the character and n is the total number of shared characters. Missing values are taken into account. For a pair of objects, i,j only those values for k are used for which X_{ki} and X_{kj} are both present. This means that different elements of the resulting dissimilarity matrix may be based on different sample sizes. Thus, average coefficients deal well with incomplete matrices. Although there were few missing data values in the data matrix, this is an added advantage of the average Manhattan distance coefficient. The Manhattan distance analysis produces a triangular data matrix listing the level of dissimilarity among all the individual OTUs. In order to visualise this matrix of dissimilarity the data was fed into a clustering program.

All clustering programs (sometimes called "greedy algorithms") basically work in the same way (Rohlf 1992):

1. Search the input matrix for a pair of objects (i,j) that are the most similar (or least dissimilar)
2. Merge these objects into a new cluster
3. Update the matrix to reflect the deletion of the pair of objects, i and j, that are merged and the addition of a new "object" corresponding to the new cluster. Similarities or dissimilarities have to be computed between the existing objects and the new cluster (the different clustering methods differ only in the formulas used at this step).
4. Go back to step 1 if the new matrix is greater than 2 X 2, else stop. Note that two objects are deleted and one is added at each step, so this algorithm must terminate.

The problem with clustering analysis is that the data are distorted to fit into two dimensions and the best algorithm is the one that results in the least degree of distortion. The unweighted pair-group method using arithmetic averages (UPGMA) algorithm, which is commonly used because it has been shown that it produces the least distortion of inter-OTU distances during clustering (Rohlf 1970), was used to construct a phenogram. The distortion was tested using a co-phenetic variation analysis. The correlation value between the phenogram matrix and the

similarity is r = 0.78 which is a fairly good fit (Rohlf, 1993). The delimitation of groups or clusters on the phenogram is based on relatively longer branch lengths subtending them.

2.4.1.2. Ordination

Ordination methods are designed to reveal continuous and overlapping patterns of variation (Sneath and Sokal, 1973). Ordination is based on the maximisation of variance of linear combinations of variables. Most of this variation is usually summarised with only a few components. Each axis is a combination of several taxonomic characters, which are reduced by the computer mathematically into a dimensional hyperspace i.e. plotting of OTU's against a linear combination of characters. By examining the factor loading, one is able to determine which characters account for the maximum variation.

Principal components analysis (PCA) was chosen as an ordination method for this study because it works better on continuous data and describes a large proportion of the observed character variance without utilising a *priori* knowledge about group boundaries unlike other ordination methods such as canonical variates analysis which only test the validity of groups assigned before-hand. A correlation matrix was first plotted from the matrix of standardised data; then eigen values and eigen vectors were computed from the symmetric triangular matrix of correlation coefficients. Principal components were then computed and the projection of the 84 OTU's on the first three PC's was shown in two-and three-dimensional model plots. Using the groupings located by the cluster analysis, groups were distinguished by drawing boundaries or borders that would assemble individuals from the same cluster together.

2.4.2. **Univariate and bivariate plots**

Univariate and bivariate methods were used to complement the analysis of variation provided by multivariate methods. Multivariate methods can be criticised for being arbitrary in the way similarity or dissimilarity between objects is analysed because the choice of algorithm largely influences the results. This is primarily because different distance coefficients may show

different clustering results for the same data set and this makes necessary the demonstration that a distribution is well supported by the original data set.

Bivariate plots were used to test if ratios between selected characters agree with the pattern produced by multiple characters since Gould (1966) has shown that plants can be distinguished by their relative sizes of parts rather than absolute size. Scatter plots were constructed for nut width versus nut length, petal length versus nut length, petal with of outer segment versus petal length, petal width of inner segment versus petal length, spikelet width versus spikelet length and bract width versus bract length, for solid and hollow specimens.

Similarly, univariate plots prove particularly useful for examination of the extent of variation in each of the individual characters. Box-and-whisker plots were used to graphically show the degree of variation within and between specimens.

2.5. Phylogenetic analyses

Contrary to phenetic analysis which show patterns of overall resemblance and difference among organisms based on many heritable characteristics, phylogenetic analysis show how the phenetic pattern changes with time on a branching tree (Abbott *et al*, 1985). Phylogenetic analyses primarily retrieve the sequence of speciation events.

A cladistic analysis was done on morphological data set to place the complex within the context of other species in the genus and also to see whether its segregates constitute distinct taxa, rather than peaks in a continuously variable set of characters.

2.5.1. **Choice of outgroup**

In this phylogenetic reconstruction, character polarity was determined using the outgroup method of Nixon and Carpenter (1993). As outgroups, *Hypodiscus aristatus* (Thunb.) Krauss , *Willdenowia glomerata* (Thunb.) Linder and *Ceratocaryum pulchrum* Linder were used, based on the phylogeny of Linder (1991). The outgroups selected share the possession of more inclusive synapomorphies with the ingroup, which is consistent with the suggestion of

Linder and Kellogg (1995) that it is useful to have an outgroup taxon not too distant from the study taxa. If the outgroup is too isolated, it may be confused by extensive homoplasy for morphological analysis (Les *et al.*, 1991).

Willdenowia, Ceratocaryum and *Hypodiscus* are sister groups to *Cannomois,* with the striking features in common between them being the presence of hyaline female perianth lobes, and a conditional synapomorphy which is the possession of simple culms.

2.5.2. **Data set**

The data set (Table 2.4) was made up of 21 morphological characters and 5 anatomical characters, of which 8 are quantitative characters. Character states for quantitative measurements were delimited by a gap in the distribution of a character. The ideal case used was a gap between the ranges (Data shown in appendix 3). This is consistent with the notion that a gap demarcates mutually exclusive sets of values, without any statistical or mathematical manipulation (Swiderski *et al.*, 1998). Coding was also allowed if a few taxa contain individuals that are on each side of the gap (these taxa would be polymorphic), but no taxon can have individuals within the gap. Following the recommendations of Platnick *et al.* (1991) unknown data and inapplicable data were coded as missing, polymorphic characters were given codes of the alternative states.

Some morphological data for the species in the genus *Cannomois* were extracted from a thesis by Wagenfield (1997) and verified from the specimens housed in the Bolus Herbarium. In addition, further original observations were made to improve and expand the morphological data set and to locate new characters.

Non-additive coding for multistate characters was restricted to cases where no character state adjacency hypothesis could be proposed, and not simply used as a default for multistate characters. This was done as both additive and non-additive coding make assumptions, and using non-additive coding for characters which are additive might result in wrong information. In this study, all quantitative and two qualitative multistate characters (17 & 23) were coded as additive.

Table 2.4. Morphological data set and characters used in the cladistic analysis. Question mark (?) indicate missing values.

Taxa	Characters					
Willdenowia glomerata	1 2 0 0 1	1 1 0 0 0	0 0 0 0 0	0 2 1 0 0	0 0 1 0 1	0
Hypodiscus aristatus	1 2 0 0 1	0 1 0 1 1	0 0 2 0 0	1 0 1 0 0	1 0 1 0 0	1
Ceratocaryum pulchrum	1 2 0 0 0	2 0 0 1 0	0 0 2 0 0	0 1 1 0 0	1 0 0 1 0	0
NW-Swartberg	0 0 1 1 2	1 1 0 1 0	1 1 1 0 0	0 2 1 1 1	1 0 1 1 1	1
Coastal	1 2 1 0 2	0 2 0 1 0	1 1 1 0 0	0 1 0 1 0	0 0 1 0 1	0
Caledon-Langeberg	1 2 1 0 2	0 2 0 1 0	1 1 1 0 0	0 2 0 2 1	1 0 1 1 1	0
Cannomois scirpoides	0 1 1 1 1	2 0 1 0 1	0 1 1 1 1	1 0 1 0 0	0 1 2 1 0	0
Cannomois taylori	0 1 1 1 1	2 0 1 0 1	0 1 1 1 1	1 0 1 1 1	0 1 2 0 0	1
Cannomois parviflora	0 1 1 1 1	2 0 1 0 1	0 1 1 1 0	1 0 1 0 0	? 1 2 0 0	1
Cannomois congesta	0 1 1 1 2	? 1 1 0 0	1 1 1 1 0	1 0 0 0 1	1 0 1 0 1	1
Cannomois aristata	0 1 1 1 2	2 0 1 0 0	2 1 1 0 0	1 0 1 0 0	0 1 2 1 0	0
Cannomois nitida	0 1 1 0 2	0 1 0 1 0	2 1 1 0 0	1 0 1 0 1	1 1 1 0 0	1

Characters:

1. Nut outline: barrel shaped = 0, rounded = 1
2. Nut width to length: < 0.43 mm = 0, 0.43 - 0.53 = 1, > 0.53 = 2
3. Flat, compressed adaxial nut side: absent = 0, present = 1
4. Elaiosome length: short (< 1/10 of nut length) = 0, long (> 1/10 of nut length) = 1
5. Elaiosome condition: absent = 0, collared = 1, shrunken = 2
6. Petal length to nut length: 1 - 0.65 = 0, 0.65 - 0.2 = 1, < 0.2 = 2.
7. Petal width of outer segment: < 1.5 mm = 0 1.5 - 2.5 mm = 1 > 2.5 mm = 2
8. Petal apex appearance: entire = 0, not entire = 1
9. Spikelet length: less than 30 mm = 0, more than 30 mm = 1
10. Spikelets per inflorescence: single, rarely to three = 0, two to many = 1,
11. Bracts shape: acute = 0, acuminate = 1, long-acuminate = 2
12. Number of fertile bracts: one = 0, two to three = 1
13. Bract number: less than 8 = 0, 8 - 12 = 1, more than 15 = 2
14. Spathe length: shorter than spikelet = 0, longer than spikelet = 1
15. Spathe colour: brown = 0, dark brown = 1
16. Fertile culms: branching = 0, simple = 1
17. Degree of fertile culm branching: nil = 0, sparingly = 1, much-branching = 2 (additive)
18. Culms: distinctly hollow = 0 solid or with a small central cavity = 1
19. Plant height: ca. 1 m = 0, 1- 2 m = 1, > 2 m = 2
20. Fire response: coppice = 0, seed = 1
21. Rhizome: spreading = 0, short = 1
22. Stomata: superficial = 0, sunken = 1
23. Epidermal cell shape: square = 0, rectangular = 1, elongated = 2 (additive)
24. Epidermal cells: tanniferous = 0, not tanniferous = 1
25. Chlorenchyma: cell layers obscure = 0, cell layers distinct = 1
26. Parenchyma: continuous = 0, interrupted = 1

2.5.3. **Descriptions of characters used in cladistic analysis**

Nut morphology

[1]. Nut outline: barrel shaped = 0, rounded = 1

The majority of the species in *Cannomois* have barrel shaped nuts except the Coastal and Caledon-Langeberg groups in the *Cannomois virgata* complex, and the outgroups which possess round nuts.

[2]. Nut width to length: < 0.43 mm = 0, 0.43 - 0.53 = 1, > 0.53 = 2

This character describes the variation in the size of the nuts. Nuts with ratios less than 0.43 are narrow and include the NW-Swartberg, whereas nuts with ratios between 0.43 - 0.53 are average and include those for *C. taylori*, *C. scirpoides*, *C. parviflora*, *C. aristata* and *C. nitida*. Those nuts with width to length ratio of more than 0.53 are stout and include the outgroups, Coastal and Caledon-Langeberg taxa. The delimitation of these states is shown in Figure 1a.

[3]. Flat, compressed adaxial nut side: absent = 0, present = 1

All the species of *Cannomois* have nuts with flattened, compressed adaxial sides. This state does not exist in the outgroups.

[4]. Elaiosome length: short (< 1/10 of nut length) = 0, long (> 1/10 of nut length) = 1

The species were coded as having elaiosomes short or long, and measurements were made to define accurately the two states (Figure 1b). The outgroups, *C. nitida*, and the Coastal and Caledon-Langeberg groups within the *C. virgata* complex have short elaiosomes. All other species have long elaiosomes.

[5]. Elaiosome condition: absent = 0, collared = 1, shrunken = 2

The *Cannomois virgata* complex groups, *C. nitida*, *C. aristata* and *C. congesta* possess shrunken elaiosomes, whereas the two outgroups and the rest of the *Cannomis* species have collared elaiosomes with the exception of *Ceratocaryum pulchrum* where the condition is absent. These states are easily seen, with shrunken elaiosomes showing infoldings whilst the collared elaiosomes are somewhat covered with perianths-like structures.

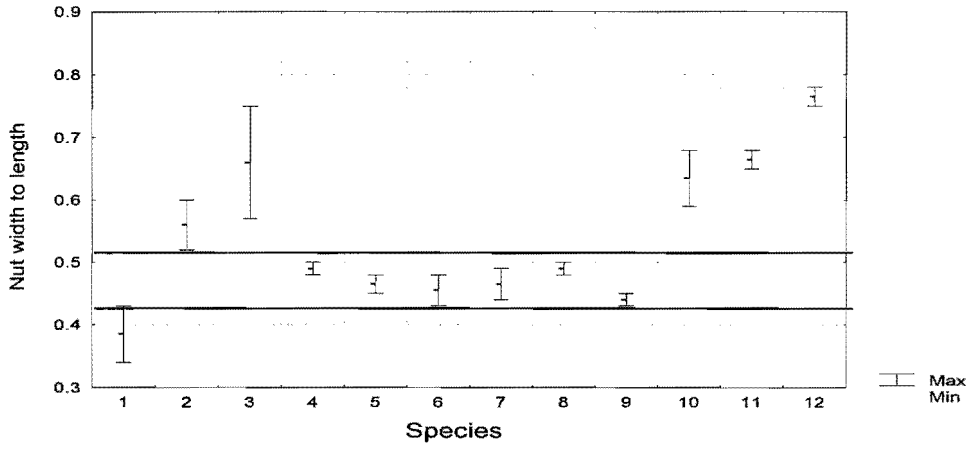

Figure 1a. Ranges in nut width to length for *Cannomois* species and the outgroups. The average of three measurements is indicated by a dash. The solid lines at 0.43 and 0.53 indicate the point of distinction between states 0, 1 and 2. Species according to numbers are as follows: 1 NW-Swartberg, 2 Coastal, 3 Caledon-Langeberg, 4 *C. nitida*, 5 *C. congesta*, 6 *C. aristata*, 7 *C. scirpoides*, 8 *C. taylori*, 9 *C. parviflora*, 10 *Willdenowia glomerata*, 11 *Hypodiscus aristatus* and 12 *Ceratocaryum pulchrum*.

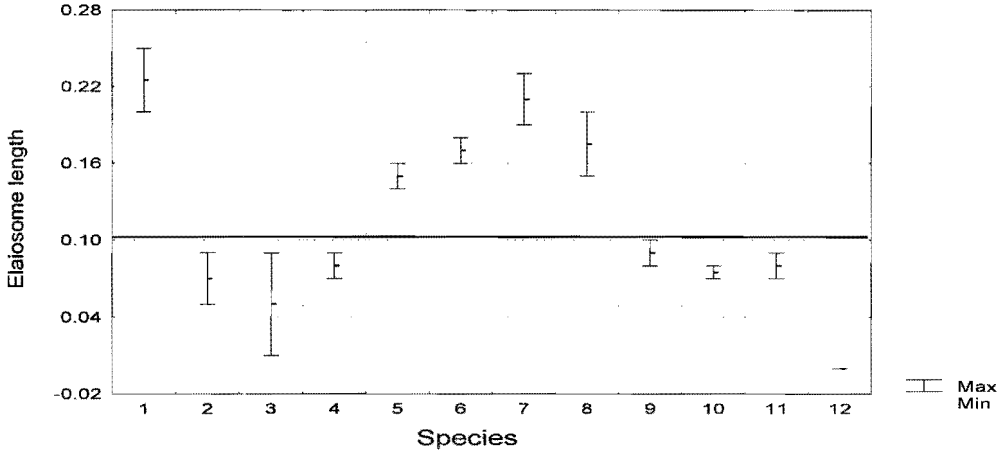

Figure 1b. Ranges in elaiosome length of *Cannomois* species and outgroups. The average of three measurements indicated with a dash. The solid line at 0.10 indicates the point of distinction between states 0 and 1. Species as in Figure 1a.

Floral and inflorescence morphology

[6]. Petal length to nut length: 1 - 0.65 = 0, 0.65 - 0.2 = 1, < 0.2 = 2.

State delimitation (Figure 1c) shows that *C. nitida*, *Hypodiscus aristatus*, the two complex groups Coastal and Caledon-Langeberg have their petal length to nut length ratios between 1 and 0.65. The NW-Swartberg group, *C. congesta* and *Willdenowia glomerata* have their ratios ranging between 0.65 and 0.20. The rest of the *Cannomois* species and *Ceratocaryum* have petal length to nut length ratios below one-fifth.

[7]. Petal width of outer segment: < 1.5 mm = 0 1.5 - 2.5 mm = 1 > 2.5 mm = 2

The character state delimitation (Figure 1d) shows that *C. taylori*, *C. scirpoides*, *C. parviflora*, *C. aristata* and *Ceratocaryum pulchrum* have petal width measurements of less than 0.5 mm. *Hypodiscus aristatus*, *Willdenowia glomerata*, NW-Swartberg, *C. nitida* and *C. congesta* range between 1.5 and 2.5 mm, while Coastal and Caledon-Langeberg, in the *C. virgata* complex have petal widths above 2.5 mm.

[8]. Petal apex appearance: entire = 0, not entire = 1

The *Cannomois virgata* complex taxa, *C. nitida* and the outgroups have entire petal apices. All the other species of the genus *Cannomois* have their petal apices either toothed, dentate or crenate.

[9]. Spikelet length: less than 30 mm = 0, more than 30 mm = 1

Variation in spikelet length is extensive within the *Cannomois virgata* complex groups. However, in all the groups spikelet length is above 30 mm, and the same applies for *C. nitida*, *Ceratocaryum pulchrum* and *Hypodiscus aristatus*. The rest of the *Cannomois* species and the outgroup *Willdenowia* have shorter spikelets less than 30 mm. Figure 1e indicates state delimitation.

[10]. Spikelets per inflorescence: single, rarely to three = 0, two to many = 1,

Most species of *Cannomois* have a single spikelet per inflorescence, with only *C. taylori*, *C. scirpoides* and *C. parviflora* having two to many spikelets, and NW-Swartberg and Caledon-Langeberg taxa having either single or two to many spikelets. All the outgroups possess a single spikelet per inflorescence except *Hypodiscus* which has either a single or two to many spikelets.

[11]. Bracts shape: acute = 0, acuminate = 1, long-acuminate = 2

Cannomois congesta and the groups in the *Cannomois virgata* complex have acuminate bracts, whereas *C. nitida* and *C. aristata have* long-acuminate bracts. Acute bracts are found in the outgroups and the remaining *Cannomois* species.

[12]. Number of fertile bracts: one = 0, two to three = 1

A common development in the female inflorescence is the reduction of the number of flowers per spikelet, finally resulting in a single fertile flower enclosed in a bract (fertile bract) subtended by numerous sterile bracts. This phenomenon is observed in the outgroups which possess a single fertile bract. All *Cannomois* species have two to three fertile bracts.

[13]. Bract number: less than 8 = 0, 8 - 10 = 1, more than 15 = 2

The trend within *Willdenowia* is toward a reduction in the number of bracts, mostly 6 relative to more than 6 to 10 in the ingroup. The other two outgroups have bract numbers exceeding 15. Bract number 8 and 10 were used to delimit states (Figure 1f)

[14]. Spathe length: shorter than spikelet = 0, longer than spikelet = 1

The genus *Cannomois* contains species either with spathes which are longer than spikelets, i.e., *C. scirpoides*, *C. taylori*, *C. parviflora* and *C. congesta*, or spathes shorter than spikelets as in the rest of the species. In the outgroups, the spathes are reduced, and shorter than spikelets. Character states are delimited based on the proportion of spathe length to spikelet length (Figure 1g).

[15]. Spathe colour: brown = 0, dark brown = 1

This character is very distinctive for separating *C. scirpoides* and *C. taylori* with pronounced dark brown spathes from the rest of the *Cannomois* species and the outgroups.

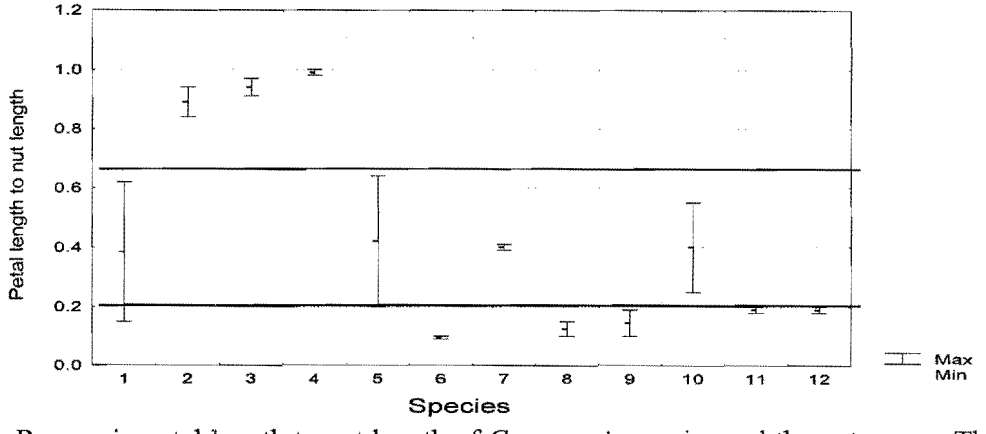

Figure 1c. Ranges in petal length to nut length of *Cannomois* species and the outgroups. The average of three measurements is represented by a dash. The solid lines at 0.2 and 0.65 indicate the point of distinction between states 0, 1 and 2. Species as in Figure 1a.

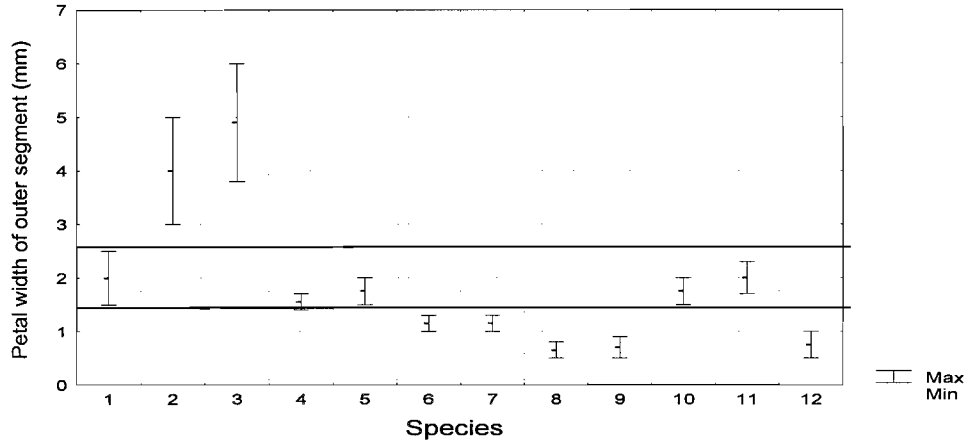

Figure 1d. Ranges in petal width of outer segment of *Cannomois* species and the outgroups. The average of three measurements is represented by a dash. The solid lines at 0.5 and 2.5 indicate the point of distinction between states 0, 1 and 2. Species as in Figure 1a.

