EVOLUTIONARY PATTERNS IN *THAMNOCHORTUS* (RESTIONACEAE):

A STUDY OF SPECIATION IN THE CAPE FLORISTIC REGION

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DISCUSSION

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ABSTRACT

Patterns of speciation and potential evolutionary pressures and constraints were investigated in the genus *Thamnochortus*. Phenetic methods were used to define boundaries of species prior to cladistic analyses. Comparative techniques were employed to investigate aspects of dispersal biology and fire survival habit. Methods of historical biogeography were used to evaluate vicariance and dispersal hypotheses. The broader understanding of species evolution gained in such a comparative study is important in conservation of species or areas, forming a basis for further ecological and genetic predictions.

The majority of *Thamnochortus* species have well-defined species limits; however, those of *T.comptonii*, *T.platypteris* and *T.scabridus* are more diffuse. For this species complex a matrix of 94 specimens, nine quantitative and sixteen qualitative characters was investigated, using cluster and ordination analyses, to define species boundaries.

Thirty-four species of *Thamnochortus*, with three species of *Rhodocoma* as the outgroup, were used in the cladistic analysis. There were forty-three qualitative characters and ten quantitative characters.

The number of species, height, reproductive output and geographic area were compared between sister lineages of seeding and resprouting species. In species classified as resprouters individuals survive fire by resprouting from the rhizome. In a post-fire environment seeding species recruit from seed and not by resprouting. Resprouters were significantly taller than seeders and covered a significantly larger distribution area. There was no significant difference in the amount of seed produced by seeding and resprouting lineages or in the geographic area covered by winged and keeled lineages.

Correlated evolution tests indicated that wings of seeds evolved independently of the seeding condition, although the probability of wings evolving randomly was low. The evolution of keels was significantly associated with a switch to resprouting.

There are few distinct ecological differences between the seeding and resprouting habits in soil type or rainfall; however, the inference is that resprouters do occupy habitats in higher rainfall areas than the sister seeders.

Biogeographic analysis of species distributions, using cluster methods with a Jacard similarity coefficient, defined four phytogeographic areas which were considered to be areas of endemism. A concentric ring method recognised narrow areas of endemism and illustrated the overlap of species distributions between areas. The defined areas of endemism and similarity were used in general area cladograms to determine area relationships. The primary differentiations on the general area cladogram of areas of similarity distinguished a summer rainfall region (south coast) from a winter rainfall region (south western Cape extending up the west coast). Within the winter rainfall region there is separation into a mesic (Cape Peninsula and south western mountain range) and an arid region (Cedarberg and Koue Bokkeveld). This analysis of *Thamnochortus* gives the first indication that the primary differentiation was between summer and winter rainfall, followed by the differentiation of the winter rainfall region into mesic and arid areas.

Comparison within clades of distribution and habitat profiles indicated that, where distributions of closely related species overlap, there is niche differentiation in flowering time and substrate texture.

Fire survival habit does not appear to have influenced speciation in *Thamnochortus*. There is, however, an evolutionary relationship between fire survival habit and female outer tepal specialization. Evidence from the general area cladogram indicates that speciation patterns in *Thamnochortus* may have been influenced by changes in rainfall in the Miocene. Habitat profiles of sister species indicate that alterations in flowering time and substrate texture are key factors in ecological differentiation of species.

INTRODUCTION

EVOLUTION, SPECIATION AND BIODIVERSITY

Evolution, Darwin's "descent with modification", is the result of the interaction of natural selection, genetic drift and mutation. Natural selection is a complex interaction of biotic and abiotic factors acting on different time scales (Altaba 1991), for example, climate change overlaying competition for a particular habitat. The combination of these pressures and genomes result in speciation (Brooks and Mclennan 1994), which is reflected in diversity (Pearson and Juliano 1993). Thus, an investigation into the process of speciation should include as many factors as possible.

The legacy of speciation and evolutionary pressures are reflected in several patterns. Firstly, incomplete divergence within populations produces species complexes (Hoelzer and Melnick 1994). Secondly, speciation results in patterns of character distribution and these can be investigated using phylogenetic systematics (Roff 1994). Adaptational pattern reveals biological and environmental interaction (Wanntorp *et al.* 1990). Finally, current distribution patterns may reflect past vicariance and dispersal events (Ladiges *et al.* 1989). These patterns, individually and in combination, may lead to hypotheses on the evolutionary pattern in the lineage under study (Brooks and Mclennan 1994).

Integrated studies - the historical approach

The importance of integrated studies has been expressed with increasing frequency in the literature (Gould and Lewontin 1979; Altaba 1991; Harvey and Pagel 1991; Pearson and Juliano 1993; Losos 1994; Wanntorp *et al.* 1994; Wainwright and Reilly 1994). The inclusion of the historical aspect, in particular, has been emphasised in studies concerned with organismal design (Altaba 1991; Wainwright and Reilly 1994) and on a larger scale, species co-occurrence and biodiversity (Pearson and Juliano 1993). Phylogenetic systematics is recognised as the best approach in developing evolutionary hypotheses which can be tested (Coddington 1988; Wainwright and Reilly 1994; Brooks and Mclennan 1994; Diaz-Uriarte and Garland 1996). However, evolutionary based studies have been limited by the availability of appropriate phylogenies (Brooks and Mclennan 1994; Pearson and Juliano 1994; Losos 1994).

Use of phylogeny in comparative studies has the advantage of statistical integrity (Diaz-Uriarte and Garland 1996), specifically with regard to replicates. Phylogenetic studies identify independent evolutionary events, preventing the use of spurious replicates and correlations in comparative studies (Harvey and Pagel 1991). An additional advantage is clarity of pattern. By using phylogenies it is possible to determine interdependence of certain characters and the relationship of cause and effect (Maddison 1990). Thus, a comprehensive view of the interactive effect of intrinsic and extrinsic factors on the direction of evolution may be obtained from a study of speciation and evolutionary pressures which employs a comparative method based on phylogeny.

The purpose of understanding the existence of species from a holistic point of view is not entirely academic. Selection of species or areas for conservation can benefit from a broader understanding of species evolution (Brooks and Mclennan 1994). Using the phylogenetic approach creates a more integrated study, with contemporary observations contributing to historical studies in such a way that ecological and genetic predictions can be made from the interpretations of systematic studies (Coddington 1988; Ladiges *et al.* 1989; Wanntorp *et al.* 1990; Baum and Larson 1991; Hodges and Arnold 1994).

THE AREA OF STUDY - THE CAPE FLORISTIC REGION

The high beta and gamma diversity of the Cape Floristic Region (Fig. 1) has made it the subject of several investigations into explanations of high plant diversity (Rourke 1972; Linder 1985a; Manning and Linder 1990; Cowling 1990; Cowling *et al.* 1994; Simmons and Cowling 1996). Although the advantage in using the phylogenetic methodology has been recognised (Midgley 1988; Donoghue 1989; Cowling and Holmes 1992; Johnson 1992; Malusa 1992; Mustart and Cowling 1992; Pearson and Juliano 1993; Hodges and Arnold 1994), there have been only a few studies (e.g. Linder and Vlok 1991; Manning and Linder 1990; Kurzweil *et al.* 1992) which have approached this natural phenomenon from a historical perspective.