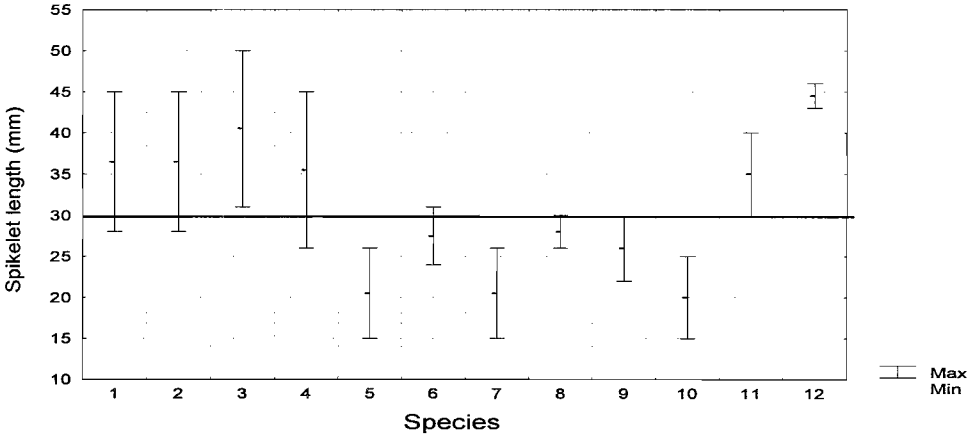

Figure 1e. Ranges in spikelet length for *Cannomois* species and outgroups. The average of three measurements is represented by a dash. The solid line at 30 indicates the point of distinction between states 0 and 1. Species as in Figure 1a.

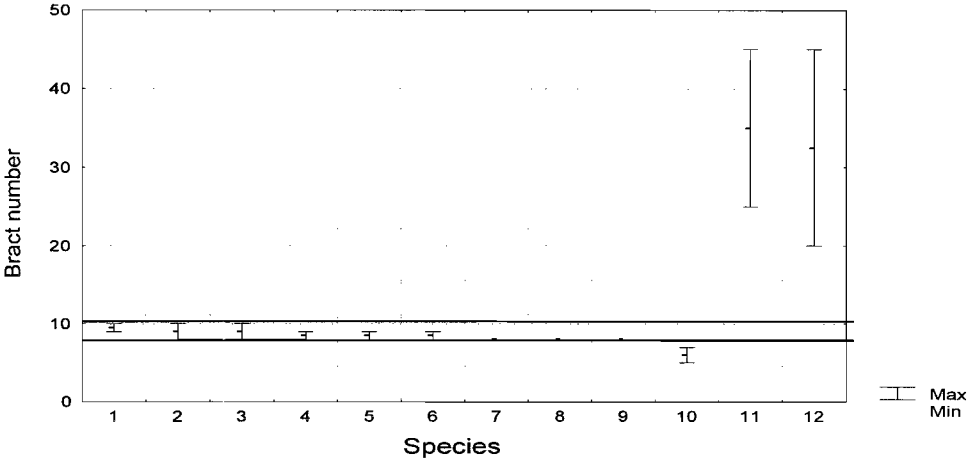

Figure 1f. Ranges in bract number for *Cannomois* species and outgroups. The average of two measurements is represented by a dash. The solid lines at 8 and 10 indicate the point of distinction between states 0, 1 and 2. Species as in Figure 1a.

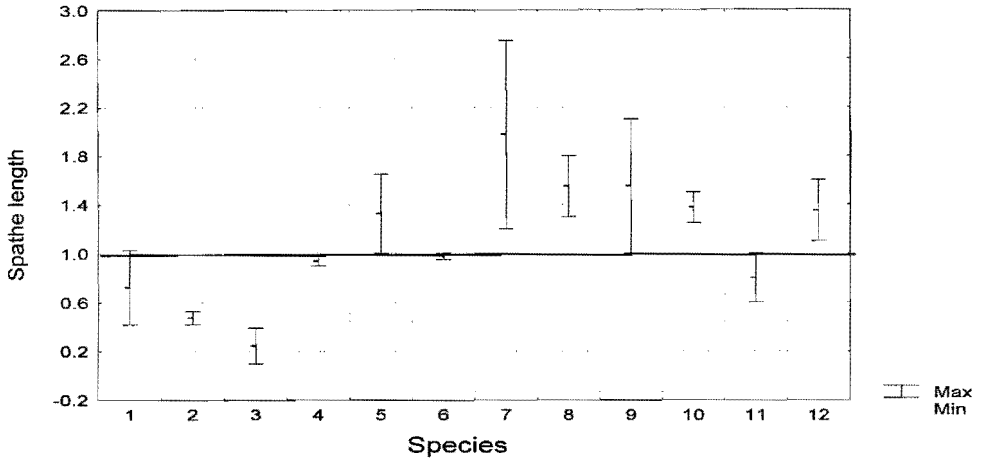

Figure 1g. Ranges in spathe length for *Cannomois* species and outgroups. The average of three measurements is represented by a dash. The solid line at 1.0 indicates the point of distinction between states 0 and 1. Species as in Figure 1a.

Culm morphology

[16]. Fertile culms: branching = 0, simple = 1

In the species of *Cannomois*, only the groups falling within the *C. virgata* complex have branching culms. This state is also shared by the outgroups with the exception of *Hypodiscus*. The remaining species of *Cannomois* have simple culms.

[17]. Degree of fertile culm branching: nil = 0, sparingly = 1, much-branching = 2

Cannomois species with simple culms and *Hypodiscus aristatus* do not exhibit any branching. Among the branching species, the Coastal taxon and *Ceratocaryum pulchrum* have a sparingly branching pattern manifested by the presence of primary branching with very minimal secondary branching if any, on the fertile culm, whereas NW-Swartberg, Caledon-Langeberg and *Willdenowia* are much-branched showing pronounced secondary branching.

[18]. Culms: distinctly hollow = 0 solid or with a small central cavity = 1

The Coastal group, Caledon-Langeberg group and *C. congesta* possess distinctly hollow cavity stems or culms with hollow cavity to culm diameter ratio of more than three-tenths, whereas the remaining species of *Cannomois* and the outgroups have culms either solid or with a negligible central cavity.

Growth habit

[19]. Plant height: ca. 1 m = 0, 1- 2 m = 1, > 2 m = 2

The majority of species in *Cannomois* and the outgroups are tussocked plants not more than 1 metre tall. Only the Coastal taxon has a plant height between 1 and 1.5 metres. NW-Swartberg and *C. taylori* have plant heights between 1.5 and 2 metres. The Caledon-Langeberg group is an exception with plant height above 2 metres. Character states were delimited at 1 and 2 metres (Figure 1h).

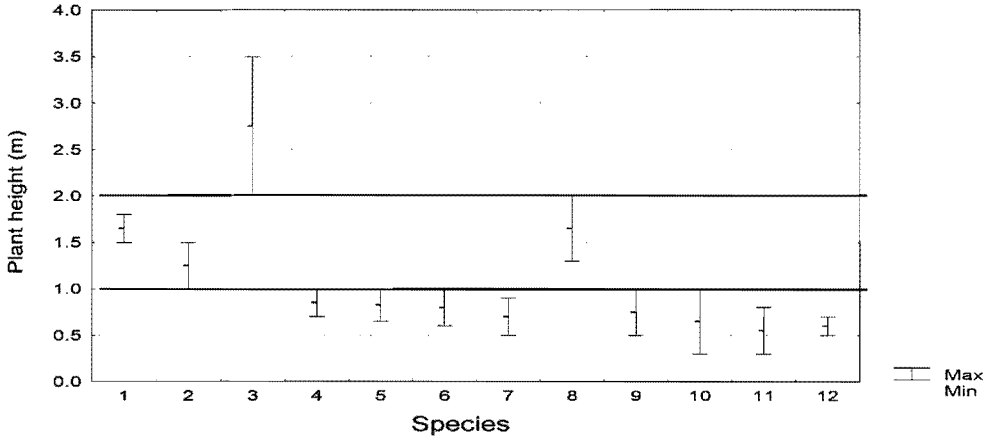

Figure 1h. Ranges in plant height for *Cannomois* species and outgroups. The average of three measurements is indicated with a dash. The solid lines at 1 and 2 m indicate the point of distinction between states 0, 1 and 2. Species as in figure 1a.

[20]. Fire response: coppice = 0, seed = 1

All the outgroups have the ability to resprout after fire. Within the *Cannomois* species, only the Coastal group in the *Cannomois virgata* complex, *C. scirpoides*, *C. parviflora* and *C. aristata* are resprouters, and the majority are reseeders.

[21]. Rhizome: spreading = 0, short = 1

All the species of *Cannomois* are rhizomatous, differing only in whether the rhizomes are short or spreading. All the species in the genus *Cannomois* and the outgroups have spreading rhizomes, with the exception of *C. congesta, C. aristata,* NW-Swartberg, Caledon-Langberg, *Ceratocarum pulchrum* and *Hypodiscus aristatus* which have short rhizomes.

Anatomy

[22]. Stomata: superficial = 0, sunken = 1

The stomata are superficial in the *C. virgata* complex taxa, *C. congesta* and the outgroups, whereas in the rest of the *Cannomois* species they are sunken.

[23]. Epidermal cell shape: square = 0, rectangular = 1, elongated = 2 (additive)

Ceratocaryum pulchrum is the only species with square epidermal cells; the other outgroups, *C. congesta*, *C. aristata* and *C. virgata* segregates have rectangular cells. The remaining species of *Cannomois* have elongated cells. Rectangular cells are defined as having length to width ratios from 2 to 3 whereas elongated cells have length to width ratios of 4 or more.

[24]. Epidermal cells: tanniferous = 0, not tanniferous = 1

All the species show tanniferous epidermal cells except *Ceratocaryum pulchrum*, NW-Swartberg, Caledon-Langeberg, *Cannomois scirpoides* and *Cannomois aristata*.

[25]. Chlorenchyma: cell layers obscure = 0, cell layers distinct = 1

Within the genus *Cannomois* this character separates *Cannomois congesta* and the *C. virgata* taxa showing distinct cell layers from the rest of the species. In the outgroups, only *Willdenowia glomerata* shows clear chlorenchyma layers.

[26]. Parenchyma layer: continuous = 0, interrupted = 1

The parenchyma layer is interrupted for *Hypodiscus aristatus*, NW-Swartberg taxon, *C. taylori*, *C. parviflora*, *C. congesta* and *C. nitida* and for all the remaining species it is continuous.

2.5.4. **Cladistic analysis**

The data set was analysed using PAUP version 3.1.1 for Macintosh (Swofford, 1993). Methods for finding the maximally parsimonious or minimum length tree(s) fall into two categories. The first one is for small to medium-sized data sets of up to about 20 taxa, exact methods which are branch-and-bound and exhaustive that guarantee the discovery of all optimal trees can be used. The second category is for larger data sets in which heuristic

methods must be employed. In this analysis, the data set is small with 12 taxa requiring the use of exact methods. However, both heuristic and branch-and-bound search algorithms were used. A heuristic search procedure, with swap = tbr, multipars, addseq = simple and 1000 random addition replicates was used to specify an upper bound for the branch-and-bound search algorithm.

The branch-and-bound algorithm is guaranteed to find all minimum-length trees and usually runs quickly for 12 or few taxa. The branch-and-bound search strategy followed in PAUP included (1) setting initial upper bound to 55, (2) keeping all minimal trees only, (3) saving all optimal trees (MULTrees) and (4) applying addition sequence with furthest search option in effect.

Character state changes were traced using MacClade version 3.07 (Maddison and Maddison 1992) which provided a suitable optimisation algorithm, and the accelerated transformation (ACCTRAN) option was used.

2.5.5. **Support for the tree topology**

Internal support of the data set for the nodes of the tree topology was assessed by bootstrap analysis (Felsenstein, 1985; Sanderson, 1989), implemented on PAUP version 4.0b2 using a branch-and-bound search algorithm. Bootstrap analysis performs random sampling of characters with replacement. The strategy for the bootstrap resampling method included setting the number of replicates to 500, retaining all groups including those with frequency less than 50%, computing via stepwise with addition sequence at furthest, keeping all minimal trees only and saving all optimal trees (MulTrees). The use of bootstrapping as a means of assessing confidence limits on phylogenies has been questioned, since characters are not randomly sampled from independent populations (Carpenter, 1992,1996; Kluge and Wolf, 1993; Siddall and Kluge, 1997). However, bootstrap values were used as a means to discover ambiguity in the data and as qualitative estimates of accuracy. Bremer support values or indices (Bremer 1988) were determined using AutoDecay (Eriksson, 1996). AutoDecay is a utility, which helps in performing 'decay analysis' of all (or at least almost all) nodes of a cladogram or consensus tree using the reverse constraint option in PAUP. It aids in the

determination of decay or support indices by generating a PAUP (Swofford, 1993) command file with (1) a constraint statement for each node in a given shortest or strict consensus tree and (2) commands to search for trees inconsistent with each of these constraint statements in turn. Compared to the shortest unconstrained tree, the number of additional steps required in the shortest tree(s) that is inconsistent with a given node is the decay index for that node. The branch-and-bound search was implemented to get the constraint statements. The decay index represents how many extra steps are required to find trees that do not contain a particular group. It provides a relative measure of how much the homoplasy in the data affects support for a particular group.

The stability of monophyletic groups was further tested using the method of sequential character removal (Davis, 1993). Characters were removed one at a time, and the data set re-analysed using branch-and-bound search. After each analysis the characters were replaced, so that in each analysis there was just one character excluded. The advantage of the character removal method, over the Bremer support or bootstrap is that it is able to identify characters that are crucial to the resolution of the clade.

Furthermore, the effect of removing taxa was assessed in order to identify how critical each taxon is to the resolution of the tree as recommended by Siddall (1995). The procedure used is a Jack-knife approach (Lanyon, 1985) similar to character removal, and is a way of determining the stable portions or subsets of the estimated phylogeny. Ten computer runs of the branch-and-bound search were made. In each run, a single taxon was deleted until all ten ingroup taxa were completed. After each run, calculation of the strict consensus tree was performed and compared with the strict consensus tree calculated when all taxa were included. Changes in the increase and decrease of the total number of parsimonious trees were noted. When deleted, taxa causing an increase in the total number of parsimonious trees were identified as critical whereas those causing a decrease were identified as problematic.

2.5.5. **Alternative topology**

The 'all rootings' option in MacClade was used to examine the effect of moving the taxa within the *C. virgata* complex to different positions on the shortest tree. The aspects examined were the cost (extra steps required) of moving a taxon to particular branches and the number of branches to which it could be moved with minimum cost.

2.5.6. **Character mapping**

Environmental and vegetative characters i.e., plant response, plant height and rhizome were mapped in MacClade version 3.07 (Maddison and Maddison, 1992), which provided a suitable optimisation algorithm. The accelerated transformation (ACCTRAN) option was used.

2.6. Description and diagnostics

Formal taxon descriptions were prepared from the information extracted from herbarium specimens. In order to establish the correct application of the name *Cannomois virgata*, the original materials were searched. These include type specimens described under the following synonyms: *Restio virgatus* Rottb. in Descriptiones Plantarum Rariorum 10 (1772), *Restio scopa* Thunb. in Diss. Restio 19 (1788), *Restio elegans* Poir. in Lam., Encycl. 6 : 171 (1804); *Cannomois cephalotes* Desv. in Annls Sci. nat., ser. 1, 13 : 43 (1828) and *Thamnochortus robustus* Kunth in Enum. Pl. 3 : 436 (1841).

3. RESULTS

3.1. Phenetic analysis

3.1.1. **Multivariate analyses**

Cluster analysis of the full data set retrieved three major groups namely A, B and C (Fig. 2.1). According to their geographical distributions, group A is the NW-Swartberg group (northwestern to Swartberg mountains), group B the Caledon-Langeberg mountain group and group C the Coastal mountain group. The cluster marked H was observed to share some few characters with the Coastal group. However, the dendrogram shows that it is embedded in the NW-Swartberg group with which it shares most of its characters.

The main clusters A, B and C are separated by long branch lengths. Cluster A is separated from clusters B and C by a dissimilarity coefficient of 1.51, and in turn the branch lengths separating cluster B and C has a dissimilarity coefficient of 1.08. Within each cluster, the branches are shorter, with a dissimilarity coefficient of at most 0.87.

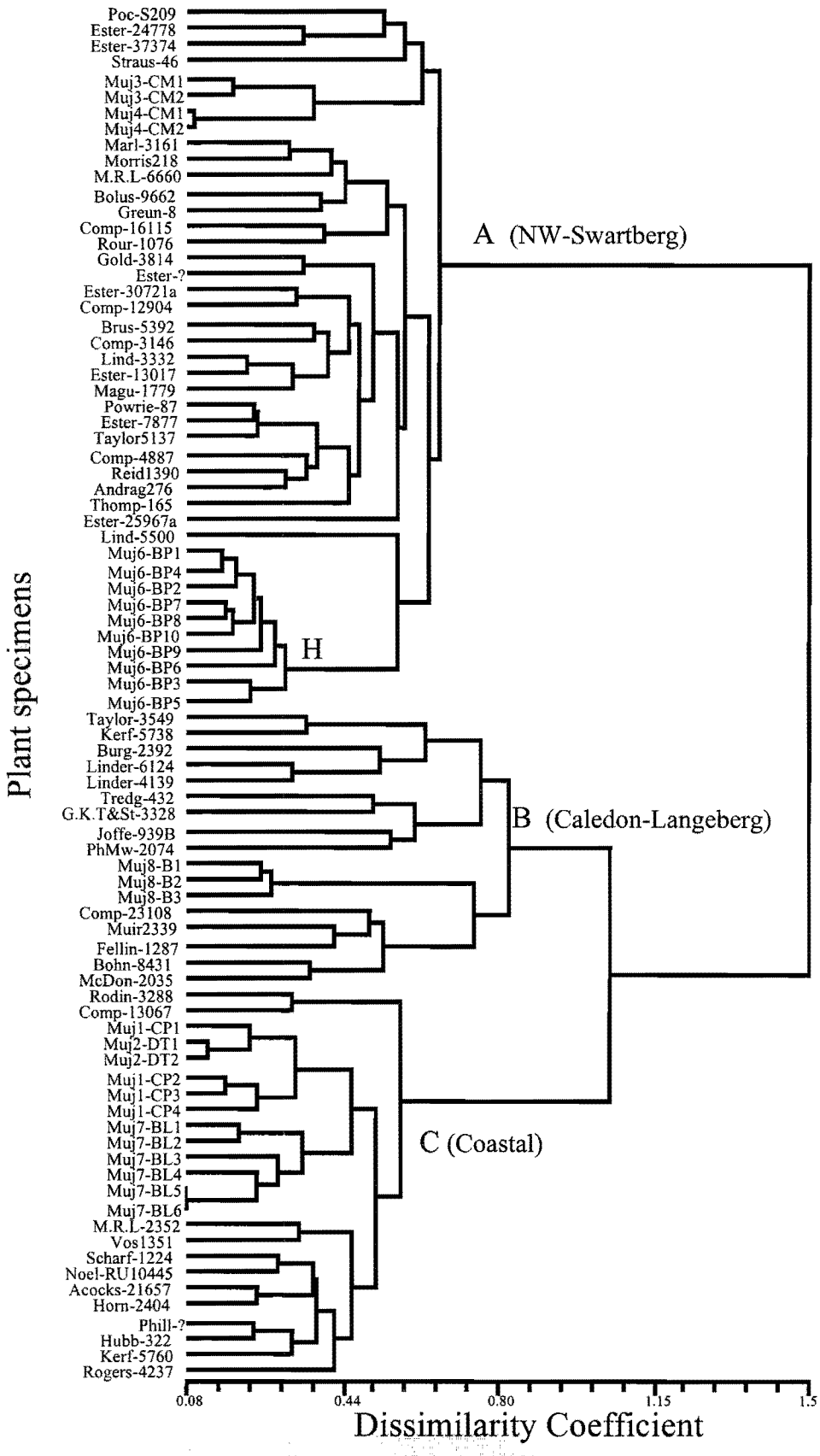

Figure 2.1. Cluster analysis of the *C. virgata* complex showing three major segregates (A, B and C). Specimen codes are according to Tables 2.1 and 2.2.

Ordination based on principal components analysis of the data set revealed the same discrete clusters of specimens (Figure 2.2), corresponding to the three taxa from Northwest-Swartberg mountains (A), Caledon-Langeberg mountains (B) and Coastal mountains (C) respectively.

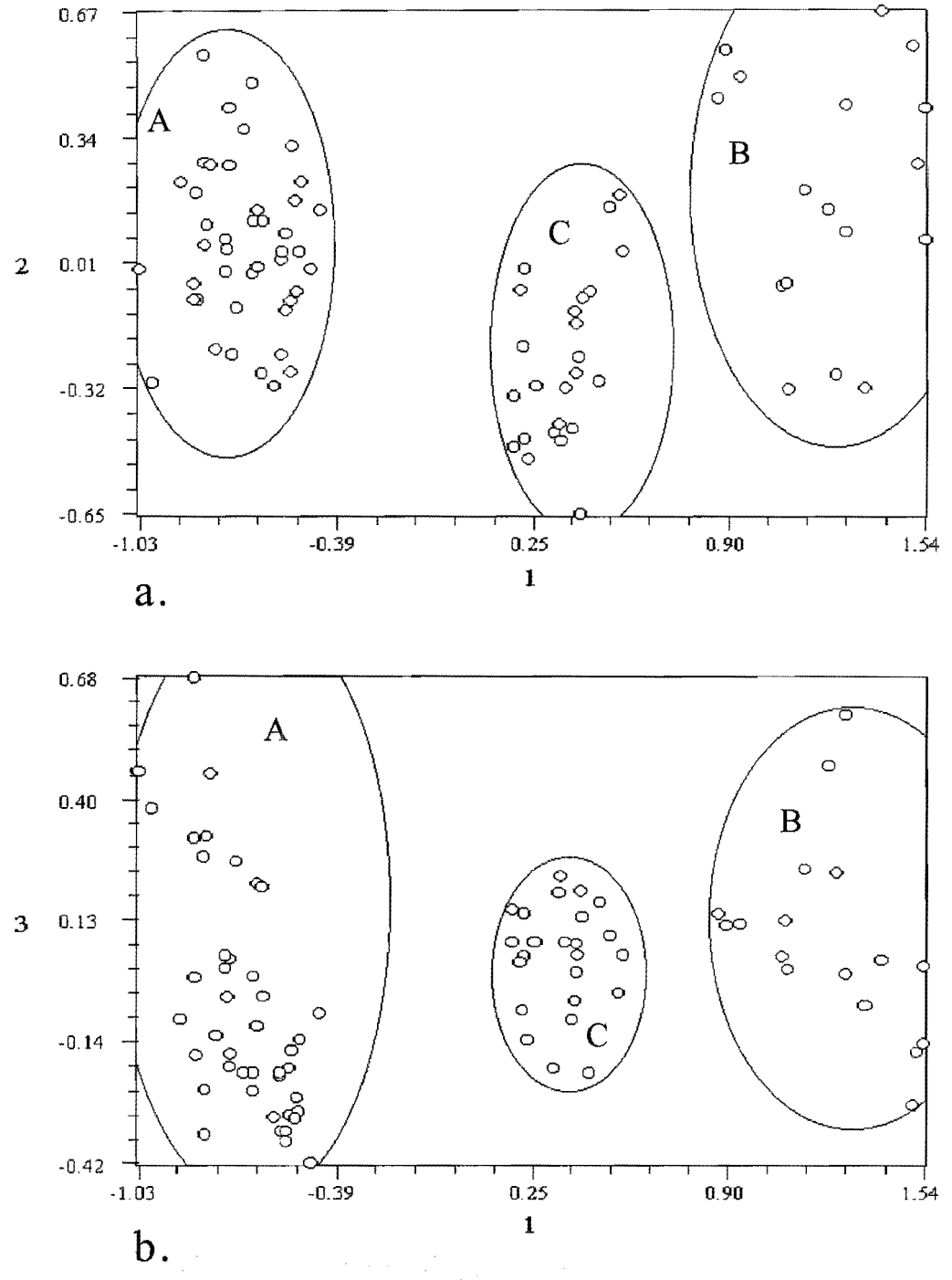

Figure 2.2. Principal component analysis of the *C. virgata* complex in 2-dimensional model plots. Plot **a** represent component 2 versus 1, and plot **b** represent component 3 versus 1. A = NW-Swartberg group, B = Caledon-Langeberg group and C = Coastal group.