Several environmental features are postulated to influence the species richness in the Cape Floristic Region (Linder 1985a; Cowling 1990). While the climate of the area is considered to be mediterranean (Dell *et al.* 1986), with predominantly winter rainfall, these conditions are restricted to the south-western corner of the region (Huntley 1984). Moving north and east there is a shift in rainfall patterns, northwards to a considerable reduction in year round precipitation and eastwards into a summer rainfall regime (Campbell 1983; Huntley 1984). The shift in rainfall patterns to the east is accompanied by an increase in soil nutrients (Campbell 1983). These climatic differences are mirrored in patterns of regional richness which is found to be higher in the south-west than the south-east of the region (Cowling *et al.* 1992). It is, however, possible that the combination of reliable rainfall, physiographic and habitat diversity, and nutrient poor soils, contributes to species richness of the south-west (Deacon 1992). Habitat heterogeneity is thought to be one of the driving forces of evolution, promoting micro-habitat specialists (Linder 1985a).

Fire is a more ephemeral selection pressure in fynbos, with fire intervals being measured in years (Kruger and Bigalke 1984). Nevertheless the regularity of fire events may have influenced the evolutionary direction of certain traits and features (Cowling 1987; Pate *et al.* 1991; Schutte *et al.* 1995). In particular, fire survival habits, such as seeding and resprouting, have become strongly linked with modes of reproduction in plant life histories (Keeley 1986; Schutte *et al.* 1995; Bell and Pate 1993; Bond *et al.* 1992).

Resprouters and seeders are two of five fire survival categories defined by Pate *et al.* (1990). Resprouters, or sprouters, are thought to repeatedly survive fire by resprouting from epicormic buds on lignotubers, root crowns or trunks. Seeders are defined as those species which succumb to fire and recruit in the post-fire environment from canopy or soil-stored seed banks. The terminology of resprouting and seeding is misleading in that resprouters do produce seed, albeit less than seeders, which may recruit in the post fire environment (Hansen *et al.* 1991). Thus, the terminology could be adjusted to resprouters and non-resprouters. For the sake of brevity, however, I am using the convention of resprouters and seeders.

Fire intensity and frequency

There is great variation in the intensity of fynbos fires depending on the season, fuel load and climatic conditions. Slow burns of low intensity are more common, but very intense fires have been recorded where hot windy conditions prevailed in combination with a highly combustible fuel load (Kruger and Bigalke 1984; le Maitre and Midgley 1992). The effects of different fire intensities on seeding and resprouting plants is best understood in terms of the impacts of extreme intensities. It is suggested that high fire intensities kill resprouter adults which may favour the establishment of seeders, usually woody shrubs. In contrast it is thought that low fire intensities would favour resprouters, particularly graminoids or restioids herbs (Kruger and Bigalke 1984).

Fire frequency is usually expressed in number of years, with the most common fire frequency being once every twenty years (Kruger and Bigalke 1984). Low fire frequency has been found to favour an abundance of seeders in comparable environments, while resprouters are generally favoured by shorter fire intervals (le Maitre and Midgley 1992). Unusually short fire intervals may restrict the reproductive output of seeders and resprouters. Seeder species are supposedly dependent on relatively large seed sets for recruitment, limitations in seed set size could favour resprouters which, by definition, are relatively more resistant to fire events. Extended fire intervals may lead to senescence amoungst resprouting adults. This scenario could be of great advantage to seeders as dead resprouter adults may be replaced by seedlings of seeders following the next fire (Keeley 1986; le Maitre and Midgley 1992).

The compounded variables in fire events and lack of experimental data limit the predictions regarding fire as an evolutionary pressure. Although there are no quantitative data available, it is suggested that fire frequency increased with the advent of the summer drought climate in the Miocene (Linder *et al.* 1992; Bruyns and Linder 1991), and more recently through the impact of fire stick farming (Hall 1984; Cowling 1987). An increase in fire frequency may favour the evolution or persistence of the resprouting habit. Increasing the disturbance frequency for seeding species could promote both speciation and extinction (Cowling *et al.* 1992).

The opportunity for speciation and extinction arises from the potential for fire to act as a disruptive force leading to fragmentation of populations in space and time (Cowling 1987; Schutte *et al.* 1995). Given that adults of seeding species are killed by fire and regeneration is from seed, fire events may fragment populations of seeders and prevent interbreeding of cohorts (Schutte *et al.* 1995). In contrast, if resprouting adults survive fire and persist in the landscape, the probability that populations will be disrupted is low and there is the opportunity for gene exchange across age cohorts. Thus, according to present definitions, the resprouter habit appears to be more adaptive in a fire prone environment, but does not promote speciation in resprouting lineages (Cowling *et al.* 1992).

SUITABILITY OF THE STUDY GROUP - *Thamnochortus* Berg.

Thamnochortus is one of nineteen genera of African Restionaceae (Linder 1984). Members of the Restionaceae are found on every continent of the southern hemisphere but only in southern

Africa do they dominate vegetation types to such an extent that they are used in physiognomic descriptions of the landscape (Taylor 1978).

All of the genera belonging to the African Restionaceae are present in the South-western Cape. *Thamnochortus*, with 33 species, is distinguished by being the second most speciose restioid genus in southern Africa and one which has economic importance in the thatching, horticultural and cut-flower industries (Linder 1985b).

The distribution of *Thamnochortus* species lies predominantly within the Cape Floristic Region (Linder 1985b). There are only two species whose distribution extends outside of this area. *T.bachmanii*, a west coast species, has been collected from the Khamiesberg area, and *T.glaber*, a south coast species, specimens are recorded from the Dwessa area in the Eastern Province.

Species within the genus occupy a diverse array of ecological niches and geographical areas. All species are wind-pollinated and dispersed and the genus exhibits none of the specialisations associated with myrmecochory or serotiny. However, two fire survival habits are evident; seeding and resprouting. Observations indicate that the majority of *Thamnochortus* species fall into one of the fire survival habit categories. Evidence from observation, however, indicates that two species, *T.scabridus*, a resprouter, and *T.pulcher*, a seeder, may continually reseed (i.e. recruit between fires). This is not an uncommon phenomenon in the Restionaceae (Linder 1985b).

As a genus of fynbos Restionaceae, *Thamnochortus* represents several key aspects of taxa common to this region. Firstly, it has a large number of species, secondly these species are diverse in terms of geographical distribution and ecological niches and finally the species exhibit two key responses to fire; resprouting and seeding. Thus, *Thamnochortus* is suitable for an investigation into speciation and selection pressures in the Cape Floristic Region.

OBJECTIVES OF STUDY

The following aspects of the evolutionary portfolio of *Thamnochortus* are investigated to locate and study speciation patterns in the genus.

Species complex: The establishment of species limits in the *T.comptonii*, *T.platypteris*, *T.scabridus* species complex of *Thamnochortus* prior to cladistic analysis.

Evolutionary history: The formulation of a hypothesis on the evolution of *Thamnochortus* using phylogenetic techniques.

Comparative Biology: The utilization of the phylogenetic hypotheses to investigate the characteristics of, and evolutionary pressures on fire survival habit, seeding or resprouting as well as interactions with specialization of female outer tepals into wings or keels. Both characters are connected with the life cycles of *Thamnochortus* species.

Biogeography: The determination of present day phytogeographic and endemism patterns to establish areas of similarity and areas of endemism for *Thamnochortus*. The defined areas can then be used in general area cladograms to determine area relationships and develop hypotheses on vicariance and dispersal events.

Ecological differentiation: A description of the degree of niche specialisation in sister species gives an indication of ecological differentiation and ecological patterns of speciation.

METHODS

THE STUDY GROUP

Pillans (1928; 1942; 1945; 1952) recognised 35 species which Linder (1985b) reduced to 28 by placing *T. lewisiae* Pillans, *T. nervosus* Pillans and *T. plumosus* Pillans (1952) in *T. guthrieae* Pillans (1928); *T. comptonii* Pillans (1945) within *T. platypteris* Kunth (1841); by including *T. similis* Pillans, *T. piketbergensis* Pillans and *T. muticus* Pillans (1952) in *T. sporadicus* Pillans (1952); and by combining *T.dichotomous* and *T. papillosus* to form *T. lucens* Poir (Linder). Two additional species were described: *T. arenarius*, *T. rigidus*. Linder (1990) added a further two species, *T. amoena* and *T. karooica*, thus raising the number of species to 33.

The taxonomy of Linder (1985b; 1990) was followed except for a group consisting of *T.bachmanii*, *T. stokoei*, *T. schlechteri*, *T. scabridus* and *T. platypteris* which was investigated phenetically to reassess species limits. *T.comptonii* was separated from *T.platypteris*. Thus, in the cladistic analysis a total of 34 species of *Thamnochortus* was used.

PHENETIC METHODS

Sampling

The west coast species complex consists of *T.bachmanii*, *T.stokoei*, *T.schlechteri*, *T.scabridus* and *T.platypteris*. Eighty-seven of the 96 herbarium specimens, located in the Bolus herbarium, were examined. Specimens were omitted if they were duplicates of a single collection or if the specimens contained only male material - the number of informative specimens per species in indicated in Table 1. Each specimen was treated as a separate entity and no data were averaged. Distribution maps were constructed from locality information on specimen labels.

Table 1. Number of specimens available for each species and the number of representative specimens used in the study.

Species	No. of specimens	No. specimens used
T. bachmanii	29	27
T.platypteris & T.comptonii	18 + 12	18 + 12
T. stokoei	18	17
T. scabridus	10	7
T. schlechteri	9	4

Twenty-five characters were scored, of which sixteen were qualitative and nine were quantitative (Table 2 and 3).

Table 2. Qualitative characters and a description of character states.

Character	States
Culm surface	rugulose or smooth
Culm surface	ridged or smooth
Sterile branches	absent or present
Male inflorescence shape	lorate or elliptic
Female spathes	prominent or decayed/absent
Spikelet number	many or solitary/paired
Female inflorescence shape	v-shaped or elliptic
Female bract colour	cream, tan, red brown
Female bract texture	chartaceous-membranous or coriaceous-cartilaginous
Female bract	homogenous or with hyaline margin
Outer tepal	small wings or large wings
Outer tepal	visible either side of bract or hidden by bract
Outer tepal texture	coriaceous, chartaceous or membranous
Outer tepal margin texture	coriaceous, chartaceous or membranous
Outer tepal apices	distinctly apiculate or not apiculate
Colour of outer tepal	brown, tan or cream

Table 3. Quantitative characters.

Characters
Culm width at base
Culm width at apex
Length of female flower
Ratio of length to breadth of female flower
Length of odd outer tepal
Breadth of odd outer tepal
Ratio of length of odd outer tepal to length of flower
Length of pedicel
Ratio of length of pedicel to length of flower

The patterns of variation were determined using Principle Component Analysis (PCA) and cluster analysis, in NTSYSpc (Rohlf 1993). Ordinations are effective in detecting general patterns in variation while formal taxonomies may be determined using cluster analysis (Sneath and Sokal 1973). PCA ordinations give a spatial representation of relationships between terminal units, with units being placed on axes according to their relative similarities. In contrast, the SAHN clustering methods, such as UPGMA, construct a hierarchical representation of relationships, grouping terminal units according to similarity (Abbott *et al.* 1985).

The assumption of hierarchical structure in the data raises the possibility that unnatural clusters may be created (James and McCulloch 1990). The use of both ordination and cluster analysis serves as partial corroboration of the results (Sneath and Sokal 1973). Furthermore, ordination may elucidate those aspects of relationships which are not fully illustrated, or are complicated, by particular clustering techniques, i.e. non-overlapping or overlapping cluster analyses (Sneath and Sokal 1973).

Principle Component Analysis

PCA has been widely used in systematics (Sneath and Sokal 1973; Abbott *et al.* 1985; James and McCulloch 1990; Chang and Giannasi 1991). In PCA analysis variables are summarised into representative components which define a particular space (Abbott *et al.* 1985). The taxa or terminal units are then arranged within this space, relative to the component axes, according to similarity (Sneath and Sokal 1973).

A correlation matrix (CORR) is constructed from the character standardised matrix (Sneath and Sokal 1973). Eigenvectors and eigenvalues were then calculated using the EIGEN function. Eigenvectors are the weightings of each variable on each component while eigenvalues are used to calculate the extent to which each component accounts for the total multiple variance (Abbot *et al.* 1985). Ordination coordinates were calculated using the eigenvectors and the final results presented as a scatterplot.

Caution should be exercised in the interpretation of PCA results as the original variables in PCA are usually less independent of one another than the representative components (Abbott *et al.* 1985). Thus, the distance between points in the defined space should not be considered as a direct reflection of the spatial separation of the original variables. Furthermore, there is a debate concerning the criteria for determining which axes are taxonomically meaningful (Sneath and Sokal 1973).

Cluster Analysis

Grouping of the specimens was achieved using the principles of the sequential, agglomerative, hierarchic, non overlapping clustering methods (SAHN) (Sneath and Sokal 1973). The properties of the techniques employed in this group of methods provide several advantages in practical situations.

Firstly, employing a sequential clustering procedure is more likely to lead to optimal clusterings according to predefined criteria (Sneath and Sokal 1973). Secondly, the agglomerative algorithm, which begins with separate entities and groups them according to similarity (Sneath and Sokal 1973), is more suitable than a divisive algorithm in studies, such as *Thamnochortus*, where there are a large number of shared character states and no one condition is required to allow admittance to a group (Abbott *et al.* 1985).

Finally, consideration should be given to the relative advantages of overlapping and non-overlapping techniques. Non-overlapping techniques (in conjunction with hierarchic classification) may distort phenetic relationships, but the results are easier to interpret and understand than those arising from overlapping techniques (Sneath and Sokal 1973).