The three-dimensional model plot (Figure 2.3) shows the relationships of the OTU's in hyperspace, in which there are only three clear groups. The intermediate group H marked on the dendrogram is inseparable from the NW-Swartberg group.

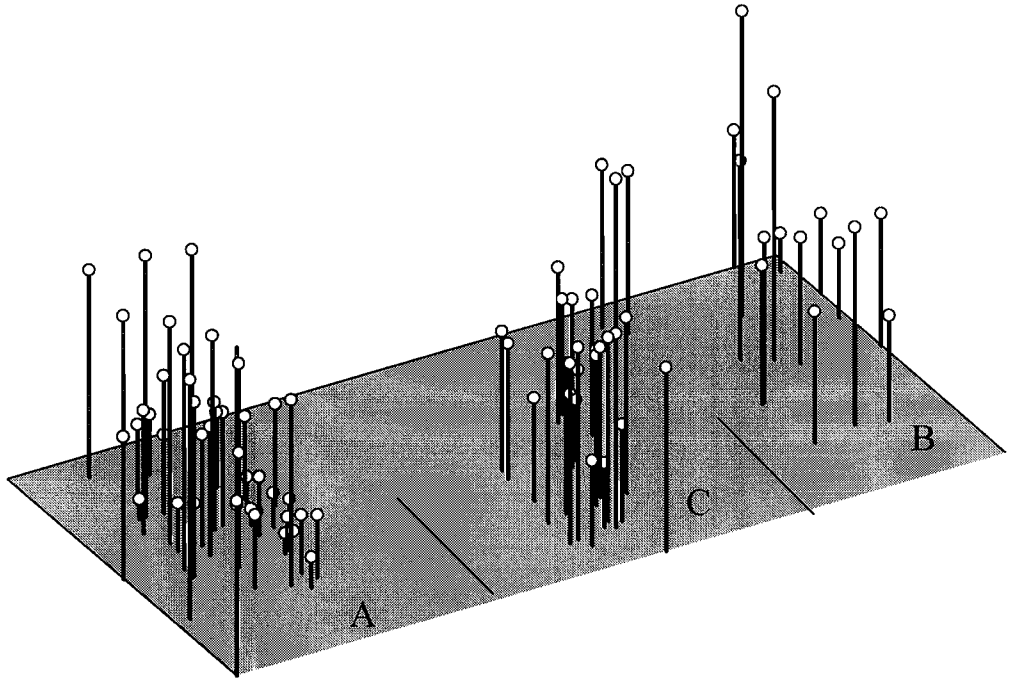

Figure 2.3. Three-dimensional model plot for components 1, 2 and 3. A is NW-Swartberg group, B is Caledon-Langeberg group and C is Coastal group.

The first three components accounted for 79.06% of total character variation (Table 3.1(b)) with 16 and 2 characters having their loading factors of more than 0.7 contributing to the first and second principal axes respectively (Table 3.1(a)). Individually, they contributed 64.35%, 8.57% and 6.13% of the variance in the data. The three main characters contributing to each component are nut width, petal length and bract width for the first axis; spikelet length, bract length and spathe length for the second axis, and ratio of spathe length to spikelet length, spathe length and branch base diameter for the third axis. The 16 characters contributing to the first principal axis express a huge variation which is due to size factor, as indicated by the correlation observed on scatterplots (Figure 2.2.). Perhaps, if a scatterplot involving the third principal axis versus the second principal axis was constructed, it would indicate the contribution due to shape variation.

Table 3.1. (a) Eigenvector matrix for PCA using all characters.

Bolded figures under each component signify 3 characters contributing the most variation for each principal component.

	1	2	3
Nut length	0.7724	0.2912	0.0749
Nut width	**0.9462**	0.1053	0.1523
Petal length	**0.9425**	-0.0305	0.0177
Petal width of outer segment	0.8983	-0.0096	0.2258
Petal width of inner segment	0.8295	0.0550	0.1056
Spikelet length	0.1544	**0.8429**	-0.0333
Spikelet width	0.8934	0.2497	-0.0261
Bract Length	0.2967	**0.7761**	-0.1295
Bract width	**0.9206**	0.1344	0.0366
Spathe length	-0.6758	**0.2966**	**0.6166**
Elaiosome length	-0.7427	0.2939	-0.2896
Culm diameter at apex	0.7872	0.2076	0.0989
Branch-tip diameter	-0.8584	0.1572	0.1555
Branch base diameter	-0.7331	0.1776	**0.3696**
Ratio of nut width to length	0.8926	-0.0688	0.1583
Ratio of petal length to nut length	0.8996	-0.1741	-0.0220
Ratio of spikelet width to length	0.7300	0.0430	-0.1154
Ratio of bract width to length	0.8803	-0.1741	0.0854
Ratio branch tip to base diameter	-0.8787	0.0203	-0.2502
Ratio of hollow cavity to culm diameter	0.9098	-0.0147	-0.0541
Ratio of spathe length to spikelet length	-0.6480	-0.0533	**0.6601**
Ratio of elaiosome length to nut length	-0.8300	0.2226	-0.2374

(b). Character variation on the first three components using all characters.

i	Eigenvalue	Percent	Cumulative
1	14.15770322	64.3532	64.3532
2	1.88630334	8.5741	72.9273
3	1.34955323	6.1343	79.0616

3.1.2. **Univariate analysis**

3.1.2.1. Scatter plots

Scatter plots (Figure 3) revealed discontinuous variation in eight pairs of metric characters among the specimens. The variation is illustrated by the separation of three distinct clusters on the basis of two characters.

A scatter plot of nut width against nut length (Fig. 3A) as a measure of nut shape, showed that individuals belonging to the Caledon-Langeberg, Coastal and NW-Swartberg segregates form discrete clusters on account of their nut width, with the former having distinctly broader nuts and the latter slender narrow nuts. Nut length shows overlap between the three segregates. A scatter plot of petal length against nut length (Fig. 3B) as a measure of petal size, shows that individuals forming the Caledon-Langeberg and Coastal segregates have long petals as compared to individuals of the NW-Swartberg segregate. A gap in petal size is explicit from the scatter plot distinguishing NW-Swartberg individuals from the other two. Figure 3C indicates that wider and longer outer petals are characteristic of individuals belonging to the Coastal and Caledon-Langeberg segregates. It is apparent that specimens from the Caledon-Langeberg areas have much wider and longer petals, though there is extensive overlap in this character with the Coastal ones. Specimens from the NW-Swartberg area have short and narrow petals. Similarly, figure 3D expresses almost the same variation as figure 3B. Only petal length measurements contribute to the discontinuous variation, which is vital for delineating *C. virgata* complex groups. Scatter plots of spikelet width against spikelet length (Fig. 3E) and bract width against bract length (Fig. 3F) illustrate enormous variation among the groups of *C. virgata* complex. This variation can be partitioned between plants, those from the Caledon-Langeberg and Coastal mountains with both broad bracts and spikelets, and those from the NW-Swartberg mountains with narrow bracts and narrow spikelets. Scatter diagrams Fig. 3G and Fig. 3H show that elaiosome length and branch-tip diameter respectively are important characters separating the groups and show little overlap. In both cases, individuals belonging to the Coastal group form a discrete cluster between the NW-Swartberg and the Caledon-Langeberg individuals. Most individuals belonging to Caledon-Langeberg have both short elaiosomes and smaller branch-tip diameter compared to the other

two groups. The scatterplot (Fig. 3H) shows branch base diameter to overlap broadly among the groups.

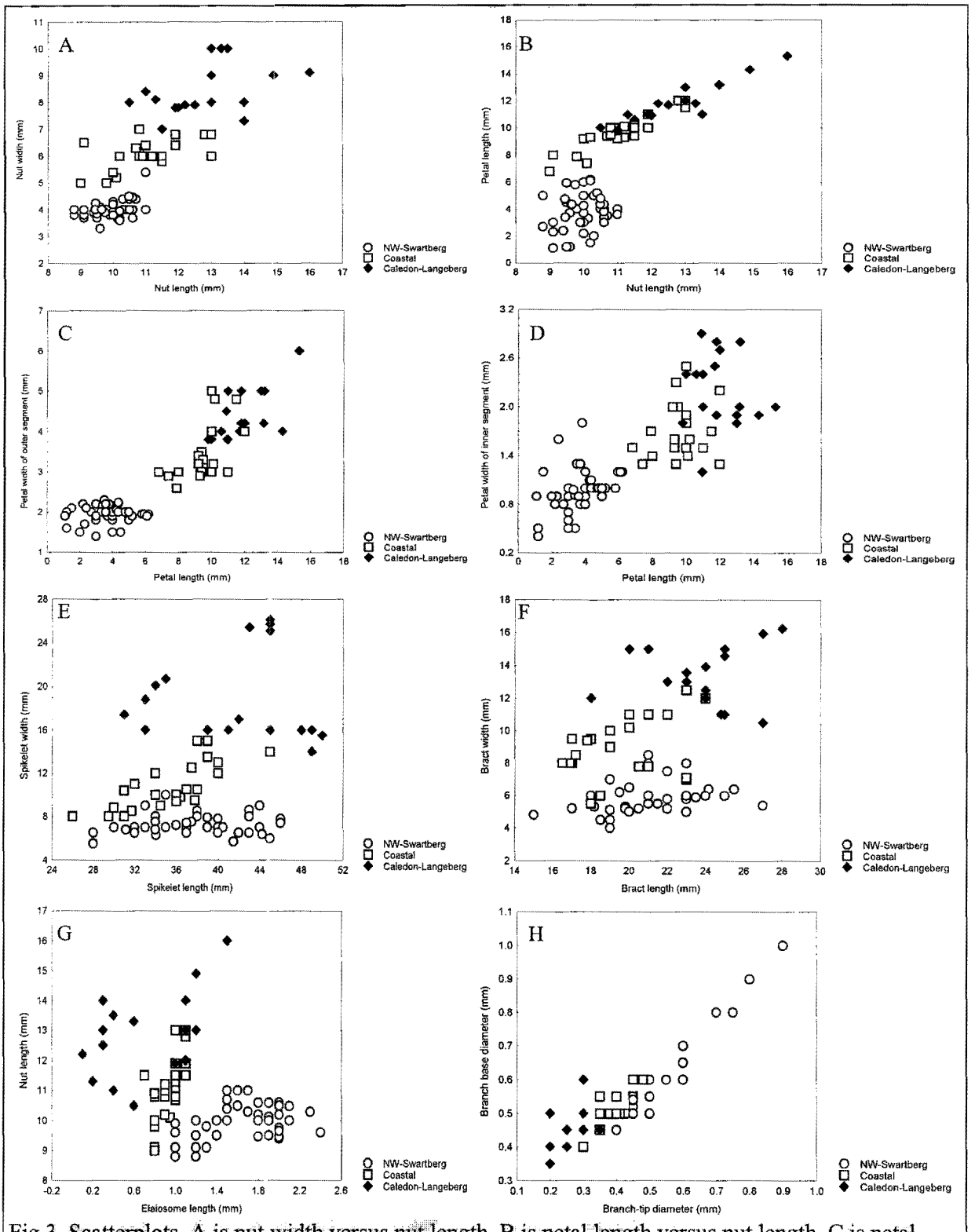

Fig.3. Scatterplots. A is nut width versus nut length, B is petal length versus nut length, C is petal width of outer segment versus petal length, D is petal width of inner segment versus petal length, E is spikelet width versus spikelet length, F is bract width versus bract length, G is nut length against elaiosome length and H is branch base diameter against branch-tip diameter.

3.1.2.2. Box-and-Whisker plots

Medians, ranges (maximum and minimum) and frequency of distributions of all individual characters used in the analyses are presented for groups (Figure 4a-d). The plots revealed ten discrete characters which include nut width (2), petal length (3), petal width of outer segment (4), spikelet width (7), bract width (9), branch-tip diameter (13), ratio of nut width to length (15), ratio of petal length to nut length (16), ratio of hollow cavity to culm diameter (20) and ratio of elaiosome length to nut length (22) for separating NW-Swartberg, Coastal and Caledon-Langeberg groups. Other remaining characters show continuous variation with overlap between all the groups and hence are not useful in separating the *C. virgata* complex groups.

Nut width and spikelet width indicate insignificant clear discontinuities between the Coastal, Caledon-Langeberg and NW-Swartberg plants. Bract width separates NW-Swartberg from Caledon-Langeberg while a smaller overlap is shown between these two groups and the Coastal group. Generally, Caledon-Langeberg plants have broadest nuts, spikelets and bracts, followed by the Coastal plants. Characters 4, 15, 16 and 22 isolate the NW-Swartberg group from the other two, whereas character 22 only distinguishes the Caledon-Langeberg group from the rest of the *C. virgata* complex groups.

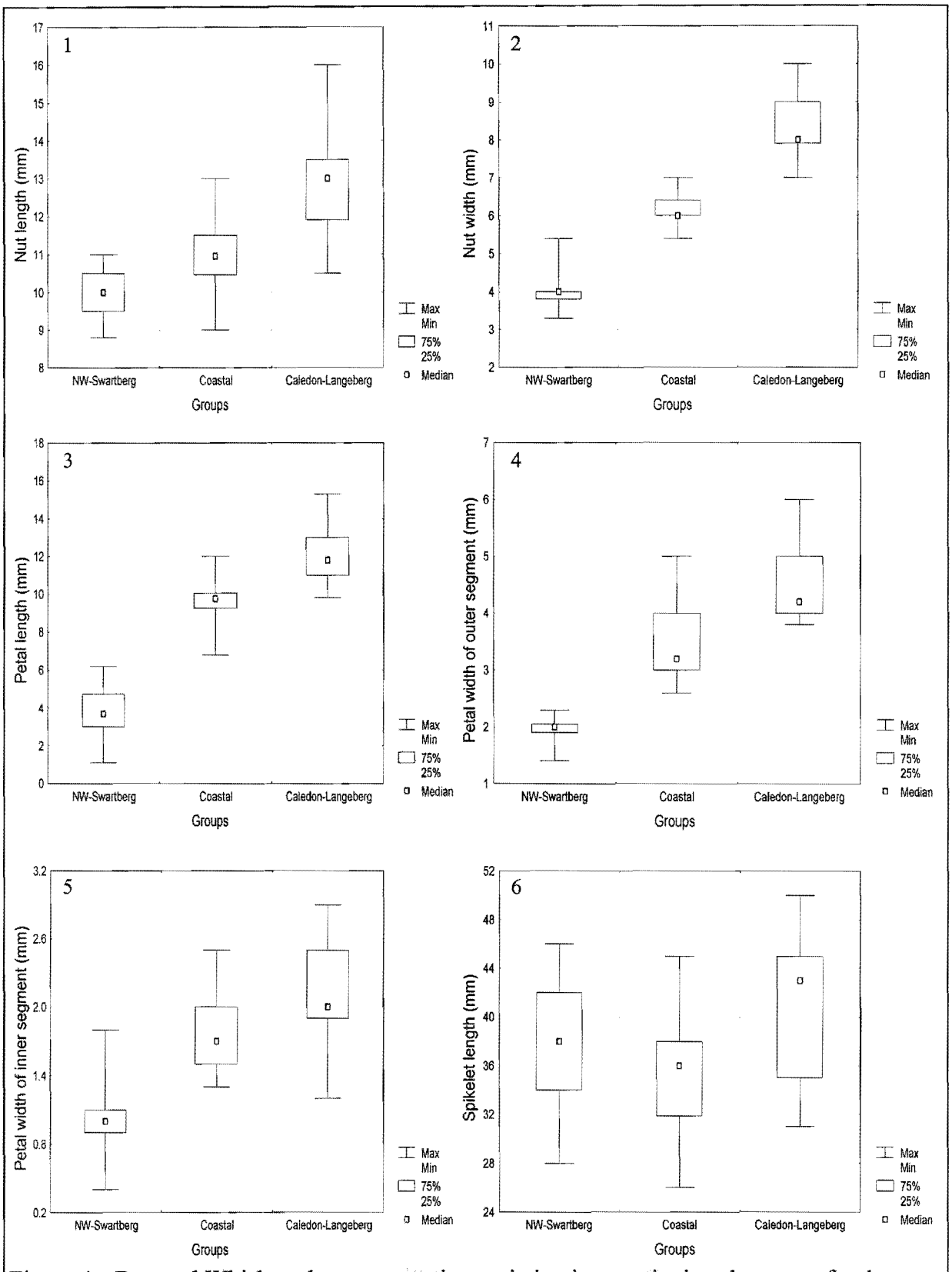

Figure 4a. Box and Whisker plots representing variation in quantitative characters for the phenetic groups. Groups are indicated along the X-axis, character variation along the Y-axis. The numbers inside the graphs correspond to the character as per Table 2.3.

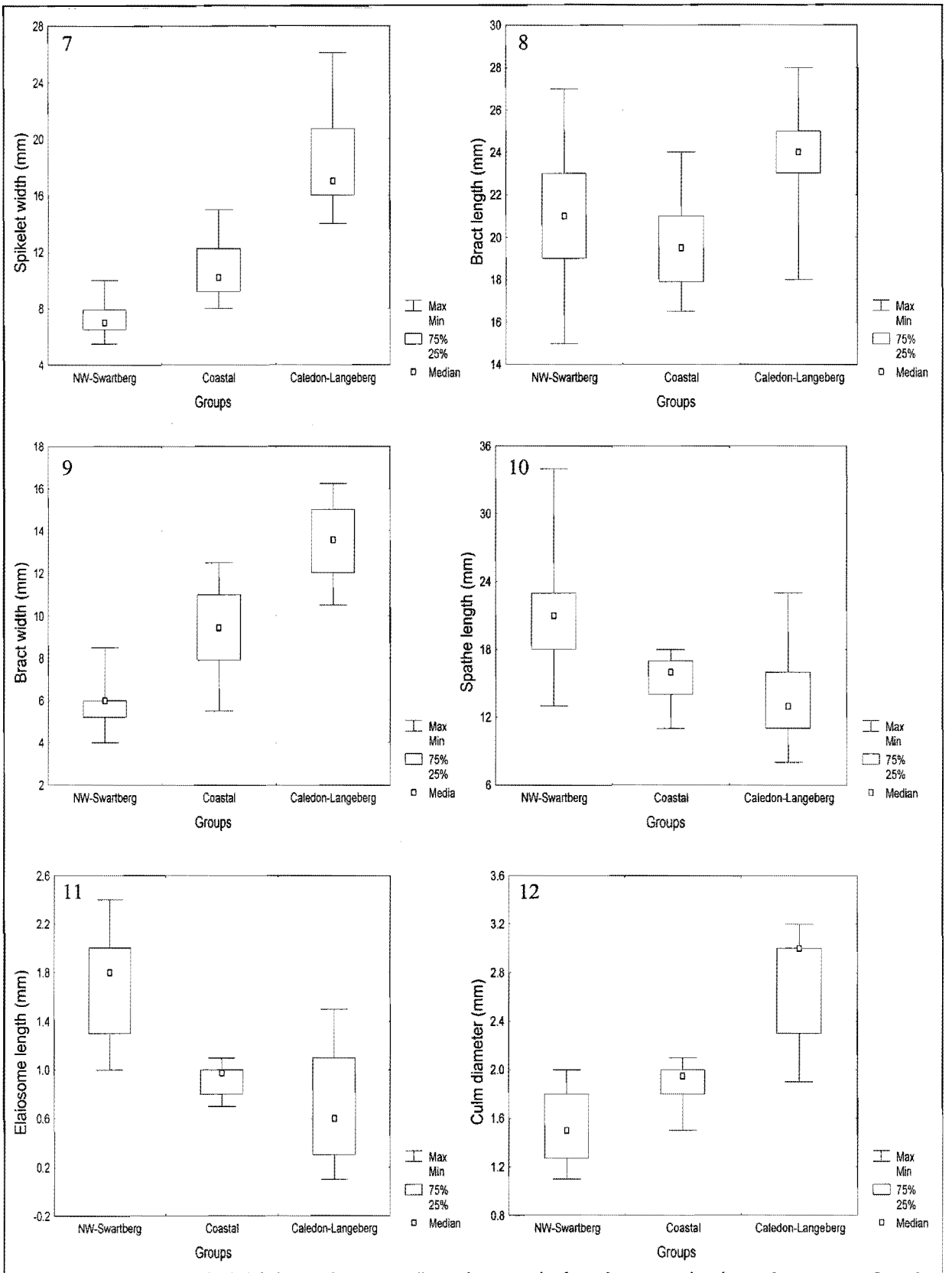

Figure 4b. Box and Whisker plots representing variation in quantitative characters for the phenetic groups. Groups are indicated along the X-axis, character variation along the Y-axis. The numbers inside the graphs correspond to the character as per Table 2.3.