The SAHN clustering strategy UPGMA (unweighted pair group method using arithmetic averages; Sokal and Sneath 1973), was used in this study. The method has also become known as the Group-Average cluster analysis (Abbott *et al.* 1985). For the purposes of this study, however, it will be referred to as UPGMA.

The data matrix was submitted to NTSYS (Rohlf 1993) and standardised by character (STAND). The similarities between the OTU's (operational taxonomic units) were calculated using distance analysis (in SIMINT using average taxonomic distance DIST). The distance measures between pairs are tabulated and provide an appraisal of the relationship between pairs of OTU's (Abbott *et al.* 1985). This method is appropriate where characters are both discrete and continuous (Rohlf 1993). In UPGMA the grouping algorithm then evaluates the average similarity, or dissimilarity, of each OTU to an existing cluster (Sokal and Sneath 1973), grouping those OTU's which are most alike first.

UPGMA, or group average cluster analysis, is the most commonly used clustering analysis in both ecology and systematics (James and McCulloch 1990; Abbott *et al.* 1985; Sneath and Sokal 1973). In many cases it is chosen as it contains more intermediate attributes lacking in other more extreme methods, such as single-linkage or central point grouping; however, it has been rejected for the same reasons (Abbott *et al.* 1985).

CLADISTIC METHODS

Outgroups

Three species belonging to the genus *Rhodocoma* Nees. were used as an outgroup to the genus *Thamnochortus*. *Rhodocoma* is the sister-group to *Thamnochortus* (Linder 1984) linked to it by the following apomorphies: scattered cavities in the central ground tissue, similarities in pollen structure, epidermal cells with thickened anticlinal walls and simple culms with pendulous male spikelets.

The genus *Rhodocoma* consists of six species with disparate growth forms (Linder and Vlok 1991). *R. fruticosus* was selected on the basis of its wide distribution pattern, while *R. gigantea* and *R. arida* were chosen as representatives of markedly different habit types and morphologies.

Sampling

Morphological and anatomical data were collected primarily from herbarium specimens housed in the Bolus Herbarium and supplemented by field observations. An initial sample of two to three specimens per species was used to identify suitable morphological characters. Representative specimens with portions of both male and female plants were selected. These specimens were chosen to reflect the extremes of the morphological and geographical variation within each species. All detailed data collection (both morphological and anatomical) was made from these specimens. Subsequently the consistency of the morphological characters and the character states was confirmed by inspecting the characters on all the material available for each of the 34 species, excluding those specimens considered to be oddities (Stevens 1991). Table 4 lists the number of herbarium specimens consulted for each species.

Cutler (1969) documented anatomical variation in the Restionaceae, with most variation being evident in transverse culm sections. Sections were cut from the base of the culm of the two specimens initially selected as representative. A 1-2cm portion of the culm was taken from a near basal internode of the dried specimens, rehydrated and softened in boiling water for 10 minutes. The boiled culm was then clamped in cork and cut with a sledge microtome. The culm was sectioned at 25 micrometers except for a few species which were sectioned at 30 micrometers. The sections were stained in a Safranin-Alcian blue stain for approximately 20 minutes, rinsed and dehydrated using an alcohol sequence, soaked in xylene and then DPX for approximately 20 minutes before being mounted in DPX on a slide. Sections were examined using a Zeiss microscope and all variable features recorded. These features are identified and described in Appendix 1.

Morphometric data included the basal culm diameter, internode length, plant height, epidermal cell width, number of parenchyma and sclerenchyma rows and aspects of female and male floral morphology. Measurements of culm diameter were made in the middle of the most basal culm internode using callipers accurate to 0.02mm. In the few cases where the basal parts of the plant were not available, the internode furthest from the inflorescence was measured. Internode length, on the second internode below the inflorescence, was measured in millimetres with a ruler. Two measurements were taken from each of three different specimens for each species.

Table 4: The number of herbarium specimens examined to confirm morphological characters and character states.

Species	Number of specimens
T. acuminatus	10
T. amoena	2
T. arenarius	27
T. bachmanii	29
T. cinereus	40
T. comptonii	12
T. dumosus	17
T. ellipticus	4
T. erectus	38
T. fraternus	19
T. fruticosus	28
T. glaber	13
T. gracilis	27
T. guthrieae	23
T. insignis	27
T. karooica	9
T. levynsieae	9
T. lucens	46
T. muirii	8
T. nutans	5
T. obtusus	36
T. paniculatus	9
T. papyraceus	7
T. pellucidus	11
T. platypteris	18
T. pluristachyus	8
T. pulcher	13
T. punctatus	23
T. rigidus	18
T. scabridus	10
T. schlechteri	9
T. spicigerus	13
T. sporadicus	50
T. stokoei	18

Height measurements were based on field observations, published descriptions and data from herbarium specimen labels.

The cells of the epidermis were measured at 40x magnification using an eyepiece micrometer. Counts were made of the number of rows of parenchyma and sclerenchyma in each species. There were two replicate specimens for each species, two sections of each replicate were examined and three counts in each section were made.

For detailed male and female floral morphology, three specimens per species were rehydrated, dissected and drawn at x12 magnification using a Zeiss microscope. Length and breadth measurements of the inflorescence, spikelet, bract and flower were made in millimetres using a ruler. Measurements of the fruit were made with callipers accurate to 0.02mm. At least three replicate observations were made for each feature on each specimen, but additional measurements were made to corroborate data if there was great variation. Ranges recorded in the published descriptions were incorporated into analyses of the floral morphometric data.

Character delimitation

Twelve quantitative and 47 qualitative characters were investigated. The final data matrix consisted of 10 quantitative and 43 qualitative characters. There are both non-additive and additive multistate characters and binary characters.

In the definition of characters and character coding the arguments of Pimentel and Riggins (1987) and Thiele (1993) were considered. Pimentel and Riggins (1987) regard the features of organisms to be cladistic data. Characters are those features that have two or more mutually exclusive and ordered, homologous states between the organisms. Thiele (1993) considers the features of organisms as attributes. Within a taxon the state of a particular attribute may vary. The state of the taxon is determined by the frequency distribution of the attribute's states within the taxon. Thus, according to Thiele (1993), cladistic characters are the frequency distribution of values of attribute states scored over a sample of individuals of a taxon. When the cladistic character changes the frequency changes. The importance of Thiele's (1993) extended definition is more evident with the delimitation of character states, particularly in quantitative data.

Qualitative characters

Due to the nature and extent of variation of features within and between taxa, one of the most important considerations is the manner in which the features are defined as characters. Redundant repetition of characters defining an aspect may present ambiguous information. The example given by Pimentel and Riggins (1987) describes the situation of red and blue petals. If the feature of colour is considered as two separate characters, pink petals and blue petals, with the character states defined as presence and absence, the definition of `absent' is not clear implying both loss and the existence of the other colour. Thus, to avoid loss of information and poor resolution of the cladogram, absence should only be used as a character state description in the context of loss. Resolution may also be impaired if many different aspects of a feature are lumped into a few states. To circumvent these problems Pimentel and Riggins (1987) advocate the use of multistate characters with careful consideration of the effects of non-additive and additive coding. Additive coding is considered to be preferable as it preserves the form and direction of the character state trees.

While the above arguments were considered in the selection and definition of the characters describing the species within the genus *Thamnochortus*, the predominant criterion was to delimit characters and states in the most direct and accurate manner possible, while still accounting for the observed variation. Towards this end it was not always possible to avoid indirectly coding a feature, which might be construed as a single character, twice. Similarly, the question of character being additive or non-additive was not always simple to resolve. Each character was considered on a case by case basis and if sufficient evidence indicated that a particular sequence was additive, the character was coded as such in the analysis (Appendix 1).

In determining the additive and non-additive nature of the characters, the assessment of character descriptions and the delimitation of character state delineation, the principles of character state trees (Mickevich 1982) and transformation series analysis (Pogue and Mickevich 1990; Mickevich and Weller 1990) were used.

Character state delineation

The primary character matrix of *Thamnochortus*, with characters described by synthetic character states (Pogue and Mickevich 1990), was analysed using Hennig86 cladistic analysis (Farris 1983). The nature of synthetic character states is such that highly variable features are described by a few character states. In the Cochylini, Pogue and Mickevich (1990) found that this method of lumping variation produced unsatisfactory results. Examination of the character distribution on the cladogram pinpointed the characters where variation was obscured. The variation was generally misrepresented in two ways, either by character descriptions which combined several conditions into a single state, or through the combination of independent characters into one (Pogue and Mickevich 1990). Reassessment of the synthetic characters led to the delineation of a set of reflective characters. Reflective characters circumscribe the observed variance, and are usually multistate.

Each character was assessed in the context of non-additive or additive coding (Mickevich and Weller 1990). The descriptions of characters, the logic of the delimitation of the states and the nature of the evolutionary sequence of the characters are discussed in detail for each character in Appendix 1.

Quantitative characters

Controversy surrounds the use of quantitative characters in cladistic analysis (Almeida and Bisby 1984; Archie 1985; Pimentel and Riggins 1987; Cranston and Humphries 1988; Baum 1988; Chappill 1989; Farris 1990; Stevens 1991; Thiele 1993). Criticisms are predominantly concerned with the continuous nature of the data, particularly the application of homology tests and statistical analyses to quantitative data, and the interpretation of results (Almeida and Bisby 1984; Archie 1985; Cranston and Humphries 1988; Pimentel and Riggins 1987; Thiele 1993).

According to Pimentel and Riggins (1987) measurements do not represent a whole feature, merely dimensions of a feature. Thus, measurements are indirect representations of a feature and do not comply with the criteria set for homology tests. The restrictions on homology are compounded by the continuous nature of morphometric data (Cranston and Humphries 1988). The limitations on sampling and relevance of statistical methods used in the transformation of morphometric data are questioned and the manipulation of data is considered to amount to data massaging (Stevens 1991).

These criticisms are countered with an evaluation of loss of information versus preconceptions surrounding the quality of cladistic data (Chappill 1989; Thiele 1993). Chappill (1989) contends that the results of the similarity tests for any particular character are only hypotheses that must be corroborated by examining the congruence with any other character. The limitations and dangers of statistics are acknowledged, but the likelihood that all variation is not represented is not seen as a reason for excluding data. Furthermore, while it is recognised that distortion occurs in the translation of continuous data to discrete states it is argued that this cannot outweigh the opportunity to include additional information in the analysis.

Despite the differences in opinion (Chappill 1989; Pimentel and Riggins 1987; Thiele 1993) there are similarities in the conclusion; quantitative characters should only be used when the choice is between examining them or abandoning the analysis. There is specific reference to such cases where morphology alone is unable to resolve a phylogeny due to high levels of homoplasy or lack of significant morphological variation. Recent evidence in favour of incorporating continuous characters show that these characters contribute to the resolution of clades, which were not resolved by discrete qualitative characters, without contradicting the topology established using only the qualitative characters (Malusa 1992). This scenario could certainly describe the situation in *Thamnochortus* where prior to the inclusion of quantitative characters, the cladogram lacked resolution due to homoplasy.

The controversy in the literature concerning inclusion of morphometric data indicates caution should be exercised in selection of characters, the sample size and methods used to code the characters (Pimentel and Riggins 1987; Chappill 1989; Stevens 1991; Thiele 1993). The morphometric data for *Thamnochortus* consisted of ranges, gleaned from descriptions, and measurements which were designed to incorporate as much of the morphological and biogeographical diversity in a limited sample size following the admonition of Chappill (1989). As these are range data, methods requiring statistical data could not be used, and so the methods outlined by Almeida and Bisby (1984) and Baum (1988) were used. The absence of statistical manipulation of data overcomes one of the major objections of Pimentel and Riggins (1987) concerning the manipulation of raw data into sample statistics (Chappill 1989), for example, as required by Archie (1985). To complement these methods and ensure that the observed groupings were not solely a function of the chosen technique, a method suggested by Stevens (1991) was also implemented.

The methods of Baum (1988) and Almeida and Bisby (1984) are similar in the manner in which the data are initially ordered. Baum (1988) orders the ranges first by the minimum then the median or the mean. Almeida and Bisby (1984) orders the data by the median alone. Chappill (1989) considers that the method of Almeida and Bisby (1984) to be more suitable than that of Baum (1988) where the taxa are ranked according to minimum values alone. This may result in taxa being miscoded as different when the means are the same or vice versa. However, this preference is unfounded as Almeida and Bisby (1984) proposes that the median be used to order the ranges while Baum (1988) specifically states that both the minimum value and the mean or median should be used when ordering the ranges. For a similar reason Thiele's (1993) criticism of Baum (1988) is also unjustified. Thiele (1993) states that Baum (1988) utilizes only part of the data contained within a quantitative character, e.g. the mean. In the study of *Thamnochortus* the range data were ordered first by the minimum value and then by the median (Baum 1988). It was not possible to use an average as in most cases the data consisted of the range, from descriptions, and three measurements.

Once the ranges are ordered, Baum (1988) assigns codes; ranges with the same minimum and maximum value receive the same coding. However, in *Thamnochortus* the variation ranges is complex and applying this method would result in many meaningless states being formed. For this reason the logic of Almeida and Bisby (1984) was employed to define the states; the ranges are presented graphically, and boundaries are placed at the gaps or dips present in the diagram.

The method of Thiele (1993) is designed to incorporate elements of the original data in cladistic analysis. However, the procedure of the gap-weighting method results in a multistate character where the gaps between the states have been weighted in relation to the differences in the raw data. Considering the nature of the data and the number of taxa involved, Thiele's (1993) method was deemed inappropriate as it showed the potential to generate an extreme number of states, leading to uninformative multistate characters. Arguably Thiele's (1993) method could be seen to include too much information, possibly more than can be found in the data. Heeding the caution of Pimentel and Riggins (1985) against data massaging adds strength to the argument against using the method of Thiele (1993).