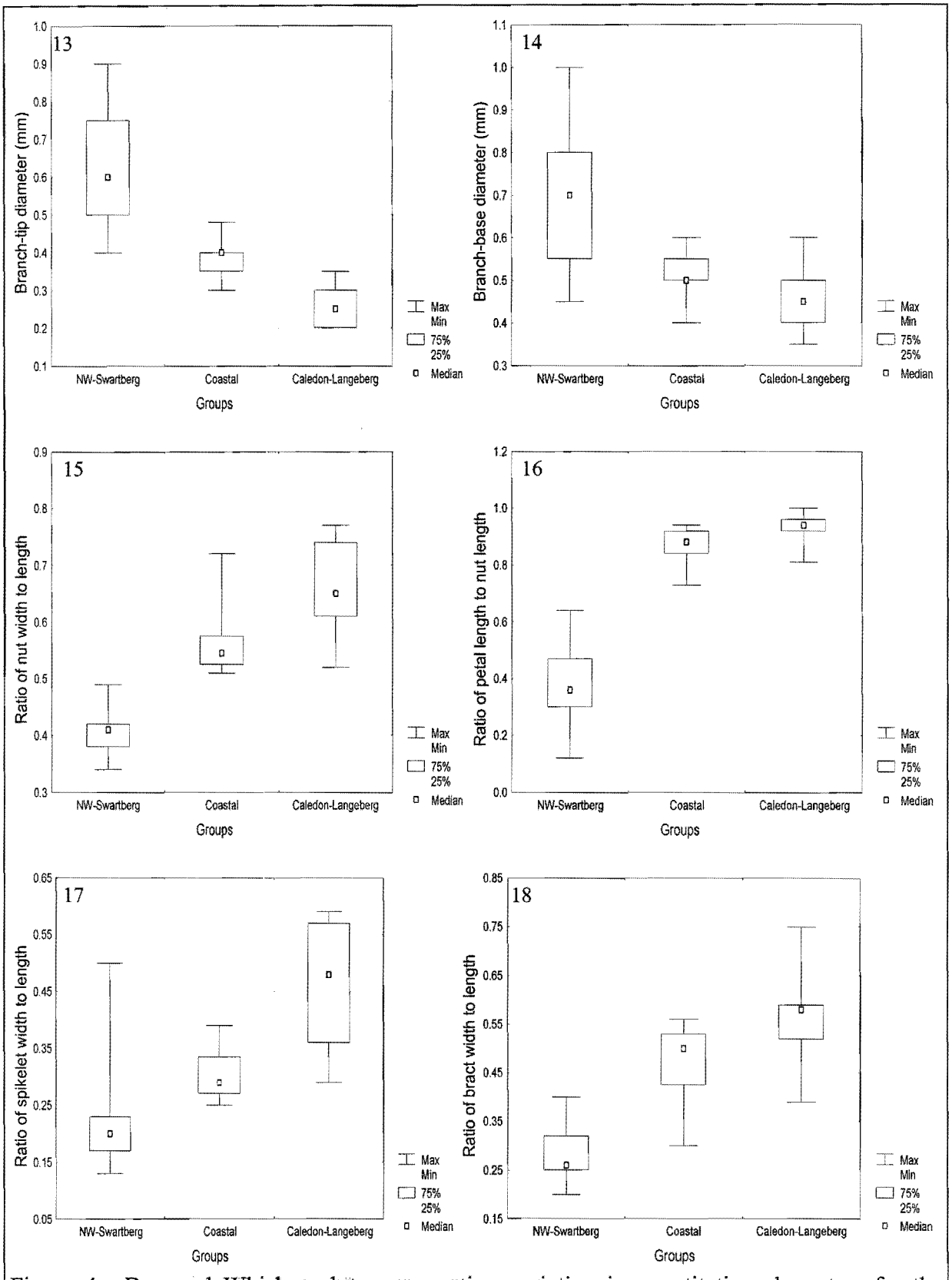

Figure 4c. Box and Whisker plots representing variation in quantitative characters for the phenetic groups. Groups are indicated along the X-axis, character variation along the Y-axis. The numbers inside the graphs correspond to the character as per Table 2.3.

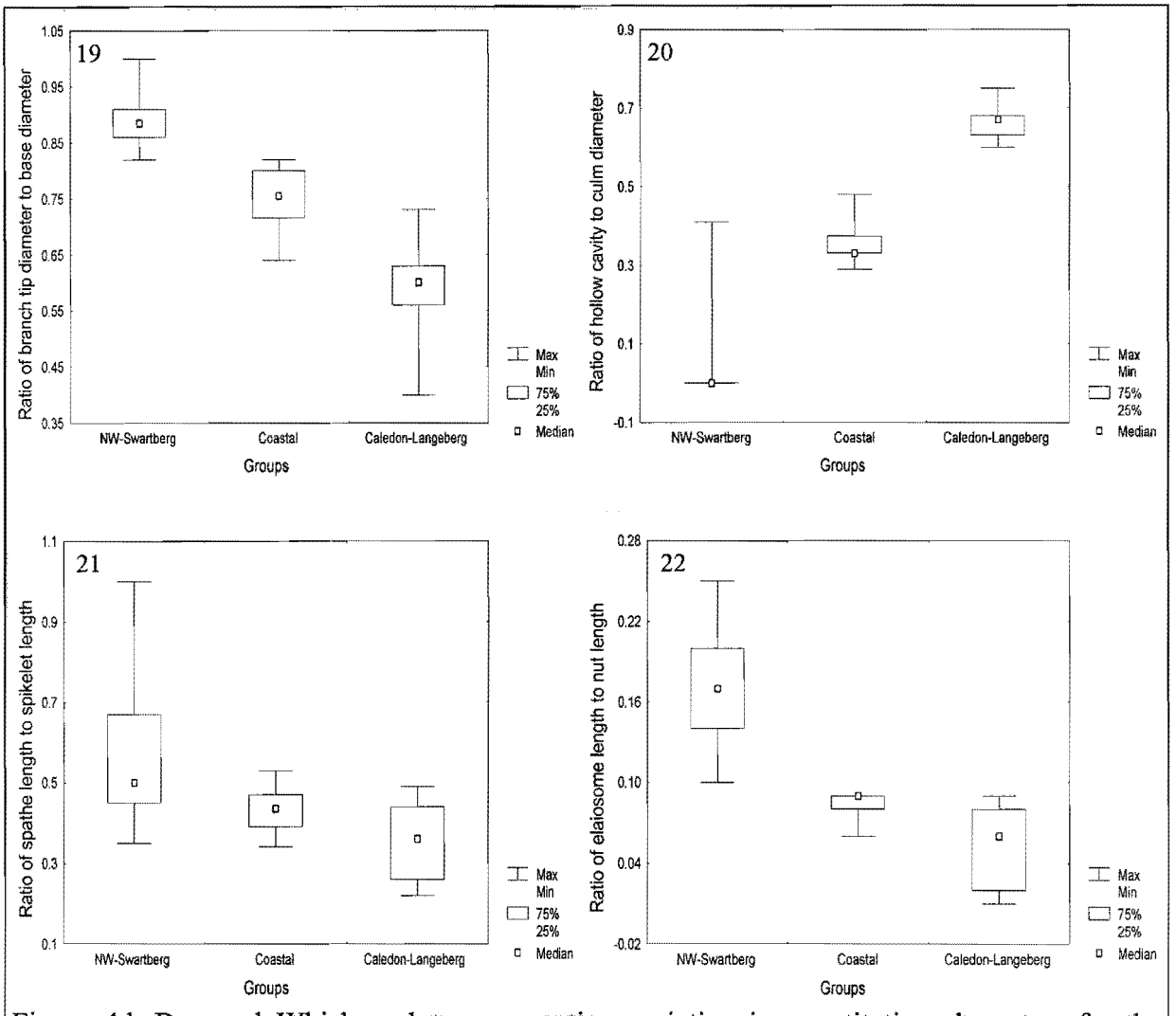

Figure 4d. Box and Whisker plots representing variation in quantitative characters for the phenetic groups. Groups are indicated along the X-axis, character variation along the Y-axis. The numbers inside the graphs correspond to the character as per Table 2.3.

3.2. Field observations and distribution of the phenetic groups

3.2.1. **Field observations**

3.2.1.1. Growth habit variation

The groups in the *Cannomois virgata* complex differ strikingly in their habits (Table 3.2). Generally, all plants within the complex have branching culms. However, the Coastal group has massive, mat forming and occasionally branching rhizomes, forming extensive tussocks whereas the remaining groups possess short rhizomes and form compact tussocks. They also differ in plant height, rhizome diameter, culm spacing and base diameter.

Table 3.2. Comparison of the habits of the groups in the *Cannomois virgata* complex

Feature	NW-Swartberg	Coastal	Caledon-Langeberg
Tussock ht.	1.0 - 1.8 m	1.0 - 1.5 m	2.0 - 3.5 m
Base diameter	0.3 - 0.5 m	3 - 5 m	1.0 - 1.5 m
Appearance	compact	spreading	compact
Culms	erect	erect	drooping
Rhizomes	short	spreading	long
Rhizome diameter.	4.0 - 5.0 mm	6.0 - 10.0 mm	10.0 - 15.0 mm
Culm spacing	adjacent	to 35.0 mm	to 10 mm
Culm base diameter.	5.0 - 8.0 mm	5.0 - 8.5 mm	12.0 - 20.0 mm
Inflorescence to foliage height	above	below	above
Inflorescence per plant	many	few (mostly single per culm)	many

3.2.2. **Distribution of the phenetic clusters**

The distributions of the phenetic clusters are given in Figure 5. It is clear that clusters may occur in sympatry. For example the Coastal morphotype is frequently found near Caledon-Langeberg, but it is always associated with wet mountain slopes, while the other occupies dry mountain slopes close to streams. However, the NW-Swartberg group has a more inland distribution as compared to the other two. The distribution of the NW-Swartberg group has its northern limit in the Hantam and Cedarberg. In the southern-central side of the Cape Floristic Region it is found along Ceres and Bains Kloof mountains. The Coastal group is prevalent in the South coast areas, with patches also found in the Hantam, Worcester, Cape Peninsula, Caledon through Du Toits Kloof and Bains Kloof mountain ranges to the Great Swartberg, whereas the Caledon-Langeberg group is distributed from Caledon mountains (around Jonkershoek), through the Bains Kloof mountains to the Langeberg mountains. Patches of the Caledon-Langeberg group are also found in the Swartberg mountains and Outeniqua mountains on the dry-north facing slopes.

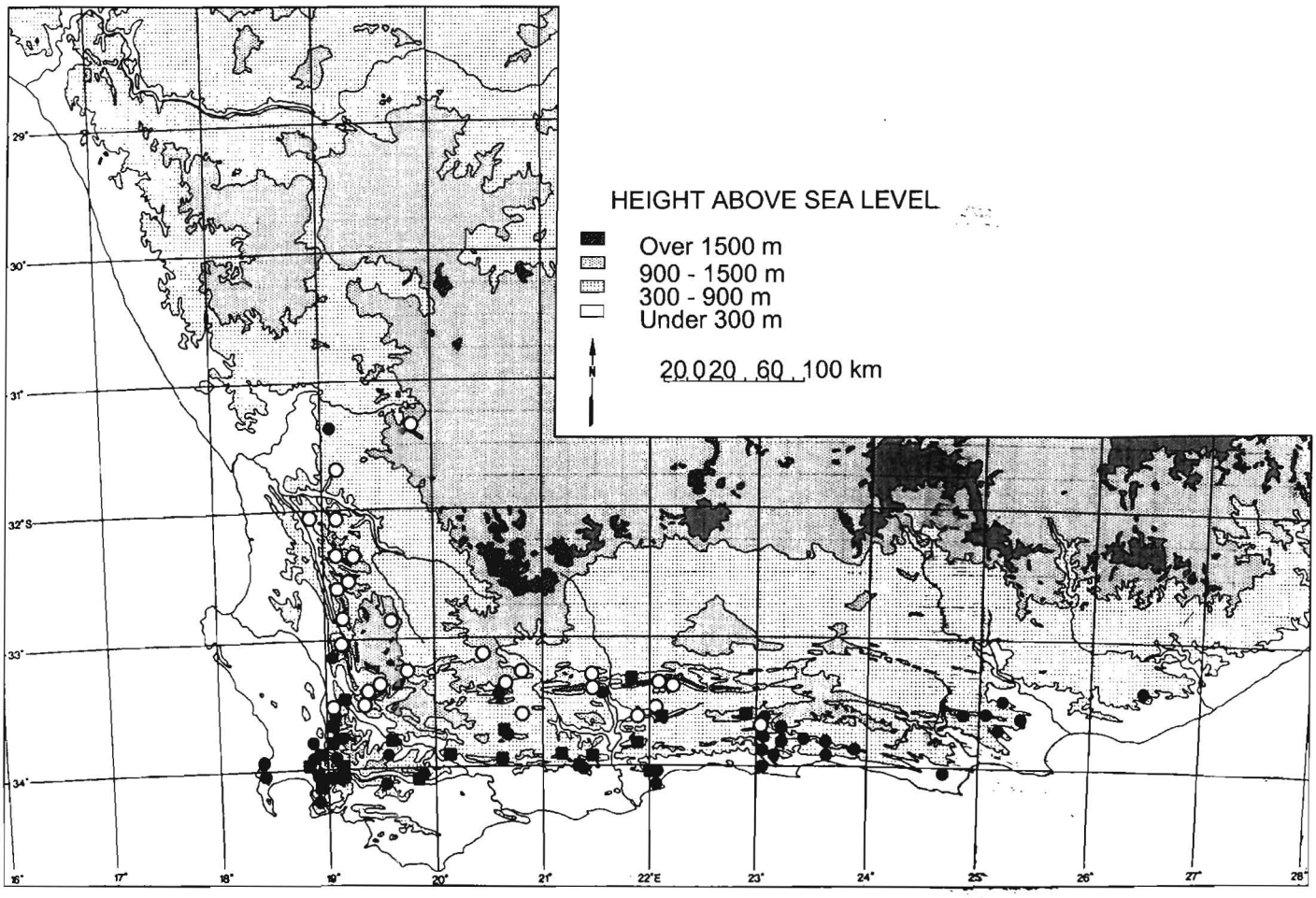

Figure 5. Distribution of the *Cannomois virgata* complex groups

- ■ Caledon-Langeberg
- ○ NW-Swartberg
- ● Coastal

3.3. Culm anatomical observations

3.3.1. **Epidermis**

The epidermis (Fig. 6) is a single layer of waxy cells in all the *C. virgata* complex segregates and the other species in the genus *Cannomois*. The shape of the cells varies from rectangular in *C. virgata* segregates, *C. parviflora*, *C. congesta* and *C. nitida* (as in Fig. 6 A, B, D & E) to elongated in *C. taylori, C. scirpoides* and *C. aristata* (as in Fig. 6 C & F).

3.3.2. **Stomata**

The stomata are paracytic and vary in the position of the guard cells with respect to the epidermal layer. In the *C. virgata* complex segregates and *C. congesta* the guard cells are flush with the outer wall of the epidermis (Fig. 6 B), whereas in the remaining species they are sunken (Fig. 6 C), almost occupying the intermediate position between the outer and inner epidermal walls.

3.3.3. **Chlorenchyma**

The chlorenchyma (Fig. 6 B & C) consists of 2 layers of cells in all the *Cannomois* species. The inner and outer layers are dissimilar with the former having shorter cells. The layers are clearly visible in the *C. virgata* complex segregates whereas they are obscure in the other species of *Cannomois*.

3.3.4. **Protective cells**

These cells are partially lignified cells lining the substomatal cavity. In all the species of *Cannomois*, one layer of protective cells (Fig. 6 D) is developed, the cells of which are somewhat longer than the chlorenchyma cells, and bone shaped, forming a basket not reaching the parenchyma layer.

3.3.5. **Parenchyma layer**

This layer varies from one cell wide to two cells wide. Only *Cannomois scirpoides* has a layer which is one to two cells wide (Fig. 6 C). Most species have globular somewhat rounded cells, except *C. taylori* with rectangular to almost elongated cells (Fig. 6 F). The parenchyma layer is continuous in the Coastal segregate, Caledon-Langeberg segregate, *C. scirpoides* and *C. aristata*, whereas in other species it is interrupted by ridges cutting through it into the chlorenchyma cells. In all the species of *Cannomois*, the parenchyma cells are larger than the epidermal cells.

3.3.6. **Sclerenchyma cylinder**

The structure varies within the genus *Cannomois*, from simple (Fig. 6 A) to formation of ridges which penetrate into the chlorenchyma cells (Fig. 6 B & F). The sclerenchyma sheath form ridges which alternate with vascular bundles in the *Cannomois* species.

3.3.7. **Central ground tissue**

In all the species a central cavity is present in the central ground tissue; it only has a size difference between species. The vascular bundles (Fig. 6 E) are arranged approximately in a ring round the periphery of the central ground tissue.

3.3.8. **Silica**

The silica bodies are generally found in cells on the outer edge of the sclerenchymatous sheath particularly on ridges or parenchymatous sheath (Fig. 6 D & E).

3.3.9. **Tannins**

Within the *Cannomois virgata* complex, distribution of tannins separates the three taxa. The Coastal group has tannins in the epidermal cells, whereas the Caledon-Langeberg group has tannins distributed in the central ground tissue (Fig. 6 E). The NW-Swartberg is not tanniferous. Other species of *Cannomois* with tannins on the epidermis (Fig. 6 F) include *C. nitida*, *C. taylori*, *C. parviflora* and *C. congesta*.

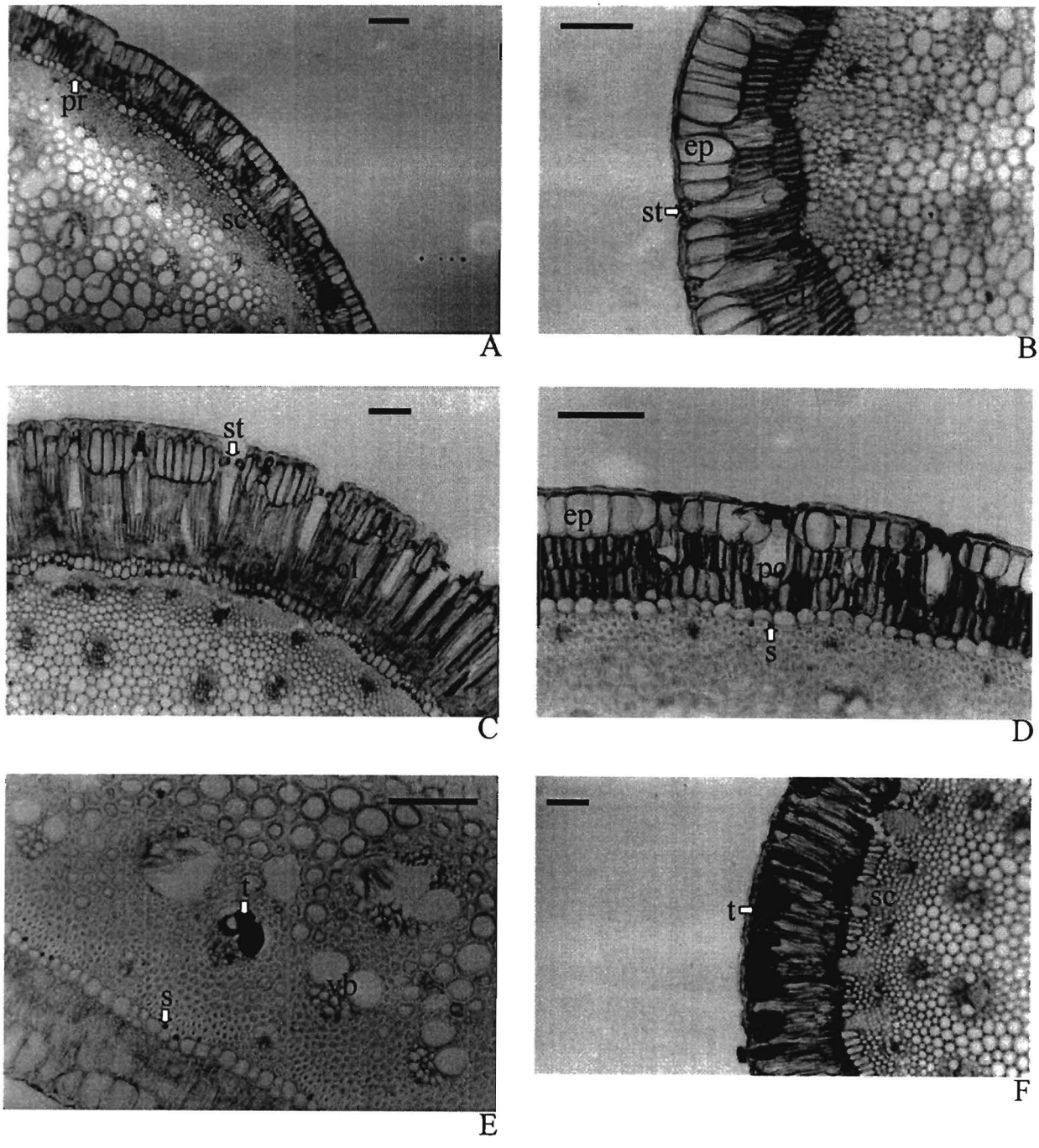

Figure 6. Variation in culm anatomy for the species of *Cannomois* (*C. virgata* segregates included). A, Coastal group (MUJAJU 1); B, NW-Swartberg group (MUJAJU 3); C, *Cannomois scirpoides* (LINDER 5317); D & E, Caledon-Langeberg group (MUJAJU 8); F, *Cannomois taylori* (LINDER 4471). Anatomical features labelled are as follows: **s**, silica; **pr**, parenchyma layer; **sc.**, sclerenchyma; **st**, stoma; **ep**, epidermis; **cl**, chlorenchyma; **pc**, protective cell; **vb**, vascular bundle; **t**, tannin. Scale bar: 100 μm.

3.4. Phylogeny

3.4.1. **The most parsimonious tree**

Cladistic analysis retrieved a single most parsimonious tree (Figure 7), 65 steps long, with a consistency index (CI) of 0.538 and retention index (RI) of 0.667. The tree shows two basal clades for the ingroup taxa, the Caledon-Langeberg - Coastal clade and the one made up of NW-Swartberg – (*C. nitida, C. congesta, C. aristata, C. parviflora, C. taylori, C. scirpoides*). The latter clade has five subclades which include ((*C. congesta, C. nitida, C. aristata, C. parviflora, C. taylori, C. scirpoides*), (*C. nitida, C. aristata, C. parviflora, C. taylori, C. scirpoides*), (*C. aristata, C. parviflora, C. taylori, C. scirpoides*), (*C. scirpoides, C. taylori, C. parviflora*) and (*C. scirpoides, C. taylori*)).