Using the procedure of Almeida and Bisby (1984) to code the data ensures that real groups are identified. Archie (1985) and Chappill (1989) both comment that the simple gap-coding method recognition of gaps is a function of sampling and codes may be affected if more taxa are added. Chappill (1989) considers that this criticism can be extended to the generalized gap coding method of Archie (1985). Farris (1990) concurs with this assessment and adds that the segment coding advocated by Chappill (1989) may have the same effect, assigning different coded states to samples that do not differ significantly.

The method of Almeida and Bisby (1984) defines groups according to the gaps or intervals that are evident in the graphs. In *Thamnochortus*, while gaps are preferable in defining character states, the reality is that intervals, i.e. points of reduced overlap in ranges, are more common. A method of quantifying the observation was established in order to ensure that intervals were defined according to similar criteria. Counts were made of the number of ranges crossing the observed intervals and the number of ranges abutting onto the interval. Ratio's of these counts were compared for all the intervals observed. Generally, a difference of a three or more between the counts was considered suitable.

The morphometric data, including those which had already had states determined, were analyzed as suggested by Stevens (1991) to determine the best possible state definitions. The range data for each character were plotted onto a cladogram that had been generated prior to the inclusion of the morphometric data. This related the measurements and ranges to hypothesised groupings, identifying states which may have been overlooked in the original morphometric analysis. In conjunction with the method described above, Stevens' (1991) technique identified and confirmed the best possible breaks to define character states for the morphometric characters (Appendix 1).

Cladistic Analysis

Four multistate characters are polymorphic. There is no facility in Hennig86 (Farris 1983) for cells in the matrix to be polymorphic, so these cells have to be scored according to the predominating state or as unknown for that character. Pimentel and Riggins (1987) strongly advocate against coding a species with variable states as either one or other of the states. Coding species as unknown for certain characters only detracted from the resolution of the tree. Another option described by Pimentel and Riggins (1987), is the division of the terminal unit into two, but this would also increase the number of terminals, resulting in a matrix too large to analyse efficiently.

PAUP allows polymorphic codings (Swofford 1993) and was thus used. Characters are described in detail in Appendix 1. Due to the large data matrix (Appendix 2) the simple addition sequence (Farris 1990) of the heuristic procedure in PAUP was used to construct a single initial tree. This was analyzed using the tree bisection-reconnection branch (TBR) swapping routine to locate shorter or more trees of equal length. Only those trees of minimal length were stored.

Testing cladogram

Bootstrap analysis

A bootstrap analysis was performed to determine comparative support within the data set for the nodes retrieved by the parsimony analysis (Felsenstein 1985a; Sanderson 1989; Linder 1991; Hillis and Bull 1993; Sanderson 1995). As a result of the resampling technique employed by this analysis, characters may be represented several times or omitted from any of the new data sets which are created. The new data sets are analyzed to obtain an estimate of the phylogeny, and to determine the frequency with which each node was retrieved (Felsenstein 1985a).

It is assumed that poor bootstrap support in the cladogram is directly related to homoplasious characters (Sober 1988). However, confidence in the bootstrap analysis as a statistical test of a cladogram is decreasing (Hillis and Bull 1993; Kluge and Wolf 1993; Sanderson 1995) and several aspects of the bootstrap analysis are questioned, such as the random nature of the selection process, the inherent by untestable assumptions made about evolution and process and the discarding of information in the random selection process (Sanderson 1995). In addition to the general mistrust of basic assumptions of bootstrap analysis, there are particular assumptions which would not favour a situation where characters are inherently homoplasious. These assumptions, such as random replication and omission, where characters are omitted and other, possibly weaker characters are inserted, may underestimate the robustness of the cladogram providing a conservative measure of accuracy (Hillis and Bull 1993; Sanderson 1995). Alternatively, bootstraps may provide overestimates of confidence (Hillis and Bull 1993), if the rates of change are highly unequal and are high enough to randomize characters with respect to history, or there is a systematic bias.

Allowing for the limitations on the interpretation of bootstrap percentiles, the technique may still indicate a degree of confidence through the relative ranking of degree of support for each of the recovered clades (Sanderson 1989; Hillis and Bull 1993), thus providing a reference point for comparison of clade stability.

Deletion of difficult taxa

The possibility that *T.insignis*, *T.bachmanii* and *T.punctatus* may cause instability in the tree was investigated by reiterative deletion and reinsertion of *T.insignis*, *T.bachmanii* and *T.punctatus* and combinations of these species, followed by cladistic analyses of the adjusted matrices.

COMPARATIVE BIOLOGY AND EVOLUTION

Sampling

Flowering time, height, and fire survival strategy was obtained from herbarium label notes and from field observations of 28 of the 34 species.

The maximum and minimum number of flowers per culm was calculated for each species by multiplying the maximum number of spikelets with the maximum number of flowers per spikelet for each species and the minimum number of spikelets with the minimum number of flowers per spikelet. This represented the maximum and minimum reproductive output of the each species. The variation in flower and spikelet number varies from species to species. Large numbers of flowers per culm is not always due to many flowers per spikelet, species such as *T.erectus* have fewer flowers per spikelet but many spikelets. To place the maximum and minimum values in a biological context the range of flower and spikelet number is given.

The size of distribution area was taken as the number of quarter degree grid squares occupied by a species, based on distribution data from herbarium material in the Bolus Herbarium.

Resprouters in *Thamnochortus* lack the obvious epicormic buds (le Maitre and Midgley 1992) or specific rhizome morphology (Pate *et al.* 1991), which are commonly used to distinguish resprouters from seeders in other taxa. To determine the fire survival strategy it is necessary to observe the plants in a post-fire environment. One strategy of determining fire survival habit is to label plants in a specific population and then burn the area. This has the disadvantage that the burn is enforced and may differ in characteristics from a natural burn (Kruger and Bigalke 1984). To determine fire survival habit in *Thamnochortus* field excursions were made to populations which had been recently burnt, i.e. within the previous two to five years. In many cases only part of the population had been burnt and it was possible to determine whether seeding or resprouting was the predominant fire survival habit by observing burnt tussocks, and any regeneration, and the numbers of seedlings present (Pate *et al.* 1991; Hansen *et al.* 1991; Schutte *et al.* 1995). Additional information on resprouting species came from herbarium collections where burnt culms were present on the specimens (Kornas 1978; Medwecka-Kornas and Kornas 1985).

Non-phylogenetic and phylogenetic methods

Non-phylogenetic analyses

Non-phylogenetic studies of evolution and adaptation usually involve pair-wise comparisons which tend to treat individual taxa as separate data points (Felsenstein 1985b; Peat and Fitter 1994) failing to acknowledge the number of times a trait evolved or the process of character transformation (Donoghue 1989). The pair-wise comparative method of Moller and Birkhead (1992) claims to overcome the problem of taxa being treated independently, offering an alternative to the use of poorly resolved phylogenies and the possibility of errors through parsimony reconstruction. However, in Moller and Birkhead's (1992) pair-wise comparative method species are either selected randomly, ignoring the possibility of important phylogenetic relationships, or are chosen according to the availability of data and the existence of appropriate variation in the taxa for those characters being considered. No indication is given as to how the relationships between species and or populations are determined. Even a poor phylogeny offers the framework for comparative studies that has the semblance of objectivity, can be retested and is potentially falsifiable (Coddington 1988). Thus, the non-phylogenetic method merely circumvents the issues in question, introducing new constraints that are directly linked to the subjective selection of the initial subjects of study. The outlines given guiding the choice of the closely related pairs or populations are such that the interpretation of results would be subject to the same cautions and constraints as those based on a poor phylogeny.

A minor investigation into the discrepancy in results of non-phylogenetic and phylogenetic studies was conducted using the *Thamnochortus* data. Prior to the phylogenetic comparative analyses, comparisons in height, seed number and size of distribution area were conducted for seeding and resprouting species groups of *Thamnochortus*. The size of distribution area of those species with winged female outer tepals was compared to those which had keeled female outer tepals. A Mann-Whitney U test was used. The possibility of co-dependence in the evolution of seeding and resprouting habits and winged and keeled female outer tepals was investigated by comparing numbers of seeding species with wings, the number with keels and the number of resprouting species with wings and the number with keels. A Chi-squared contingency table was used to statistically determine the relationships between the permutations.

Phylogenetic analyses

In comparative analyses scenarios are too complex to consider each species as an independent data point. There is an integration of known and unknown biological and phylogenetic variables which place different constraints upon groups of related taxa (Moller and Birkhead 1992; Brooks and Mclennan 1994). Evidence that pattern can easily be obscured by combining taxa comes from many sources (Harvey *et al.* 1995). The phylogenetic approach provides a framework in which the sequence of character evolution can be traced and the processes of speciation investigated (Roos 1987; Brooks and Mclennan 1994). Thus, the relationship of the species can be examined and the relative dependence and independence determined.

Ignoring the phylogenetic links between species can result in grave statistical errors (Felsenstein 1985b), and the assumption of independence constrains the evolutionary pattern to one of explosive radiation. The aphyletic approach fails to provide a realistic estimate of the number of times a trait has evolved, and cannot determine the direction of evolution and the order in which the characters were assembled in the lineage (Donoghue 1989). The introduction of cladograms into comparative studies not only overcomes such problems, but can lead to hypotheses that can be tested experimentally and provide framework for several different aspects of comparative study such as the rates and direction of evolution or possible limitations in variation, design or function (Losos and Miles 1994; Brooks and Mclennan 1994).

Evolutionary analysis of adaptation has been divided into the homology approach and the covergent (homoplasy) approach (Pagel 1994; Coddington 1994). The homology approach concentrates study on a single evolutionary event in a particular clade or lineage. The derived feature is compared to the ancestral state, especially with regard to function, to determine the factors which may have resulted in the evolution of the feature (Pagel 1994). The convergence approach is more general examining the repeated evolution of analogous traits in several independent lineages to locate evolutionary pattern (Pagel 1994; Coddington 1994). In the comparative biology of *Thamnochortus* the convergent approach was used.

Convergent methods employ correlations to determine the relationship between multiple and independent evolutionary events (Coddington 1994). There are several methods which use phylogeny to overcome the problem of statistical independence of characters (Felsenstein 1985b; Faith 1989; Maddison 1990; Baum and Larson 1991; Harvey and Pagel 1991; Frumhoff and Kern Reeve 1992). Each method addresses slightly different problems. In the case of *Thamnochortus* both non-directional and directional techniques were employed. The term non-directional refers to those comparisons which are between lineages, assessing the either current utility, the number of times a feature evolved, or, as in this case, the relationship between characters and other variables (Harvey and Pagel 1991). The methods of Felsenstein (1985b) and Faith (1989) fall into the category of non-directional techniques. The method of Felsenstein (1985b) compares variables between sister lineages circumscribed in the cladistic analysis. Faith (1989) considers that homoplasy may reduce the explanatory power of cladograms and suggests that multivariate analysis be used to investigate convergence in characters as a manner of revealing, and or defining an adaptational pattern e.g. convergence in morphological structures defining a particular habitat.

Directional techniques are those which trace character change down a lineage, inferring direction and rates of evolutionary change. This technique is useful in studies of adaptation and the discovery of parallel and evolutionary change (Maddison 1990; Baum and Larson 1991; Harvey and Pagel 1991).

The first procedure, non-directional, based on the precepts of Felsenstein (1985b) was used to test the following hypotheses:

1. seeders would be taller than resprouters
2. seeders would have more seed than resprouters
3. seeders would have a smaller distribution area than resprouters.
4. species with winged seeds would have a larger distribution area, independent of the fire survival habit.

The second type of analysis (Maddison 1990; Baum and Larson 1991) is more directional, comparing the presence and absence of two characters and tracing their development down the lineages. This analysis was performed to investigate the relationship between the two fire survival strategies and the presence of a wing or a keel.

In MacClade characters were mapped onto one of the fundamental trees to investigate possible links between speciation and adaptations (Felsenstein 1985b; Maddison 1990). The presence of polytomies prevented the use of the consensus tree. The characters plotted were fire survival strategy and female side tepal winged or keeled. The PAUP cladogram was used as the basis for the comparative analyses. In optimising character state transformation, the default setting in MacClade was used. The default assesses each character employing both ACCTRAN and DELTRAN optimisation. If the state of a branch is ambiguous for a character in either or both of the optimisations it is considered ambiguous. If a branch is unambiguous it is unambiguous for both optimisations.

Non-directional evolutionary analyses

The sister lineages of seeding and resprouting species were located on the consensus tree. The use of sister lineages ensures that each comparison is independent (Felsenstein 1985b; Harvey and Pagel 1991). Variables are then compared between sister lineages. The number of species in each seeding and resprouting lineage were counted and compared. In the case of the height measurements and flower counts, where the sister lineage consisted of more than one species the values of the terminal two species were averaged to their common node. This value was then averaged with the next species and so on until the basal node of the lineage was reached. The final value was then compared to that of the corresponding value in the sister lineage. This method varied from that of Felsenstein (1985b) only in that the values calculated for the ancestral nodes were not weighted by the variance in the data.

The area occupied by sister lineages was calculated in a slightly different manner. Where there was a single species of seeder and resprouter in the sister lineages, a straightforward comparison of data was possible. However, in the cases where there was more than one species in one or both of the sister lineages, the total area covered by the respective lineages was calculated prior to comparison with the sister lineage. For example, if there were four species in one lineage and one in the other, the combined area covered for the four species was computed and compared with the area covered by the single species in the other lineage. Those grid squares where more than one of the species occurred were only counted once.

The size of the area occupied by winged or keeled lineages was assessed using the same method to evaluate the differences in the biogeographic distribution of seeding and resprouting lineages. The presence of a wing or keel was mapped onto a cladogram and the total area for each lineage calculated. In this manner the dispersal advantage a wing may confer, independent of fire survival habit, was determined.

To statistically test the possible differences between seeder and resprouter lineages and winged and keeled lineages for the different variables, the data for the six sister lineages were compared using Wilcoxon paired T-test.