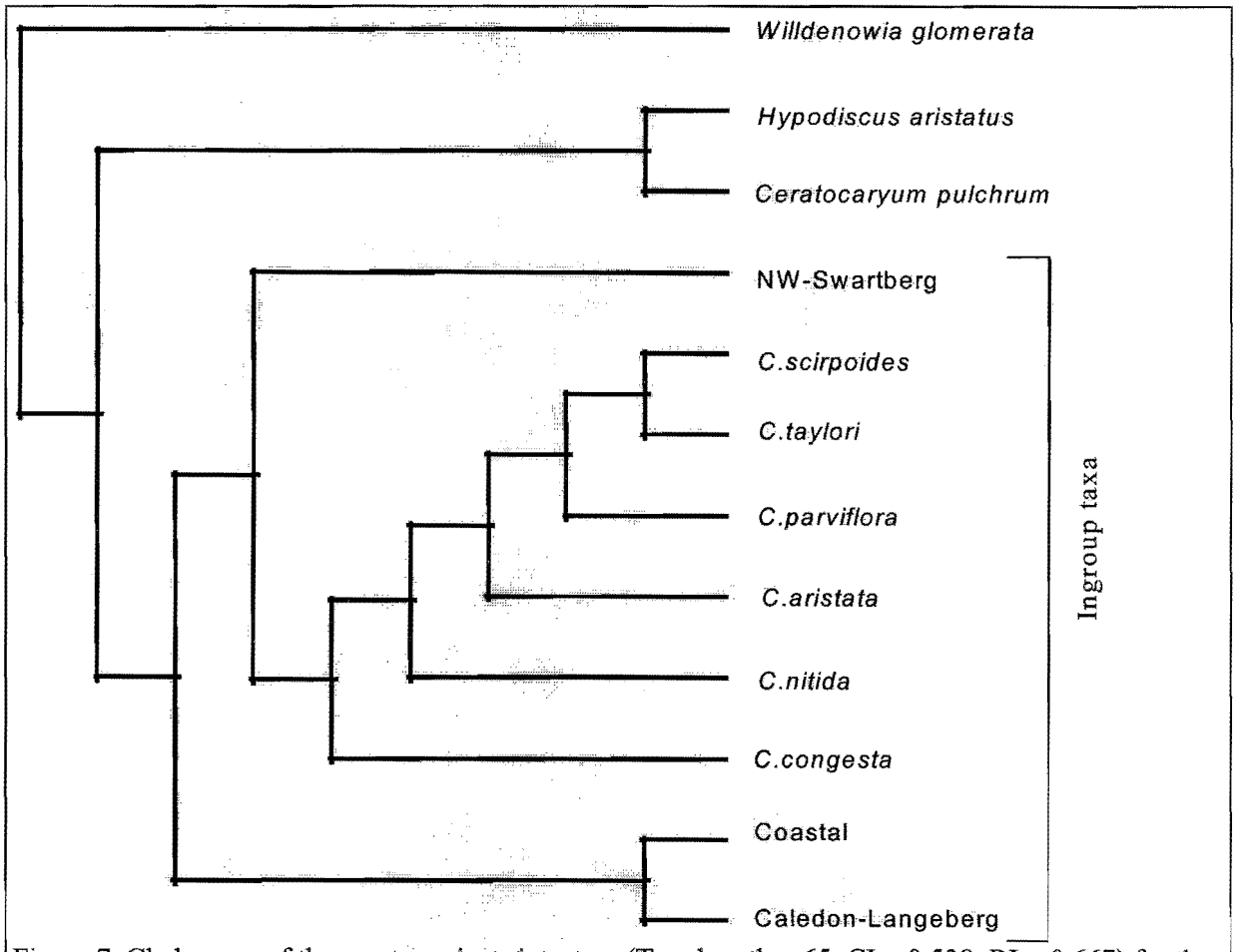

Figure 7. Cladogram of the most parsimonious tree (Tree length = 65, CI = 0.538, RI = 0.667) for the genus *Cannomois* showing the groups in *Cannomois virgata* complex with respect to the other species. Rooting was done to make the ingroup taxa monophyletic with respect to the paraphyletic outgroup taxa.

3.4.2. **Characters supporting the tree topology**

Of the 26 characters used, all were parsimony informative and the cladogram (Figure 8) shows all possible character changes supporting the tree topology. The *C. virgata* complex does not form a monophyletic group. However, the Coastal and Caledon-Langeberg taxa form a monophyletic group defined by petal width of outer segment exceeding 2.5 mm (7), culms distinctly hollow (18) and plant height more than 1 metre (19). The other basal clade of NW-Swartberg, *C. congesta, C. nitida, C. aristata, C. parviflora, C. taylori* and *C. scirpoides* is held together by the presence of barrel shaped nuts (1), nut width to length ratio less than 0.53 (2), long elaiosomes (4) and interrupted parenchyma layer (26). The two basal clades join to form the *Cannomois* clade, which is held together by three unambiguous characters. These characters include flat, compressed adaxial nut side; elaiosome condition and number of fertile bracts. The *C. virgata* complex taxa also possess autapomorphies (Figure 8).

Overall, for the ingroup taxa the cladogram shows 22 synapomorphies (unambiguous characters only). These include 2 for the Coastal - Caledon-Langeberg clade, 3 for NW-Swartberg - *C. congesta* - *C. nitida* - *C. aristata* - *C. parviflora* - *C. taylori* - *C. scirpoides* clade, 3 for *Cannomois* clade, 2 for *C. congesta* - *C. nitida* - *C. aristata* - *C. parviflora* - *C. taylori* - *C. scirpoides* clade, 2 for *C. nitida* - *C. aristata* - *C. parviflora* - *C. taylori* - *C. scirpoides* clade, 5 for *C. aristata* - *C. parviflora* - *C. taylori* - *C. scirpoides* clade, 4 for *C. scirpoides* - *C. taylori-C. parviflora* clade and 1 for *C. scirpoides* - *C. taylori* clade. In addition, 18 homoplasies were observed and include all characters except 1, 2, 3, 12, 13, 15, 22 and 23.

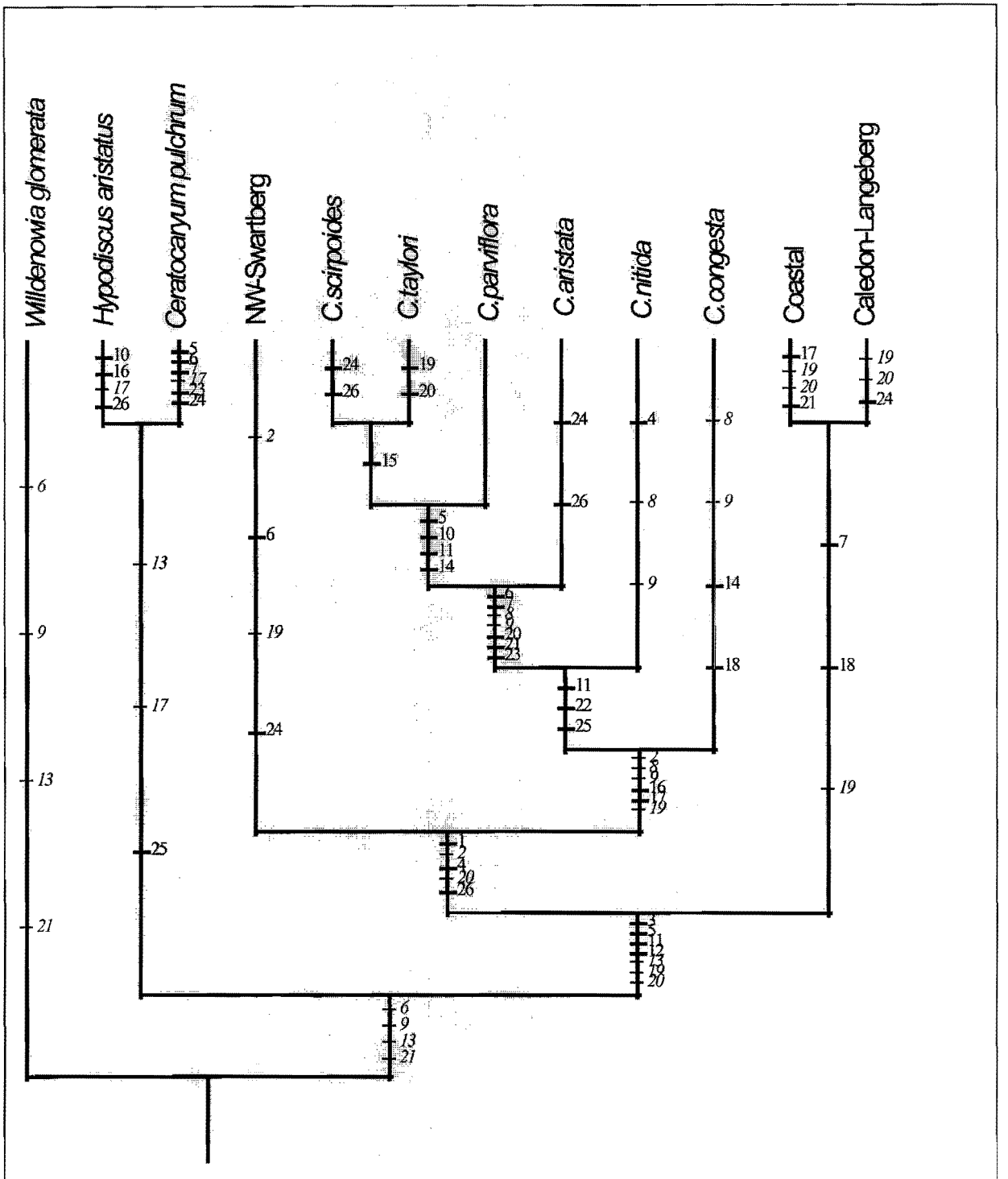

Figure 8. All possible character changes mapped on the most parsimonious tree. Characters are according to Table 2.4. Thick bars on branches show unambiguous characters only.

3.4.3. **Bootstrap and Bremer support values**

Five nodes have support of at least 59% (Figure 9). Node 8 holding the Coastal - Caledon-Langeberg clade has a bootstrap support value of 65 % and a decay value of 1, whereas the node joining NW-Swartberg to *C. congesta* - *C. nitida* - *C. aristata* - *C. parviflora* - *C. taylori* - *C. scirpoides* clade with a similar decay value, has a bootstrap support of 41%. The highest bootstrap support of 88 % is shown for the *C. aristata* - *C. parviflora* - *C. taylori* - *C. scirpoides* clade, with a Bremer support value of 4; followed by node 9 holding the *Cannomois* clade with bootstrap support of 63% and Bremer support value of 3. Nodes 1, 2 and 5 have a bootstrap support of less than 50%.

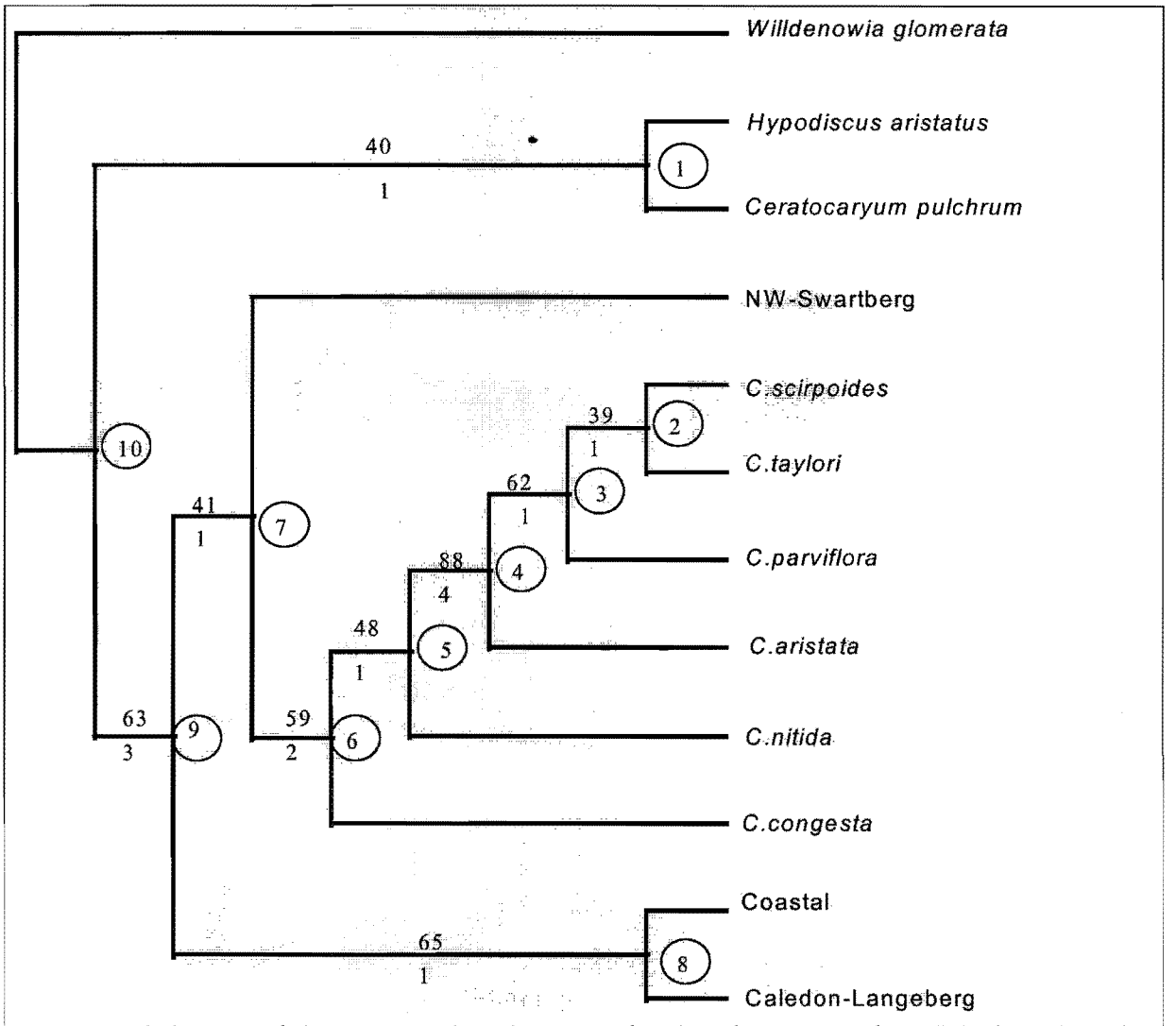

Figure 9. Cladogram of the most parsimonious tree showing bootstrap values (%) above branches and Bremer support values below. Circled numbers represent nodes.

3.4.4. **Character exclusion (Jacknife)**

Individual character exclusion of nine out of 26 characters from the analysis had an effect on the tree topology.

Excluding of characters 1 (nut outline), 5 (elaiosome condition), 10 (spikelets per inflorescence), 11 (bract shape), 15 (spathe colour), 22 (stomata) or 25 (chlorenchyma) resulted in the collapse of nodes 1, 2, 3, 5 and 7. Node 8 collapsed after the removal of either character petal width of the outer segment (7) or culms (18).

Of the remaining characters, no single character when removed resulted in a change of topology of the fully resolved tree, which confirms the robustness of all the clades.

3.4.5. **Taxon exclusion**

Successive exclusion of five taxa i.e., Coastal, Caledon-Langeberg, *C. congesta*, *C. nitida* and *C. aristata* out of ten ingroup taxa gave rise to changes in tree topology and increase in the number of the parsimonious trees (Table 3.3). The collapsing of nodes revealed changes in the topology of the most parsimonious tree. Nodes 1, 2 and 7 collapsed when either *C. congesta* or *C. nitida* or *C. aristata* was removed. Similarly, nodes 1, 2, 3, 5, 8 and 9 collapsed when NW-Swartberg was removed. The removal of the Coastal taxon resulted in the loss of node 1.

Only the removal of Caledon-Langeberg taxon within the *C. virgata* complex did not affect the resolution of the most parsimonious tree. For any given taxon in the genus *Cannomois*, its removal resulted in trees that are similar to the fully resolved tree. Furthermore, the resolution of the *Cannomois virgata* complex clade and the whole cladogram remained intact.

Table 3.3. Effects of taxa exclusion from the character matrix on tree statistics

Taxon deleted	Tree length	CI	RI	Tree number	Effect on Tree topology
none	65	0.538	0.667	1	-
NW-Swartberg	61	0.557	0.654	10	nodes 1, 2, 3, 5, 8 and 9 collapsed
Coastal	61	0.574	0.658	2	node 1 collapsed
Caledon-Langeberg	62	0.548	0.632	1	none
C. scirpoides	63	0.556	0.636	1	none
C. taylori	63	0.556	0.632	1	none
C. parviflora	65	0.538	0.625	1	none
C. congesta	61	0.574	0.675	3	nodes 1, 2 and 7 collapsed
C. aristata	62	0.565	0.663	4	nodes 1, 2 and 7 collapsed
C. nitida	62	0.565	0.671	2	nodes 1, 2 and 7 collapsed

3.4.6. **Alternative topology**

Moving each of the *C. virgata* segregates to the branches holding other *Cannomois* species produced a minimum cost when attached to *C. congesta* (Table 3.4). The least minimum cost of two extra steps was required to move the NW-Swartberg taxon to the branch holding *C. congesta*. For the other two taxa within the *Cannomois virgata* complex, movement to other branches required at least six extra steps, indicating that their current positions are stable.

Table 3.4. Summary of costs of moving *C. virgata* complex taxa (segregates) to branches of the other species within the genus *Cannomois*. Minimum cost entailed in movement to any branch on tree is indicated for each taxon.

TAXON Moved	COST OF MOVEMENT TO BRANCHES					
	C. nitida	*C. congesta*	*C. aristata*	*C. scirpoides*	*C. taylori*	C. parviflora
NW-Swartberg	5	2	10	14	13	14
Coastal	9	6	11	15	15	15
Caledon-Langeberg	9	6	11	19	19	18

3.4.7. **Character mapping**

Environmental and vegetative characters mapped onto the cladogram were considered important in the evolution of the complex and mapping of each character was done to elucidate the plesiomorphic and derived states within the genus *Cannomois*.

Mapping of fire response (Figure 10a) shows that no state can be regarded as plesiomorphic but the cladogram exhibits an equivocal condition for all the states.

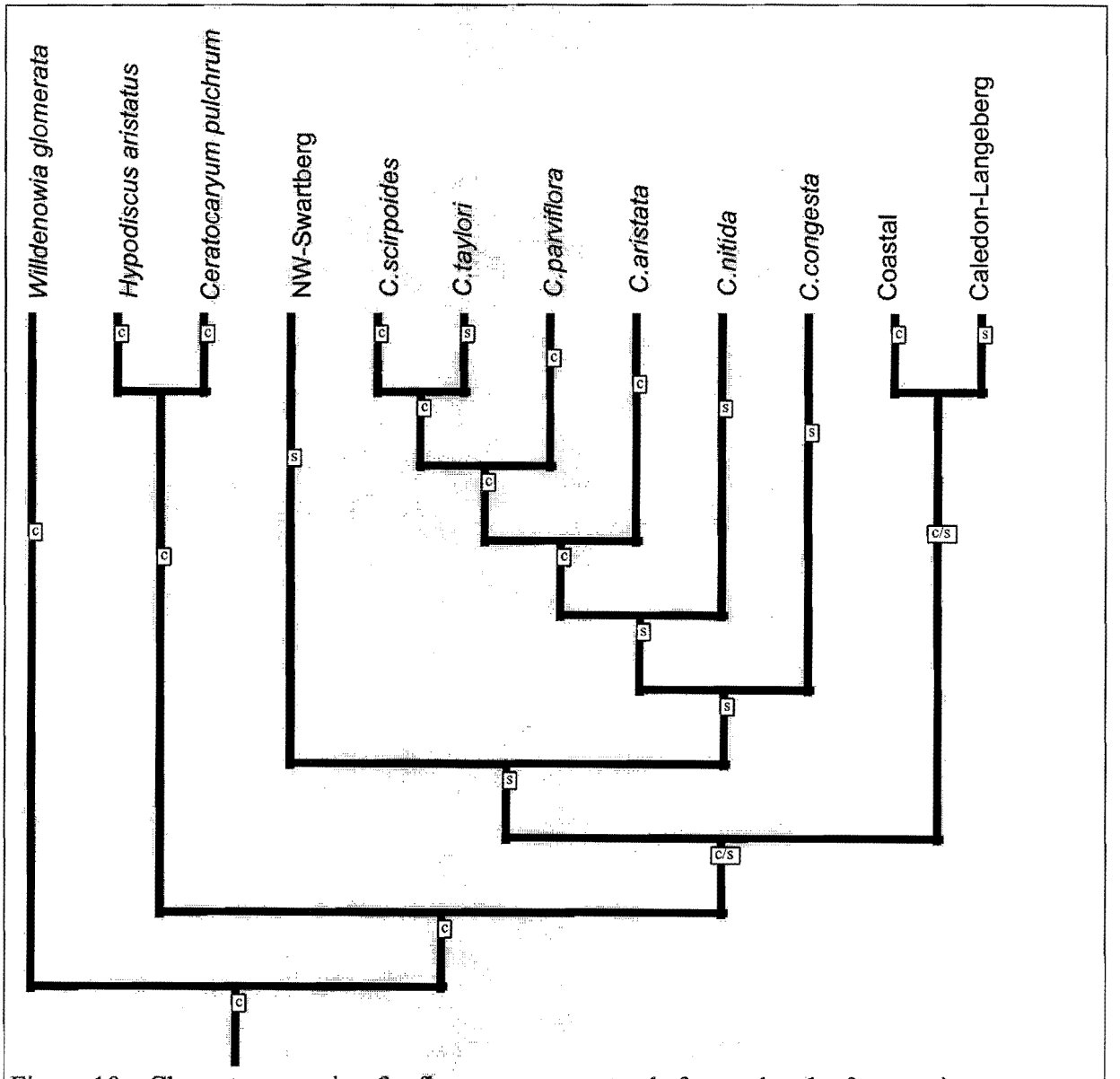

Figure 10a. Character mapping for fire response. **s** stands for seed and **c** for coppice.

Mapping of character 20 (rhizomes) (Figure 10b) shows that short rhizome is plesiomorphic in the genus *Cannomois*.

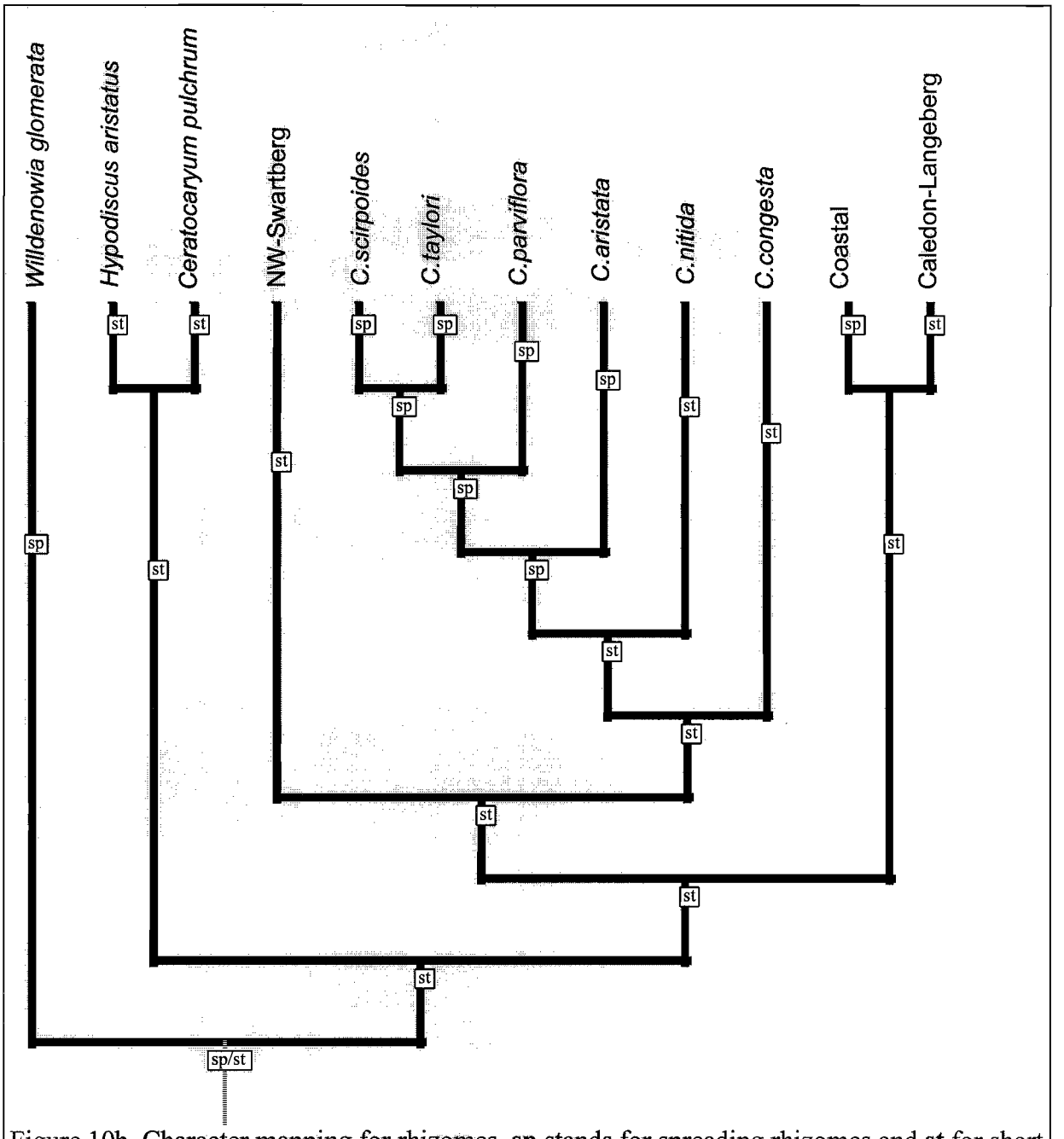

Figure 10b. Character mapping for rhizomes. **sp** stands for spreading rhizomes and **st** for short rhizomes.

Mapping of plant height onto the cladogram (Figure 10c) shows an equivocal condition for the two states, ca. 1 m and 1 - 2 m, at the basal internal nodes. It is difficult to tell the plesiomorphic state between the two. The state > 2 m in the genus is an advanced state.

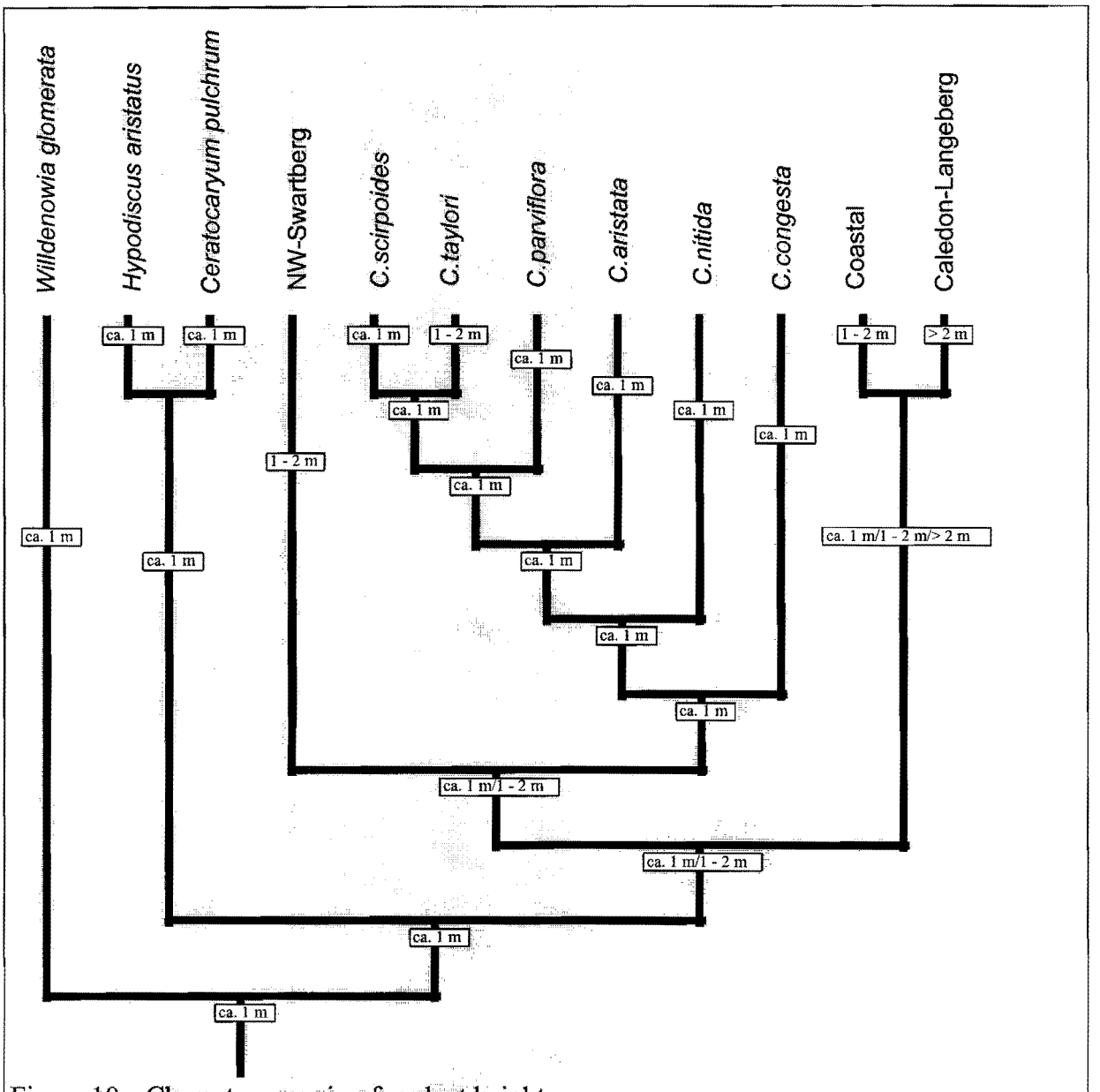

Figure 10c. Character mapping for plant height.

3.5. Nomenclatural typification

In order to assign the name *C. virgata* to the right group or segregate within the *Cannomois virgata* complex, reference was made to the type specimens previously used by Rottboell (1772), Thunberg (1788), Poiret (1804), Desvaux (1828) and Kunth (1841), under *Restio virgatus*, *Restio scopa*, *Restio elegans, Cannomois cephalotes* and *Thamnochortus robustus* respectively. According to the Code the type of the name is to be sought from the original specimens (Minghetti and Nardi, 1999).

Examinations of the type specimens have shown the presence of some of the diagnostic features used in delineating the Coastal group from the rest of the other groups, e.g. the ratio of hollow cavity diameter to culm diameter, and the foliage which overtops inflorescence and nuts.

Measurements of the type specimen at UPS for two individual culms, gave a culm diameter value of 2.7 mm and hollow cavity diameter of 0.75 mm for the first one, and a culm diameter of 2.2 mm and a hollow cavity diameter of 0.6 mm for the second culm (Roland Moberg, pers. comm.). Measurements were taken at the lowermost parts of the two culms. The ratios of hollow cavity diameter to culm diameter for the two respective set of values give 0.28 and 0.27 respectively, fitting very well within the range of the Coastal group plants. Similarly, the type specimen named *Restio virgatus* Rottb. from Copenhagen (C) had a culm diameter of 2.5 mm and hollow cavity diameter of 1 mm (Ibfriis, pers. comm.), and a resultant hollow cavity diameter to culm diameter ratio of 0.4, which also ultimately shows that it belongs to the Coastal group. Furthermore, examination of the microfiche slide Thunb. 23244 and the iconotype have shown some diagnostic features of the Coastal group i.e., foliage which overtop inflorescence and nuts, and the culms which appear to be less than 1 m in height. Measurements of the holotype specimen at Paris (P) gave a culm diameter between 2 mm and 1.5 mm, and a hollow cavity diameter of about 0.5 mm (Jean - Noël LABAT, pers. comm.), thereby giving a hollow cavity diameter to culm diameter ratio ranging between 0.23 and 0.33. The lectotype specimen Drege 1606 observed has a hollow stem with culms observed appearing to be less than 1 m tall (H. P. Linder, pers. comm.). Furthermore, this type specimen was collected from Du Toits Kloof, an area from herbarium specimens and fieldwork observations, to which may have extensive and abundant populations of the Coastal group.

4. DISCUSSION

4.1. Phenetics

Numerical phenetic analyses of morphological characters have proven useful in testing the initial hypothesis that the *C. virgata* complex may constitute three or more taxa. Both cluster analysis and ordination retrieved three groups namely: NW-Swartberg, Caledon-Langeberg and Coastal.

Cluster analysis of the data set revealed the three major clusters or groups which are separated by relatively longer branch lengths, with a coefficient of dissimilarity greater than 1.08, whereas within each cluster branch lengths were short, with a coefficient of dissimilarity less than 0.87. The long branch lengths subtending major clusters remained intact on addition of more OTUs as opposed to the short branch lengths within each cluster and hence the clusters can be concluded to constitute different taxonomic units or groups.

Ordination based on a principal component analysis has revealed the same discrete clusters of operational taxonomic units, corresponding to the three major clusters or groupings. The three-dimensional model plot explicitly reveals the intermediate group H to belong to the NW-Swartberg group. While ordination gave the same groups as cluster analysis, it proved most useful in distinguishing between OTUs of the three clusters, showing no overlap between them. The first three components contributed 79.06% of the total variation, of which 64.35% was explained by the first principal axis with sixteen characters having loadings of more than 0.7. Loading on the first component was contributed mainly by the following characters (coefficients in parenthesis): nut length (0.7724), Nut width (0.9462), petal length (0.9425), petal width of outer segment (0.8983), petal width of inner segment (0.8295), spikelet width (0.8934), bract width (0.9206), elaiosome length (-0.7427), culm diameter at the apex (0.7872), branch-tip diameter (-0.8584), Branch-base diameter (-0.7331), ratio of nut width to length (0.8926), ratio of petal length to nut length (0.8996), ratio of spikelet width to length (0.7300), ratio of bract width to length (0.8803), ratio of branch-tip diameter to base diameter (-0.8787), ratio of hollow cavity diameter to stem diameter (0.9108) and ratio of elaiosome length to nut length (-0.8300). Loading on the second component was contributed

mostly by spikelet length (0.8429) and bract length (0.7761), whereas the ratio of spathe length to spikelet length (0.6601) and spathe length (0.6166) contributed much for the third principal component. The characters that contributed most to the loading on the first two principal components were usually those that proved most useful in diagnosing the taxa.

Univariate analysis revealed discrete character distribution contributing to diversity between the clusters. It was useful in indicating the extent to which character variation shows intervals congruent with the major groups in the *Cannomois virgata* complex. Bivariate plots showing graphical representation of ratio characters have shown that the ratio of nut width to length (nut width versus length), ratio of petal length to nut length (petal length versus nut length), ratio of bract width to length (bract width versus length), ratio of branch-tip diameter to base diameter (branch-tip diameter versus base diameter), ratio of hollow cavity diameter to culm diameter (hollow cavity diameter versus culm diameter) and ratio of elaiosome length to nut length (elaiosome length versus nut length) are important characters contributing to the differentiation of the NW-Swartberg, Coastal and Caledon-Langeberg clusters. These characters retrieved were also retrieved under principal component analysis and this implies congruence between the two methods, which further supports the significance of the characters in separating the clusters. The pattern of loadings on the first principal component and the bivariate plots presented suggest that much of the variation described is due to size. Box-and-Whisker plots showed that nut width, petal width of outer segment, bract width, spikelet width, branch base diameter and hollow cavity diameter to culm diameter ratio are discontinuous characters separating NW-Swartberg, Coastal and Caledon-Langeberg groups. However, some univariate characters are distinct for a particular group, and this include culm diameter at apex for the Caledon-Langeberg and nut shape (ratio of nut width to length) for the NW-Swartberg.

Plant height, a character not included in the morphometric analyses because of limited records on herbarium specimens, may show a clear discontinuity separating the three phenetic clusters. However, plant height is a vegetative character that would be expected to show continuous variation due to phenotypic response to micro-environmental differences especially between the Coastal and Caledon-Langeberg plants growing in sympatry unless there is an important genetic component to it. The observation of the cultivated plants

belonging to Caledon-Langeberg cluster in Kirstenbosch Botanical Gardens close to the naturally occurring coastal plants indicates that plant height may well be a genetically controlled character.

4.2. Phylogeny

4.2.1. **Use of morphological data set**

Several biologists have argued that there can be no valid criteria for dividing quantitative data into discrete states because quantitative traits are inherently continuous (Felsenstein, 1988; Garland and Adolph, 1994). They claim that coding quantitative data introduces artificial distinctions even if the observed distribution is discontinuous. On the contrary, Swiderski *et al.* (1998), have shown that arguments against coding quantitatively described traits are not supported by theory and that obstacles posed by continuity are only practical problems, which are not unique to quantitative data.

Chase *et al* (1995) commented that the analysis of a morphological data set on its own highlights areas in which more research is needed, but putting more emphasis on certain characters. He suggested the use of combined data sets (with molecular data) in the analysis, which may provide insight into other characters, which would not otherwise necessarily be regarded as significant. However, this analysis using a morphological data set provides a starting point from which further study can proceed.

4.2.2. **Stability of the Cladogram**

Cladistic analysis retrieved a single most parsimonious tree of 65 steps long, a consistency index (CI) of 0.538 and retention index (RI) of 0.667, showing two basal clades for the genus *Cannomois*, the Coastal – Caledon-Langeberg clade and the NW-Swartberg - *C. nitida* - *C. congesta* - *C. aristata* - *C. parviflora* - *C. taylori* - *C. scirpoides* clade. The consistency index (CI) is the simplest and most common measure of homoplasy and equals the minimum amount of possible evolutionary change (the number of genetic switches) divided by the actual tree length (the number of actual genetic changes on the tree). In cladistics, homoplasy

is judged as character incongruence; minimally, when two characters are incompatible, they cannot both be homologues (Kluge, 1976). However, the CI is limited in that it is sensitive to uninformative characters and the number of taxa in an analysis (Judd *et al.* 1999). If many uninformative characters are added into the analysis, the overall CI would be inflated accordingly and would give a misleading impression that many characters supported the trees. In this analysis there were no uninformative characters, and therefore the value of CI is a true measure of fit for the data on most parsimonious tree. The retention index (RI) as another measure to describe how characters vary over the tree was used to circumvent another limitation of the CI. It corrects the narrower range of the CI by comparing the actual number of changes in the character to the maximum possible number of changes.

The majority of clades were relatively well supported with bootstrap values between 59% and 88% (Figure 9). The cladogram shows that the Coastal – Caledon-Langeberg is a monophyletic clade supported by a bootstrap value of 65%. The cladogram offers high support for the monophyly of *C. aristata* - *C. parviflora* - *C. taylori* - *C. scirpoides* clade with a decay index of 4 and bootstrap support value of 88%. However, branches leading to nodes 1, 2, 5 and 7 respectively have poor support, with bootstrap values less than 50% (Figure 9). Generally, bootstrap values less than 75% would not be considered "strong support" by most practitioners of systematics. According to Sanderson (1989), poor bootstrap values may be due to few characters or lack of congruence. The latter explanation applies to *Cannomois*. Another reason could be due to the effect of undersampled multistate additive quantitative characters. Horovitz (1999) has shown that when additive characters are not coded in a binary fashion, they will be undersampled compared to binary characters in relation to the amount of information they contain. This also makes clades that are contradicted by the data to appear with high frequencies (Horovitz, 1999). However, bootstrap values are regarded as poor estimates of repeatability, which can be used only as conservative measures of accuracy (Hillis and Bull, 1993). The magnitude of bias caused by bootstrapping differs from branch to branch and study to study, so that the values cannot be directly compared among studies. Hillis and Bull (1993) proposed the need to use retrospective simulation studies to calibrate bootstrap proportions so that they can be converted into acceptable measures of accuracy. Therefore, bootstrap values alone may not represent true clade stability at nodes 1, 2, 3 and 7. In addition, there is also a weak correlation between the bootstrap and the Bremer support

values. Nodes 3 and 8 with bootstrap values of 62% and 65% respectively have Bremer indices of 1 whereas nodes 6 and 9 with bootstrap values of 59% and 63% correspond to Bremer support indices of 2 and 3 respectively.

Character exclusion has shown that the presence of characters 1 (nut outline), 5 (elaiosome condition), 7 (petal width of outer segment), 10 (spikelets per inflorescence), 11 (bract shape), 15 (spathe colour), 18 (culms), 22 (stomata) and 26 (parenchyma layer) are relevant for the resolution of the most parsimonious tree. Nut outline, elaiosome condition, number of spikelets per inflorescence, bract shape, spathe colour, stomata and parenchyma layer are necessary for the stability of nodes 1, 2, 3, 5 and 7, whereas petal width of outer segment and culms are necessary for the stability of node 8. The stability of the clades in the cladogram was also tested by the iterative deletion of taxa. This is consistent with Siddall's suggestion that the stability of phylogenetic hypotheses may actually be more related to the taxa included than to the number of characters (Horovitz, 1999). The taxa NW-Swartberg, Coastal, *Cannomois nitida, Cannomois congesta* and *Cannomois aristata* are necessary for the stability of the cladogram.

The current positions of the *Cannomois virgata* complex taxa are vital for the stability of the cladogram. Movement of the *C. virgata* complex taxa to branches joining other *Cannomois* species indicates lack of alternative topologies. However, two extra steps resulting from moving NW-Swartberg taxon to *C. congesta* may suggests some uncertainty about the position of NW-Swartberg in the shortest tree.

Overall, variation in the bootstrap values among the nodes, as well as various manipulations of the data set, indicate that nodes 1, 2, 3, 7 and 8 are relatively poorly supported, while the majority of the nodes are quite robust. This suggests that the contribution of the morphometric characters to the resolution of particular clades is weak. Poorly supported nodes are sensitive to contradictory data, but not supportive data. Poor support for nodes 5 and 8 implies that the monophyly of either NW-Swartberg, *C. nitida, C. congesta, C. aristata, C. parviflora, C. taylori* and *C. scirpoides,* or Coastal and Caledon-Langeberg has poor support; but since node 6 has strong support, the members of the *C. virgata* complex will never be embedded within the rest of the genus. Also, since node 9 has strong support, the genus remains monophyletic.

4.3. Species concepts and interpretation of clusters

The 'species problem' has a long history and the advent of phylogenetic systematics (Hennig, 1966) has spawned a debate about the most appropriate units for cladistic analysis, and whether these correspond to 'species'. The central issue is whether species should be considered units of evolutionary process, products of evolution, or both (e.g., Mishler and Brandon, 1987; de Queiroz and Donoghue, 1988; Frost and Hillis, 1990). However, some cladists (Vrana and Wheeler, 1992) believe that there is no 'species problem'. Therefore all taxa are treated as equivalent and monophyletic, and are recognised only by synapomorphy. This view recognises taxa by cladistic analysis only and taken to its extreme, the only terminal units suitable for analysis can be individuals (Vrana and Wheeler, 1992). The limitation to this approach would be the discovery of spurious incongruence in the analysis of sexually dimorphic taxa. According to Crisp and Weston (1993), at least some sexually polymorphic characters would be apparent synapomorphies for gender groups rather than clades and would thus conflict with sexually monomorphic characters. Nixon and Wheeler (1990) have argued that if taxa are delimited too broadly some opportunities for cladistic analysis are lost whereas if they are delimited too narrowly the results become too spurious because they rest on polymorphic traits within populations rather than phylogenetic taxa.

The lack of agreement concerning what a species is, leaves the definition of species level taxa open to interpretation by the individual taxonomist. According to McDade (1995), the choice of species concept influences the interpretation of taxonomic pattern at the species level, and consequently it is important to state which concept is used in a study. This study empirically examines three clusters of the *Cannomois virgata* complex in the context of a well-corroborated phylogenetic hypothesis and six prevailing species concepts: phenetic concept, two reproductive concepts, two versions of the phylogenetic species concept and the ecological species concept. Predictions or implications of these various species concepts for the phenetic clusters of *C. virgata* complex are impossible without an operational definition of a species from which a working unit can be established. Nelson and Platnick's (1981: 11) operational definition of a species has been adopted in this study. Species are recognised as clusters in phenetic space based on their distinctness, owing to some underlying factor such as infraspecific polymorphism or phylogenetic divergence. Phenetic differentiation, therefore, is

the observable expression of underlying fixed qualitative differences (expected of monophyletic taxa; Nelson and Platnick, 1981) that are either observed as synapomorphies or predicted following speciation. Thus, species concepts are compared based on the sharing of a common operational practice, i.e., identification of basal or irreducible phenotypic units. Such units are suitable as terminals in cladistic analysis and have the methodological advantage of being independent from the procedure to be followed (Vrana and Wheeler, 1992). Similarly, operational units detected as phenetic clusters are compatible with all the prevailing species concepts.

Under the phenetic species concept, a species is defined as a set of organisms that look similar to each other and distinct from other sets (Ridley, 1993). Its application emphasises gaps in diagnostic characters for different taxa. Because there is complete discontinuity in multivariate morphometric space between the NW-Swartberg, Coastal and Caledon-Langeberg individuals, their respective clusters should be treated as species. In all the phenetic analyses, nut width, petal length, bract width, ratio of hollow cavity diameter to culm diameter, spikelet width and branch base diameter were most useful for diagnosing the *Cannomois virgata* complex groups. A combination of univariate analysis, bivariate and multivariate analysis have been used successfully in taxon delimitation among species complexes in other studies (Ballard and Wujek, 1994; Reinhammar, 1995). Ballard and Wujek (1994) used morphometric data scored from continuous variables in PCA, CVA and univariate analysis, to derive evidence for the recognition of *Viola appalachiensis* as distinct from *V. conspersa*. The two species were suspected to be interbreeding. Similarly, Reinhammer (1995) used clustering, PCA and canonical variates analysis to separate *Pseudochoris albida* and *P. straminea* as two distinct species. In all the diagnostic analyses, the ratio of hollow cavity diameter to culm diameter contributes most to the distinction of the dioecious plants among the NW-Swartberg, Coastal and Caledon-Langeberg individuals. However, a few intermediate plants marked H on the phenogram, part of the NW-Swartberg cluster, possess the same range of the ratio of hollow cavity diameter to culm diameter as the Coastal ones. On the contrary, the two are separated from each other by their growth habits (Table 3.2). Apart from the hollow cavity diameter to culm diameter ratio, most discontinuous characters examined are essentially useful in delimiting the species based on female plants.

Under the reproductive species concepts, the two prevailing concepts are the biological species concept of Mayr (1969) and the recognition species concept of Paterson (1985). The crucial factor for both is interbreeding, and whether this is brought about by a shared mate recognition system or an isolating mechanism is a secondary matter. In essence, interbreeding is thought to be significant as a mechanism for maintaining coadapted gene complexes; new species arise when these complexes are reorganised through selection or drift (Mayr, 1982). Sexual breeding relationships are thought to be responsible for phenotypic similarity within (recognition concept) or discontinuity between (isolation or biological concept) basal clusters (McKitrick and Zink, 1988; Templeton, 1989). This study was based largely on herbarium specimens, regarded as dead material, and hence there was virtually no data available to test whether NW-Swartberg, Coastal and Caledon-Langeberg clusters are biological species. The recognition species concept is more broadly applicable as an explanation for continuity of form among non-sympatric populations (Theriot, 1992) with gene flow as the binding agent for individuals in a species. For the three endemic clusters, there is no direct or indirect evidence that similarity among individuals within each cluster is or is not due to interbreeding, and so the recognition concept as a mechanism for maintaining similarity within a species cannot be distinguished from other explanations for the endemics. However, it seems most unlikely that gene flow can explain similarity among the widely spaced populations of the three clusters, as can be inferred from the distribution map. Linder (1985b), by extrapolating data from other parts of the world to the Cape, indicated that gene flow is too spatially limited to be of significance in maintaining species integrity.

Under the phylogenetic species concept, two concepts have evolved emphasising unique common descent or monophyly (Hennig, 1965) but identifying species with basal clusters in two different ways. In the monophyletic concept (also called autapomorphic), species are simply taxa (Nelson, 1989) and so operationally are irreducible clusters on the phylogeny diagnosed by uniquely held derived characters (autapomorphy). The application of the monophyletic species concept was described by Donoghue (1985) and De Queiroz and Donoghue (1988). The recognised species are composed of the smallest monophyletic groups of populations (or individuals in this case) defined by a number of shared derived characters. Within the *Cannomois virgata* complex clade, all three clusters have autapomorphies. NW-Swartberg is defined by having petal length to nut length ratio between 0.65 and 0.2, and non-

tanniferous epidermal cells. The presence of spreading rhizomes and the response to fire by coppicing make the Coastal group a monophyletic species. Similarly, Caledon-Langeberg is recognised as a monophyletic species by the presence of plant height more than 2 m. The other version of phylogenetic species concept by Nixon and Wheeler (1990), who amplified upon earlier contributions by Eldredge and Cracraft (1980), Nelson and Platnick (1981) and Cracraft (1983, 1989), define species as the smallest aggregation of populations (sexual) or lineages (asexual) diagnosable by a unique combination of character states in comparable individuals (semaphorants). This definition argues that individual units diagnosable by unique combinations of character states, but not necessarily derived, are phylogenetic species and will be found to be monophyletic. According to this version all the clusters qualify to be regarded as species. In theory, this version of the phylogenetic concept (autapomorphy not required) still argues for a species as a unique evolutionary entity, but operationally it is equivalent to the phenetic species concept that emphasises raw similarity without regard to history or biological processes (Sneath and Sokal, 1973).

Under the ecological species concept, a species is defined as a lineage (clone or ancestral-descendent sequence of populations) which occupies an adaptive zone minimally different from that of any other lineage in its range and which evolves separately from all lineages outside its range (Van Valen, 1976). The ecological species concept attributes the formation of discrete units to selection, which favours certain forms and removes forms that are intermediate between species. Species integrity is maintained by stabilising selection, and speciation results from adaptation to different habitats by populations originating from the same ancestor (Linder, 1985b). In this study, the phenetic clusters often co-occur in the same area but rarely in the same habitat (H. P. Linder, pers. comm.). The ecological data extracted from the notes on the herbarium specimens were too little to test whether the clusters are ecological species. However, one would expect that if the phenetic clusters show separate ecological niches, they can be regarded as ecological species.

4.4. Proposed modes of speciation in the *C. virgata* complex

Several modes of speciation have been proposed in the Cape Flora (e.g. Goldblatt, 1978; Linder, 1985b; Cowling, 1987). Recently, a number of attempts to postulate speciation modes for particular taxa based on the patterns of sister-species coexistence (i.e. Kurzweil *et al.*, 1991; Linder and Vlok, 1991; Manning and Linder, 1992) have revealed that allopatry may play a less significant role than ecological factors, although both may be involved. For the *C. virgata* complex, a classical model of geographic (allopatric) or a combination of ecological and sympatric speciation and/or hybrid speciation appears to explain speciation in species groups.

4.4.1. **Sympatric speciation**

This is evidenced by all the three members of the *Cannomois virgata* complex which are often found occurring in the same general area (Figure 5). The Coastal and Caledon-Langeberg taxa are frequently found together, although rarely occupying the same habitat. If on the same mountain, the Coastal segregate occupies the south facing slopes exposed to the moist air current from the seacoast, whereas the Caledon-Langeberg segregate occupies the dry-north facing slopes. These two taxa exemplify the ecological-sympatric model of speciation which is largely driven by the steep ecological gradients and rendering geographical isolation of less important. Hence, this may reflects the suggestion by Linder (1985b) that species and speciation are essentially consequences of the adaptation of populations to their ecological conditions, constrained only by the genetic inheritance of the populations. However, there is need of more data on the ecology of the *C. virgata* complex to test this model of speciation.

Another interesting aspect of the Coastal and Caledon-Langeberg species pair is that Coastal is a resprouter while Caledon-Langeberg is a reseeder. A noteworthy point is the increased distribution range of Coastal in comparison to Caledon-Langeberg, a possible indication of the increased survival status of a resprouter in the fire prone vegetation of the Fynbos biome. Sprouters generally seem to have extended ranges relative to non-sprouter species (Schutte *et al.* 1995). This species is dependent on fire to clear the soil surface for new individuals to germinate and establish themselves. Therefore, fire may also have played a large role in

enhancing speciation. According to Linder (1985b), fire may have increased the number of species that coexist, owing to the fact that frequent and regular disturbance prevents competitive exclusion of species, where mainly re-seeders are involved.

4.4.2. **Geographic (allopatric) speciation**

Allopatric speciation is possible when simple spatial separation interrupts gene flow. The distribution map (Figure 5) clearly indicates that the Coastal and Caledon-Langeberg taxa are allopatrically distributed with respect to the NW-Swartberg taxon in most areas. The areas in which the NW-Swartberg taxon co-occurs with the other two taxa could be a result of secondary dispersal. In this case, vicariance events could have separated the NW-Swartberg taxon from the others. This can also be evidenced by flowering time, information on which was lacking from this study. Linder (1991) has shown that closely related species, if they are sympatric, flower at different times, while if they flower at the same time, they are allopatric.

4.4.3. **Hybrid speciation**

This mode of speciation is postulated to have given rise to the intermediate plants falling under the NW-Swartberg taxon, owing to the fact that these plants possess a hollow cavity diameter to culm diameter ratio common to the Coastal plants. Hybrid speciation is poorly known in Southern Africa, however, many other genera in the flora exhibit features which suggest that hybridisation may be significant (Goldblatt, 1978). Natural hybrids are known between woody and herbaceous taxa in *Protea* and even between genera of Proteaceae (Rourke, 1976), in *Streptocarpus* (Hilliard and Burtt, 1971), *Euryops* (Nordenstam, 1968), *Erica* (Oliver, 1977) and in several genera of Iridaceae (Goldblatt, 1978). Although hybrid speciation has not been demonstrated, but only postulated for the genus *Streptocarpus*, it will most likely prove significant given the diverse environments and recurring climatic changes in the Cape flora.

4.5. Evolution of the complex

The *C. virgata* complex groups do not form a monophyletic clade. However, there are characters, which are common between the three *Cannomois virgata* segregates and include branching culms, plant height more than 1 metre and clear chlorenchyma cell layers. Each taxon within the *C. virgata* is monophyletic (held by autapomorphies) and exhibits evolutionary modifications within the complex. The branching culms and height of plants may be associated with their growth habitats and fire response. All the taxa in *C. virgata* complex are found in moist environments, either in wet mountains, or if dry mountains near streams and long streambanks in valleys, kloofs and gorges. Hence, water conservation is not critical so that they can afford to have branching culms, which would in turn enhance photosynthesis. Thus, the water availability and the enhanced photosynthesis then facilitate the growth and increase in height. However, the height differences exhibited by the taxa within the *C. virgata* complex as seen from the Coastal and Caledon-Langeberg plants cultivated in the Kirstenbosch Botanical Gardens could be a result of the genetic component attached to it.

The three taxa of the *C. virgata* complex belong to Cape fynbos ecosystem, which is prone to fire disturbances. According to Keeley (1992) the fynbos stands have 90 - 100% probability of burning before reaching the age of 25 years. Therefore, questions about the evolution of the complex and its fire-survival strategies become imperative. Within the *Cannomois virgata* segregates the Coastal plants respond to fires by resprouting while both the NW-Swartberg and Caledon-Langeberg respond by seed regeneration. Evidence as to whether sprouting after fire is a derived or ancestral condition is contradictory (Kornas, 1978; Le Maitre and Midgley, 1992). Mapping of fire response on the cladogram (Fig. 10 a) showed a single instance of reseeding evolving from a coppicing ancestor on the branch leading to *C. taylori*. This may therefore contradicts Wagenfeld's (1997) suggestion that coppicing is a plesiomorphic condition in *Cannomois*. However, the question is what are the implications of both re-seeding and coppicing in an environment where fire is a dorminant disturbing factor. According to Le Maitre and Midgley (1992), in a flora such as Fynbos, where fire is dorminant disturbing factor, the ability to resprout after fire is of great ecological and evolutionary significance. Manders and Cunliffe (1987) remarked that sprouting enables an

individual to survive fire, and may involve no reproductive or genetic process at all. Thus, by resprouting after fire, a plant is able to persist in the landscape for an indefinite period in evolutionary time. In contrast, a seeder species is more vulnerable to local extinction as a result of stochastic fire intervals, which are characteristic of the Fynbos (Le Maitre and Midgley, 1992). However, in the *C. virgata* complex, the two re-seeders (Caledon-Langeberg and NW-Swartberg) may increase their chances of survival by growing near water i.e., near streams for Caledon-Langeberg or dams and streams along stream banks for NW-Swartberg. The water therefore may act as a buffer zone reducing the effect of fires on these reseeders.

Generally reseeders tend to grow taller than resprouters do and in the *C. virgata* complex, they have inflorescences (including nuts), which overtop the foliage. Optimisation of plant height (Figure 10c) suggested that either of states, ca. 1 m and 1 – 2 m, has an equal chance of being plesiomorphic in the genus *Cannomois*. However, the branch leading to *C. taylori* shows a a single clear instance in which the character state 1 – 2 m evolved from ca. 1 m. The state > 2 m is derived. The height of the reseeder plants may be necessary to prevent the seeds from being damaged in fire. NW-Swartberg and Caledon-Langeberg taxa, the two reseeders grow to 1.8 metres and 3.5 metres respectively whereas the Coastal taxon has plants growing up to 1.5 metres. Also field observations have shown that the two reseeders spend most of their energy in producing numerous seeds or nuts, which is likely to increase the chances of some seeds escaping fire damage even during heavy fires. This, therefore, eventually increases their survival in the fire prone environment, as these reseeders will be regenerating from the remaining healthy seeds, even if whole plants are destroyed. Although the Coastal resprouter plants only grow up to 1.5 metres high, they invest much of their energy in having a widespread growth, achieving a plant diameter of at least 4.0 metres. This is made possible by the presence of spreading rhizomes, which is a derived state (Figure 10 b) in *Cannomois*. This then may imply that even if their seeds may be destroyed by fires, the plants are capable of coppicing.

The evolution of elaiosomes and petals may be necessary for dispersal. In the genus *Cannomois*, the mode of dispersal is myrmecochory and is understood to occur only when elaiosomes are present on the fruit. With myrmechorous dispersal nutlets are seldom carried more than two to three metres by ants (Bond and Slingsby, 1983). On the contrary, the

distribution of the NW-Swartberg, Coastal and Caledon-Langeberg individuals would suggest that some agents of dispersal must have been involved to facilitate long distance dispersal. According to Linder (1991), dispersal mechanisms involve two factors, i.e., dispersal to new localities and to safe sites. He suggested that myrmecochory favours the safe sites option, whilst wind-dispersed seed favours the dispersal to new localities option. Also, since Caledon-Langeberg plants are mostly found near streams, it may be that water is a more important dispersal mechanism. Similarly, the NW-Swartberg is found on stream banks and though it has a long elaiosome, which can be dispersed by ants, water can be important for its long dispersal distances. Also, Marloth suggested a means of dispersal over greater distances when he noted that many Cape shrubs are occasionally eaten by buck (Linder, 1985b).

4.6. Nomenclatural typification

Cannomois virgata (Rottb.) Steud. is the current correct name of a polymorphic species ubiquitous in the mountains of the Cape Floral Region, reaching from Uitenhage to Nieuwoudtville. According to this study, the *Cannomois virgata* complex can be divided into three main groups worthy of specific rank, that is the NW-Swartberg, Coastal and the Caledon-Langeberg groups easily recognisable by the macromorphological characters. The main taxonomic problem concerning the name *C. virgata* is its application as referring to all the groups found in the *Cannomois virgata* complex, owing to the differences established and the circumscription of the specific taxa.

The types used to circumscribe the species under *C. virgata* previously, satisfy the major diagnostic characters that are common with the Coastal group plants. These include:
1. the ratio of hollow cavity diameter to culm diameter, and
2. the foliage which overtops inflorescence and nuts.

The culms which appear to be less than 1 m tall is an indication that the plant height was less than 2 metres and by restricting the plant height between 1 and 2 metres entails that the type specimens belong to the Coastal group collections. The subcluster H belonging to the NW-Swartberg is the only exception sharing a similar hollow cavity diameter to culm diameter ratio with the Coastal plants. However, this will not qualify based on herbarium records which

revealed that it was never collected before. Also, this subcluster has the inflorescence equalling or overtopping the foliage.

These diagnostic characters, therefore distinguish all the types of this species from the NW-Swartberg and Caledon-Langeberg groups. This allows the application of the name *Cannomois virgata* to the Coastal group plants. On account of this, it is therefore necessary to name the other two taxa. Caledon-Langeberg group has been named *Cannomois grandis* Mujaju based on its giant form ranging from 2 metres to 3.5 metres high. The NW-Swartberg is distinguished by the name *Cannomois saundersii* Mujaju, in recognition of a seed collector Mr. Saunders, and is easily distinguished by slender narrow nuts and solid culms.

4.7. Taxonomy

4.7.1. **Key to the species in the *C. virgata* complex**

1a. Culm solid; nuts slender (width to length ratio < 1/2); rhizome diameter less than 6.0 mm; bracts narrow (width < 7 mm); spikelets narrow (width < 8 mm); petal width of outer segment less than 3 mm; ratio of petal length to nut length less than 0.65.

1. *Cannomois saundersii* Mujaju *sp. nov.*

1b. Culm hollow; nuts stout (width to length ratio > 1/2); rhizome diameter more than 7.5 mm; bracts broad (width > 8 mm); spikelets broad (width > 8 mm); petal width of outer segment at least 3 mm, petal length about equal to nut length.

3

3a. Ratio of hollow cavity to culm diameter between 0.25 and 0.5; plant height 1 - 1.5 m; plant diameter at least 3.0 m, mostly single or few inflorescences per plant, foliage overtops inflorescence and nuts; a resprouter.

2. *Cannomois virgata* (Rottb.) Steud.

3b. Ratio of hollow cavity to culm diameter greater than 0.6; plant height 2 - 3.5 m; plant diameter less than 1.5 m, numerous inflorescences per plant, inflorescence and nuts overtop foliage; a reseeder.

3. *Cannomois grandis* Mujaju *sp. nov.*

4.7.2. **Descriptions**

1. Cannomois saundersii *Mujaju*, sp. nov.

Plants caespitose with a narrow base, taller than wide, 1.5 - 1.8 m high with, basal diameter of 0.3 - 0.5 m and a crown diameter 0.3 - 0.5 m; plant base compact. *Rhizomes* present, not spreading, 4.5 - 6 mm in diameter, short and scarcely branched. *Fertile culms* branching, terete, solid, finely regulose, green, 5 - 8 mm in diameter at base and 1.1 - 2 mm in diameter at apex. *Sheaths* persistent on fertile culms, closely convoluted, margins coriaceous like the rest of the body, nervose striate, entire, upper 1/3 of sheath same colour and texture as the lower 2/3, 24 - 45 mm long; mucro small and penicellate, 5 - 7 mm long. *Male inflorescence* paniculate, 70 - 250 mm long, 20 - 35 mm wide and with 100 - 300 spikelets; spathes persistent and sometimes caducous, taller than spikelets and almost as tall as the branches, coriaceous, with pedicels shorter than spikelets or absent in some spikelets and terete. *Male flowers* in spikelets. *Male spikelets* pendulous, ovate, acute at apices, 5 - 8 mm long and 3 - 4.2 mm wide. *Male bracts* taller than flowers, 1.9 - 2.2 mm long including awn, ovate, acute at apices, awn minute and less than half as long as the bract body, coriaceous. *Female inflorescence* with 1 - 4 spikelets, 30 - 100 mm long and 7 - 22 mm wide. *Female spathes* shorter than spikelets and occasionally become as long as the spikelets, persistent/caducous, coriaceous. *Female spikelets* sessile, 2 - 3 flowers, linear-oblong, acute apices, 30 - 55 mm long. *Female bracts* taller than flowers, 15 - 25 mm long including awn, oblong-lanceolate, acuminate at apices, awn minute and less than half as long as the bract body, coriaceous, apical margin membranous. *Female flowers* tepals membranous, outer tepals wider than inner tepals, 1.5 - 2.2 mm wide, inner tepals 0.5 - 1.2 mm wide, lanceolate or ovate, acute tepal apices, inner and outer whorls the same length, 1.2 - 5 mm long; indehiscent ovary. *Fruits* a woody shiny brown to almost black nut, nut apex smooth without a distinct cap, nut wall smooth, flattened and compressed on the adaxial side, 9 - 13 mm long and 3.8 - 5.2 mm wide, perianth membranous and reduced; elaiosome present, white, 1.2 - 4 mm long, less than half as long as the nut body.

CULM ANATOMY. *Epidermis* uniseriate, outer wall thickened, glabrous, length to width ratio of 2.75 - 3. *Stomata* superficial, guard cells seated on top of support cells.

Chlorenchyma cells of 2 layers with a length to width ratio of 6, somewhat dissimilar. *Protective cells* not reaching to base of the chlorenchyma layer. *Parenchymatous layer* of 1 cell wide, cells smaller than the epidermal cells. *Sclerenchyma sheath* with outer margins made of ridges alternating with the vascular bundles, ridges penetrating the parenchymatous sheath into the chlorenchyma. *Central ground tissue* without scattered cavities. *Pith* with a central cavity. *Tannin* absent. *Silica* found in sclerenchyma.

FLOWERING TIME. October to November.

DISTRIBUTION. Endemic in the Cape Floristic Region of South Africa. Commonly found in the following winter rainfall areas: Namaqualand (north of Olifants – Doorn river), Northern CFR (Cedarberg, Bokkeveld), South-western mountains and Swartberg and Little Karoo.

Comments on distribution. Generally has a northwestern – Swartberg distribution within the Cape Floristic Region.

GENERAL ECOLOGY. It is commonly associated with stream-banks on sandstone, in valleys or gorges and kloofs; occurring on deep soils derived from the Table Mountain Sandstone. Altitudinally it ranges between 500 and 1 100 m above sea level. Plants are killed by fire, regenerating from seed. Its mode of seed dispersal is by ants.

ECONOMIC USE. Horticulture.

2. Cannomois virgata (Rottb.) Steud., Syn. Pl. Glum. 2 : 263 (1855); Mast. in A.DC., Monogr. Phan. 1 : 361 (1878); Pillans in Trans. R. Soc. S. Afr. 16 : 411 (1928); damson & Salter, Fl. Cape Penins. 157 (1950); Linder in Bothalia 15: 387-503 (1985). Type: Cape, without precise locality, *Kónig* s.n. male (C, holo.).

Restio virgatus (Rottb.), Descriptiones Plantarum Rariorum 10 (1772); Thunb., Fl. Cap. edn 1, 338 (1811); edn Schultes, 89 (1823). *Thamnochortus virgatus* (Rottb.) Kunth, Enum. Pl. 3 : 436 (1841).

Restio scopa Thunb., Diss. Restio 19 (1788); Thunb., Fl. Cap. edn 1, 337 (1811), edn Schultes, 88 (1823). Type: Cape, without precise locality, in herb. Thunb. 23244 (UPS, holo.).

Restio elegans Poir. in Lam., Encycl. 6 : 171 (1804). Type: Cape, without precise locality, herb. Poiret in herb. Moquin-Tandon (P, holo.).

Elegia paniculata Pers., Syn. Pl. 2 : 607 (1807), nom. illeg., superflous name for *R. elegans* Poir.

Cannomois cephalotes Desv. in Annls Sci. nat., ser. 1, 13 : 43 (1828); Kunth, Enum. Pl. 3 : 447 (1841); Mast. in Fl. Cap. 7 : 141 (1897). Type: Annls Sci. nat., 1, 13 : t.3 fig.1 (8128) (iconotype).

Thamnochortus robustus kunth, Enum. Pl. 3 : 436 (1841). Type: Cape, 3319 (Worcester): Du Toits Kloof (-CA), Drége 1606 male (B, lecto.; B, BM; K; MEL; MO; P).

Icones: Rottb., Descriptionum et Iconum Rariores t. 1 f. 2 (1773). Annls Sci. nat., ser. 1, 13 : t. 3 f.1 (1828).

Plants mat-forming with wide base, plants much wider than tall with height of 1 - 1.5 m and basal diameter of 3 - 8 m, plant base with spreading rhizomes. *Rhizomes* of 7.5 - 10 mm in diameter and somewhat branched. *Fertile culms* evenly spaced, sparingly branching, terete, hollow (0.25 - 0.48 hollow cavity diameter to culm diameter ratio), finely rugulose, green, 5 - 8.5 mm in diameter at base and 1 - 2.1 mm in diameter at apices. *Sheaths* persistent on fertile culms, closely convoluted, margins coriaceous like the rest of the body, nervose-striate, entire, upper 1/3 of sheath the same colour and texture as the lower 2/3, 25 - 65 mm long, coriaceous portion of sheath acute; mucro small and penicellate, 4 - 7 mm long. *Male inflorescence* paniculate, 200 - 400 mm long, 15 - 20 mm wide and with 100 - 210 spikelets. *Male spathes* persistent, shorter or sometimes taller than spikelets, coriaceous to chartaceous, pedicels absent. *Male flowers* in spikelets. *Male spikelets* pendulous, ovate, acute at apices, 4 - 6.8

mm long and 3 - 4 mm wide. *Male bracts* taller than flowers, 1.9 - 2.2 mm long including awn, ovate, acute at apices, awn minute and less than half as long as the bract body, chartaceous to membranous. *Female inflorescence* with 1 spikelet, 26 - 45 mm long and 8 -16 mm wide. *Female spathes* shorter than the spikelets, caducous, coriaceous. *Female spikelets* sessile, 2 - 3 flowered, oblong, apices acute, 7 - 8 sterile bracts, 26 - 45 mm long, 8 -16 mm wide. *Female bracts* taller than flowers, 16.5 - 25 mm long including awn, oblong to ovate, acuminate at apices, awn minute and less than half as long as the bract body, bony to coriaceous, apical margin membranous. *Female flowers* with membranous tepals, outer tepals wider than inner tepals, 2.8 - 5.0 mm wide, inner tepals 1.3 - 2 mm wide, linear oblong, tepal apices obtuse, entire, inner and outer whorls the same length, 6.8 - 14.3 mm long; indehiscent ovary. *Fruits* woody nuts, nut apices smooth, without a distinct cap, nut wall smooth, flattened and compressed on the adaxial side, 9 - 12 mm long and 5 - 7 mm wide, ovate, brown in colour; perianth membranous and persistent; elaiosome present, white, 0.7 - 1.1 mm long, less than half as long as nut.

CULM ANATOMY. *Epidermis* uniseriate, outer wall thickened, glabrous, length to width ratio ranging between 1.4 to 1.5. *Stomata* superficial, guard cells seated on top of support cells. *Chlorenchyma* of 2 layers of cells, length to width ratio of 4, inner and outer layers somewhat dissimilar. *Protective cells* not reaching to base of the chlorenchyma layer. *Parenchymatous layer* of 1 cell wide, cells smaller than the epidermal cells. *Sclerenchyma sheath* with outer margins made of ridges alternating with the vascular bundles. *Central ground tissue* without scattered cavities. *Pith* with a central cavity. *Tannin* present on the epidermal cells. *Silica* found in sclerenchyma.

FLOWERING TIME. November.

DISTRIBUTION. Endemic in the Cape Floristic Region of South Africa. It is distributed in the following winter rainfall areas: Namaqualand (north of Olifants – Doorn river), West Coast (False Bay to Olifants river), Cape Peninsula, South Western mountains, Bredasdorp plains, Swartberg and Little Karoo, Langeberg-Outeniqua mountains and Eastern Cape.

GENERAL ECOLOGY. Common on sandstones derived from the Table Mountain Sandstones and often form patches in over-burnt vegetation. It is occasionally found on shales. Altitudinally, it occurs between 0 to 1800 metres above sea level. Its response to fires is by coppicing from the rhizomes or base. It disperses its seeds by means of ants acting as dispersal mode.

ECONOMIC USE. Horticulture and thatching.

3. Cannomois grandis *Mujaju*, sp. nov.

Plants caespitose with narrow base, plants taller than wide with height of 2.0 - 3.5 m, a basal diameter of 1 - 1.5 m and a crown diameter 1 - 2 m. *Rhizomes* present, 10 - 30 mm in diameter, short, scarcely branched. *Fertile culms* branching, terete, distinctly hollow (> 0.60 hollow cavity diameter to culm diameter ratio), finely rugulose, green, 12 - 20 mm in diameter, at base and 1.8 - 3.2 mm in diameter at apices. *Sheaths* persistent on fertile culms, closely convoluted, margins coriaceous like the rest of the body, nervose-striate, entire, upper 1/3 of sheath differentiated from the lower 2/3, and decaying in older sheath, 40 - 92 mm long, coriaceous portion of sheath acute; mucro small and penicellate, 4 - 7 mm long. *Male inflorescence* paniculate, 100 - 400 mm long and 10 - 25 mm wide, with 200 - 350 spikelets. *Male spathes* caducous, taller than spikelets and as tall as the branches, coriaceous; pedicels shorter than spikelets, terete. *Male flowers* in spikelets. *Male spikelets* pendulous, ovate, obtuse at apices, 10 - 12 mm long and 5 - 6 mm wide. *Male bracts* taller than flowers, 2 - 2.2 mm long including awn, ovate, acute at apices, awn minute and less than half as long as the bract body, chartaceous to membranous. *Female inflorescence* with 1 to 3 spikelets, 31 - 90 mm long and 10 - 25 mm wide. *Female spathes* shorter than the spikelets, caducous, coriaceous. *Female spikelets* sessile, 1 - 2 flowers, ovate, acute apices, 30 - 55 mm long. *Female bracts* taller than flowers, 20 - 28 mm long including awn, oblong to ovate, acuminate at apices, awn minute and less than half as long as the bract body, coriaceous to chartaceous, apical margin membranous. *Female flowers* with membranous tepals, outer tepals wider than inner tepals, 3.8 - 5.0 mm wide, inner tepals 1.5 - 2.5 mm wide, lanceolate or ovate, tepal apices round, entire, inner and outer whorls the same length, 9.8 - 15.3 mm long; indehiscent ovary. *Fruits* with hard woody nuts, nut apices smooth without a distinct cap, nut wall

smooth, flattened and compressed on the adaxial side, 11 - 16 mm long and 7 - 9 mm wide, ovate, brown to black; perianth membranous and persistent; elaiosome present, white, 0.2 - 1.1 mm long, less than half as long as nut.

CULM ANATOMY. *Epidermis* uniseriate, outer wall thickened, glabrous, length to width ratio between 2.75 and 3. *Stomata* superficial, guard cells seated on top of support cells. *Chlorenchyma* of 2 layers of cells, length to width ratio of 6, somewhat dissimilar. *Protective cells* not reaching to base of the chlorenchyma layer. *Parenchymatous layer* of 1 cell wide, cells smaller than the epidermal cells. *Sclerenchyma sheath* with outer margins made of ridges alternating with the vascular bundles, ridges pushing into the parenchymatous sheath. *Central ground tissue* without scattered cavities. *Pith* with a central cavity. *Tannin* present in the central ground tissue. *Silica* found in sclerenchyma and central ground tissue.

FLOWERING TIME . October.

DISTRIBUTION. Endemic to the Cape Floristic Region of South Africa. It is distributed in the winter rainfall areas, particularly, in the Bredasdorp plains, Swartberg and Little Karoo, Langeberg-Outeniqua mountains and Eastern Cape.

Comments on distribution. Common in the mountains around Paarl, Stellenbosch through Langeberg to the Outeniqua mountains.

GENERAL ECOLOGY. Commonly found on shales between altitudes of 500 to 1100 m above sea level. Also, it is occasionally found on sand soils derived from Table Mountain Sandstones. Plants are killed by fires and they respond by regenerating from seed. Mode of seed dispersal is by ants.

ECONOMIC USE. Horticulture and thatching.

5. CONCLUSIONS

The initial hypothesis that the *Cannomois virgata* complex is made up of at least three species was supported by this study. The species are distinguished morphometrically. Ordination methods proved more useful than cluster analysis in elucidating the variation patterns of the *Cannomois virgata* into discrete clusters without overlap and ensuring that the intermediate plants marked H on the phenogram falls under the NW-Swartberg cluster. In addition, principal component analysis also assisted in the identification of diagnostic characters. However, both these multivariate methods retrieved the same groups. The operational definition of species, which is analogous to the definition of phenetic species concept, has been used to establish the working units. It allows the use of phenotypically irreducible clusters of individuals as first order estimates of species.

Cladistic analysis demonstrated that the clusters can be diagnosed by autapomorphies, and also that the clusters can be diagnosed by a combination of characters states, indicating that the three clusters are phylogenetic species. The phylogenetic concept explained these clusters as the results of unique descent, although the monophyletic species concept version insists on apomorphy as evidence for unique historical relationships and the other does not. The operational definition of species is also compatible with reproductive and ecological species concepts. Under reproductive concepts, the biological species concept explained the existence of clusters as a result of gaps formed because of isolation (in this case flowering time) within formerly interbreeding individuals or populations, whereas the recognition concept attributes existence of these clusters to internal cohesion reinforced by interbreeding. The ecological species concept identifies species as clusters occupying a unique ecological niche. However, in this study there was no data to support whether NW-Swartberg, Coastal and Caledon-Langeberg could described as either biological or ecological species.

Evolution of the complex in the fire prone Fynbos ecosystem in which it is found have shown that both sprouter and non-sprouter species have developed adaptational features i.e., increase in plant height and investing much energy in producing numerous nuts or seeds for re-seeders and long spreading rhizomes for sprouters, to facilitate their perpetual survival. Evolution of elaiosomes and petal length possibly aid in the dispersal of the *Cannomois virgata* complex segregates.

Speciation in the complex has been postulated to be sympatric (separated by occupation of different adaptational zones) for the Coastal and Caledon-Langeberg plants or geographic (allopatric) for the NW-Swartberg plants with respect to others. Hybridisation as a mode of speciation is possible and under the ecological theory hybrids would only survive if they find a suitable habitat unoccupied by either parent. Otherwise, the ecological species concept attributes the formation of discrete units to selection which favours certain forms and removes forms that are intermediate between species.

The taxonomy of the *Cannomois virgata* complex is based upon the results of both the phenetic analysis and cladistic analysis. Diagnostic characters found for each cluster, showed that the Coastal plants should be recognised as *Cannomois virgata* (Rottb.) Steud. from which the type was collected.

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APPENDIX 1. Specimens examined.

1. Northwest-Swartberg

BOL. Bolus 9662, 5481; Brusse 5392; Compton 3146, 4887; Esterhuysen 30721a, ?, 25967a, 24778, 13017, 7877, 34470a; Goldblatt 3814; Linder 3332, 5500; Maguire 1779; Mujaju 3, 4, 6; M.R.L 6660, 8097, 3958, 1930a, 2930, 4679; Phillips 7462; Powrie 87.

PRE. Humbert 9759; Marloth 3161, 10813, 3172, 12068; Pocock S209.

NBG. Andrag 276; Compton 12904, 16115; Durand 304; Esterhuysen 37374; Goldblatt 3814, 1348; McDonald 2339; Morris 218; Phillips 7462=7618; Reid 1390; Rourke 1076; Steyn and De Villiers 512; Strauss 46; Taylor 5137; Thompson 165; Van Greuning 8.

2. Coastal group

BOL. Bolus 4085, 4088; Bredenkamp 672; Burchell 7139; Esterhuysen 6819, 6621, 6819, 10603a; Fourcade 1009, 6528; Kerfoot 5255; M.R.L. 2352; Mujaju 1, 2, 7; Page 14337; Pillans 8391; Rodin 3288; Schlechter 5983; Stokoe 9571.

PRE. Acocks 21657; Andreae 1174; Bredenkamp 672; Cheadle 743; Dahlstrand 1743, 627; Davidse 33666, 33604; Davidson J24943; Faure H775; Galpin 4826, 4829; Gane 28265; Gower 37566; Horn 2404; Kruger 859a; Marloth 8288; Noel RU10445; Rogers 4237; Scharf 1224, 1637, 1218, 1726; Schlechter 5998; Theron 961; Wilson H140; Zeyher 1738.

NBG. Boucher 3402; Compton 13067; Dahlstrand 627; De Vos 1351; Jodaarn 264; Kerfoot K5760; Kruger 329, 859a; Marshall 122; Manson 276; Rode and Boucher 0083; Phillips (no collector's number); Pretorius 196; Scharf 1726, 1637; Smith 191; Van Zyl 3352; Viviers 742.

3. Caledon-Langeberg group

BOL. Bolus 7486, 11411; Burchell 5811, 8697, 1814; Burman 989; Esterhuysen 9664; Galpin 4823; Linder 6124, 4139; M.R.L. 7364; Mujaju 8; Rodin 3286; Schlechter 1973.

PRE. Burgers 2392; Galpin 4827, 4823; Greuter 22009; Kerfoot 5738; Joffe 939B, 939A; Stokoe 1201, 7209; Taylor 3549; Theron&Studente 3328; Tredgold 432, 433.

NBG. Bohnen 8431; Compton 23108; Esterhuysen (no collector's number); Fellingham 1287; Joordaan (no collector's name); Kerfoot 5738; Muir 2339; McDonald 2035; Phillip and Merwe 2074; Taylor 3549.

APPENDIX 2. Raw data used in phenetic analysis.

Twenty-two characters in rows (22L) are coded as in Table 2.3 and 84 specimens (84L) in columns coded as in Tables 2.1 and 2.2. 999 denotes missing value.

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1 22L 84L 1 999

Nut-L Nut-W Petal-L Petal-W1 Petal-W2 Spike-L Spike-W Bract-L
Bract-W Spath-L Elaios-L Culm-D BrT-D BrB-D RNW-L RPL-NL RSkW-L
RBW-L RTD-BD RHol-CD RSh-SkL REl-NutL

Poc-S209 Marl-3161 Gold-3814 Ester-30721a Ester-? Ester-25967a
Brus-5392 Lind-3332 Powrie-87 Comp-3146 Magu-1779 M.R.L-6660
Comp-4887 Bolus-9662 Ester-24778 Ester-13017 Ester-7877 Lind-
5500 Taylor-3549 Kerf-5738 Burg-2392 Joffe-939B Tredg-432
G.K.T&St-3328 Linder-6124 Linder-4139 M.R.L-2352 Rodin-3288
Scharf-1224 Acocks-21657 Horn-2404 Rogers-4237 Noel-RU10445
Muj1-CP1 Muj1-CP2 Muj1-CP3 Muj1-CP4 Muj2-DT1 Muj2-DT2 Muj3-CM1
Muj3-CM2 Muj4-CM1 Muj4-CM2 Comp-12904 Ester-37374 Morris218
Comp-16115 Straus-46 Greun-8 Reid1390 Taylor5137 Andrag276
Thomp-165 Rour-1076 Muj6-BP1 Muj6-BP2 Muj6-BP3 Muj6-BP4 Muj6-
BP5 Muj6-BP6 Muj6-BP7 Muj6-BP8 Muj6-BP9 Muj6-BP10 Muj7-BL1
Muj7-BL2 Muj7-BL3 Muj7-BL4 Muj7-BL5 Muj7-BL6 Phill-? Kerf-5760
Vos1351 Comp-13067 Hubb-322 Muj8-B1 Muj8-B2 Muj8-B3 PhMw-2074
Comp-23108 Muir2339 Fellin-1287 Bohn-8431 McDon-2035

10.2 10.7 9.6 9.1 8.8 9.6 10.3 10.6 9.5 10.5 10.6 10 10.4 9.1
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10.0 9.75 9.5 10.2 10.2 10.0 9.45 9.65 10.5 10.0 10.8 11.5 11.9
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3.7 4.4 3.3 3.7 3.8 4.1 4.4 3.7 3.9 4.4 3.7 4.3 4 3.8 4 3.7 4.0
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6.0 6.0 6.4 6.0 4.24 3.7 4.46 4.5 4.0 4.0 3.8 4.0 3.7 4.0 4 4
3.8 5.4 4.0 3.93 3.9 3.85 3.95 3.6 3.8 4.0 4.0 4.0 4.2 6.0 6.0
6.8 6.3 6.4 6.0 5.4 6 7 6.8 6 8.0 7.8 7.8 8.0 10 10 9 10 8.4

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11.8 11.7 13.2 10.6 10.96 13.16 15.3 14.3 8.0 12.0 7.4 9.30 9.4
6.8 7.9 10 10 10.2 11.5 11.0 10.1 3.39 3.3 4.35 4.36 3.7 4.0
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0.50 0.50 0.50 0.50 0.5 0.60 0.5 0.6 0.5 0.45 0.45 0.45 0.45
0.6 0.40 0.4 0.5 0.5

0.36 0.41 0.34 0.41 0.43 0.43 0.43 0.35 0.41 0.42 0.35 0.43
0.38 0.42 0.38 0.35 0.45 0.41 0.65 0.63 0.52 0.61 0.72 0.57
0.61 0.6 0.72 0.53 0.51 0.54 0.51 0.56 0.52 0.58 0.55 0.52 0.54
0.54 0.54 0.45 0.37 0.42 0.43 0.40 0.36 0.41 0.40 0.39 0.44
0.39 0.41 0.38 0.49 0.36 0.39 0.40 0.41 0.39 0.35 0.38 0.42
0.41 0.38 0.42 0.56 0.52 0.57 0.59 0.58 0.56 0.54 0.55 0.65
0.52 0.59 0.62 0.66 0.65 0.76 0.77 0.75 0.69 0.74 0.76

0.15 0.33 0.39 0.33 0.57 0.13 0.49 0.38 0.47 0.38 0.32 0.22 0.5
0.25 0.28 0.36 0.31 0.26 0.97 0.94 0.94 0.92 0.97 0.94 0.96
0.96 0.88 0.94 0.73 0.83 0.82 0.76 0.81 0.92 0.91 0.89 0.88
0.92 0.90 0.36 0.33 0.41 0.42 0.37 0.36 0.33 0.30 0.13 0.12
0.19 0.41 0.30 0.32 0.32 0.60 0.59 0.64 0.61 0.60 0.43 0.50
0.45 0.46 0.50 0.88 0.87 0.84 0.88 0.84 0.88 0.92 0.92 0.93
0.92 0.91 0.92 0.92 0.91 0.95 1.0 0.89 1.0 0.81 0.89

0.22 0.23 0.16 0.13 0.16 0.16 0.18 0.16 0.15 0.19 0.17 0.23
0.17 0.23 0.22 0.14 0.15 0.20 0.59 0.57 0.57 0.56 0.59 0.57
0.59 0.58 0.39 0.31 0.33 0.35 0.33 0.28 0.29 0.26 0.31 0.27
0.27 0.28 0.28 0.50 0.50 0.50 0.50 0.20 0.21 0.24 0.27 0.24
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0.31 0.33 0.26 0.31 0.26 0.26 0.26 0.26 0.29 0.29 0.28 0.25
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0.54 0.50 0.47 0.44 0.44 0.39 0.71 0.60 0.57 0.59 0.52 0.50

0.87 0.87 0.89 0.88 0.90 999 0.89 0.94 0.86 0.88 0.86 0.89 0.92
1.00 0.89 999 0.86 999 0.57 0.57 0.60 0.56 0.60 0.60 0.63 0.63
0.82 0.80 0.75 0.73 0.75 0.75 0.73 0.70 0.64 0.64 0.64 0.70
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999 999 999 999 999 999 999 0.41 0.44 0.46 0.43 0.34 999 999
999 0.36 0.47 0.29 0.44 0.49 0.36

0.18 0.14 0.11 0.14 0.11 0.25 0.22 0.16 0.15 0.15 0.18 0.12
0.14 0.11 0.19 0.19 0.14 0.21 0.01 0.02 0.08 0.09 0.02 0.02
0.09 0.08 0.09 0.09 0.09 0.09 0.09 0.09 0.08 0.08 0.08 0.09
0.08 0.09 0.08 0.19 0.19 0.19 0.20 0.15 0.15 0.13 0.11 0.13
0.11 0.17 0.13 0.10 0.15 0.14 0.21 0.21 0.20 0.20 0.20 0.18
0.21 0.21 0.19 0.19 0.07 0.06 0.08 0.09 0.09 0.09 0.08 0.07
0.09 0.08 0.09 0.09 0.08 0.09 0.06 0.02 0.05 0.08 0.03 0.04

APPENDIX 3. Data showing character ranges used in delimiting quantitative states. Species according to numbers are as follows: 1 NW-Swartberg, 2 Coastal, 3 Caledon-Langeberg, 4 *C. nitida*, 5 *C. congesta*, 6 *C. aristata*, 7 *C. scirpoides*, 8 *C. taylori*, 9 *C. parviflora*, 10 *Willdenowia glomerata*, 11 *Hypodiscus aristatus* and 12 *Ceratocaryum pulchrum*. Characters with reference to Table 2.4 are as follows: NW/L = 2, PL/NL = 6, EL/NL = 4, PLHT = 19, SPKL = 9, BRNO = 13, SH/SPL = 14 and PW1 = 7.

	Characters							
Species	NW/L	PL/NL	EL/NL	PLHT	SPKL	BRNO	SH/SPL	PWI
1	0.340	0.150	0.200	1.50	28.0	9	0.420	1.5
	0.385	0.385	0.225	1.65	36.5	10	0.725	2.0
	0.430	0.620	0.250	1.80	45.0		1.030	2.5
2	0.52	0.84	0.05	1.00	28.0	8	0.420	3.0
	0.56	0.89	0.07	1.25	36.5	10	0.475	4.0
	0.60	0.94	0.09	1.50	45.0		0.530	5.0
3	0.57	0.91	0.01	2.00	31.0	8	0.100	3.8
	0.66	0.94	0.05	2.75	40.5	10	0.245	4.9
	0.75	0.97	0.09	3.50	50.0		0.390	6.0
4	0.48	0.98	0.07	0.70	26.0	8	0.900	1.40
	0.49	0.99	0.08	0.85	35.5	9	0.940	1.55
	0.50	1.00	0.09	1.00	45.0		0.980	1.70
5	0.45	0.20	0.14	0.65	15.0	8	1.000	1.50
	0.465	0.42	0.15	0.82	20.5	9	1.325	1.75
	0.48	0.64	0.16	1.00	26.0		1.650	2.00
6	0.43	0.09	0.16	0.60	24.0	8	0.950	1.00
	0.455	0.095	0.17	0.80	27.5	9	0.975	1.15
	0.48	0.10	0.18	1.00	31.0		1.000	1.30
7	0.44	0.39	0.19	0.50	15.0	8	1.200	1.00
	0.465	0.40	0.21	0.70	20.5	8	1.975	1.15
	0.49	0.41	0.23	0.90	26.0		2.750	1.30
8	0.48	0.10	0.15	1.30	26.0	8	1.300	0.50
	0.49	0.125	0.175	1.65	28.0	8	1.550	0.65
	0.50	0.15	0.20	2.00	30.0		1.800	0.80
9	0.43	0.10	0.08	0.50	22.0	8	1.000	0.50
	0.44	0.145	0.09	0.75	26.0	8	1.550	0.70
	0.45	0.19	0.10	1.00	30.0		2.100	0.90
10	0.59	0.25	0.07	0.30	15.0	5	1.250	1.50
	0.645	0.40	0.075	0.65	20.0	7	1.375	1.75
	0.68	0.55	0.08	1.00	25.0		1.500	2.00
11	0.65	0.18	0.07	0.30	30.0	25	0.600	1.70
	0.665	0.19	0.08	0.55	35.0	45	0.800	2.00
	0.68	0.20	0.09	0.80	40.0		1.000	2.30
12	0.75	0.18	0.00	0.50	43.0	20	1.100	0.50
	0.765	0.19	0.00	0.60	44.5	45	1.350	0.75
	0.78	0.20	0.00	0.70	46.0		1.600	1.00

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