Directional evolutionary analysis

The possibility of evolutionary constraints in the relationship between fire survival habit and the presence of wing or keel on the female outer tepal was investigated using Maddison's (1990) method of correlated evolution. This method examines the probability that changes in one (dependent) character might be concentrated on certain branches, where the other (independent) character has a specific state, to greater degree than may be expected under the null hypothesis. The null hypothesis assumes that changes are distributed randomly on the cladogram.

Maddison's (1990) method operates through two algorithms. The first makes two counts; firstly the number of ways in which the total number of gains and losses in the dependent character can occur over the whole tree, and secondly the number of ways that the observed number gains and losses of the dependent character, found within the specified state (branches) of the independent character, can occur within the specified state of the independent character. Using these two figures the second algorithm then determines the probability of the observed number of gains and losses of the dependent character occurring within the specified state (branches) of the independent character, given the total number of gains and losses of the dependent character over the whole tree.

If data sets are too large for exact calculations, it is possible to conduct a simulation. The simulation algorithm generates changes randomly within the clade selected and the number of gains and losses in the specified state (branches) and in the clade are counted as a whole. Only those gains and losses that fit the observed total number of gains and losses are examined to see where the gains and losses are distributed (Maddison and Maddison 1992).

Optimisation of female side tepals winged or keeled and evolution of fire survival habits results in equivocal coding for some branches. As an exact count of the number of gains and losses of wings and keels respectively is required all permutations must be considered. Similarly, it is necessary to perform the correlated change test for each permutation on the cladogram displaying fire habit evolution, i.e. equivocal branch with the seeding habit and then equivocal branch with the resprouting habit. In total there are four permutations for which a probability must be calculated:

1. Winged state/Seeding state
2. Winged state/Resprouting state

3. Keeled state/Seeding state
4. Keeled state/Resprouting state

Only fully resolved cladograms can be used; thus where there is more than one fundamental tree, all should be used.

Edaphic specificity in seeders and resprouters

The relationship between fire survival habit and soil type was assessed using three substrate categories, Table Mountain Group sandstone, coastal sands and limestone. The total number of species found on each substrate was calculated. The proportion of seeding and resprouting species for each category was determined.

The different substrates of each sister seeding and resprouting lineage were compared.

ECOLOGICAL ANALYSIS

Habitat specificity

The categories of rarity of Rabinowitz *et al.* (1986) were used to determine habitat specificity amoung species of *Thamnochortus*. Eight categories are created on the basis of geographic range (wide or small), habitat specificity (broad or restricted) and population size (big and small). Species are assessed in terms of its biogeographical distribution, the altitudinal and rainfall range which it covered, the number of individuals which may be expected in any one population and assigned to one of the eight. These data are obtained from herbarium specimen sheets, descriptions and field observations, respectively.

The criteria of Schutte *et al.* (1995) were used to allocate species to categories. Species were considered widespread if the distribution area was greater than 200km, habitat specificity was determined by an altitudinal range smaller than 500mm and rainfall difference over the distribution range less than 500m. Additional information on habitat soil texture, from herbarium sheets and observations, indicated that different species were associated with particular soil conditions. If more than 50 individuals had been observed in a population, the species was considered common in the area.

Ecological PCA analyses

Groups of species with similar habitat requirements were located using the PCA ordination procedure in NTSYS (as above). The data matrix contained a range of ecological characters: altitude, rainfall and soil type.

Rainfall values were interpolated from isohyets on 1:50 000 summer and winter rainfall maps, compiled by the weather bureau, Pretoria. The data matrix was constructed with species being coded for the following characters: total rainfall, proportion of winter rainfall, minimum altitude and maximum altitude, soil type (simplified to limestone or sandstone), drainage pattern (habitat wet, applying to those plants which experience seasonally wet conditions possibly in or next to marshy ground, or dry).

Ecological profiles

A table of ecological profiles for each species was constructed. Altitude classes were created and each species was assigned according to the upper limit of the altitudinal range. Other parameters were soil type, texture and drainage.

BIOGEOGRAPHICAL ANALYSIS

Distribution maps were drawn for each species and were based on herbarium specimen locality data.

A species by quarter degree grid matrix was created containing the presence/absence data for each species. This matrix was then used to document variation in species richness and locate areas of endemism and similarity.

Grid diversity

The number of species per 1/4° grid square is an index of grid diversity (Pearson and Juliano 1993) and when plotted on a map of the southern Cape region graphically illustrates areas rich in species of *Thamnochortus*.

Areas of endemism

Areas of similarity

Areas with similar species composition were located by calculating the Jacard similarity coefficient for grid squares (Pielou 1979), as implemented in NTSYS (Rohlf 1993), and clustering them using the UPGMA algorithm. The species by area matrix was simplified by removing all grids with a single species as these show either 0% or 100% similarity, thus accentuating errors and distorting results. The phenon line was drawn to cut off six groups. The areas defined by the groupings of grid squares were delineated on a map.

Parsimony method

Areas of endemism were located using the parsimony method of Morrone (1994). The matrix was transformed into Hennig86 format with grid squares as taxa and the species as characters. The size of the matrix prohibited an efficient branch-breaker search. Consequently a strategy of `long-thin' searches was employed, using Clados (Nixon 1992) to generate 100 random entry sequences into Hennig86. Each sequence was searched with "h", and the shortest tree found entered into "bb*". The strict consensus tree of the resulting trees was calculated using the `nelsen' option and stored.

The procedure was repeated until the topology of the consensus tree found each time remained the same. Repeated use of the consensus trees is intended to locate the most robust groups and reduce the influence of widespread species (Morrone 1994). The consensus trees stored after each run of the procedure were combined in a single file. The final consensus tree was calculated from this combined tree file. Groupings of grid squares are defined by unique combinations of species associations or by species specific to those grid squares. Groups of quadrats which have at least two species unique to them are regarded as areas of endemism, and distribution boundaries of the endemic species are mapped to delineate the boundaries of each area (Morrone and Crisci 1995).

Concentric ring method

Species with a distribution area covering ten grid squares or less were selected for mapping, beginning with those covering the smallest number of grid squares. This group represented those species with restricted distributions (Table 5).

Table 5. Species selected as having restricted distributions and the number of grid squares they cover.

Species name	No. of grid squares
T.ellipticus	1
T.papyraceus	1
T.nutans	1
T.levynsieae	2
T.amoena	2
T.schlechteri	4
T.comptonii	4
T.scabridus	5
T.stokoei	5
T.pellucidus	5
T.arenarius	6
T.punctatus	6
T.dumosus	6
T.acuminatus	6
T.karooica	7
T.pulcher	8
T.spicigerus	9
T.pluristachyus	9
T.paniculatus	10
T.insignis	10

Species with similar geographic distribution patterns

Groups of species with similar distribution areas were located by using the grids as characters and the species as items (de Jong 1987). The Jacard coefficient for each species was calculated (NTSYS; Rohlf 1993)and clustered using the UPGMA algorithm. The geographical groups highlighted by the species groupings were compared to those found in the area of similarity analysis.

Area cladograms

General area cladograms were determined for areas of similarity and areas of endemism (located with the concentric ring method) using paralogy-free sub-trees which were combined in a three-area analysis (Nelson and Platnick 1991; Nelson and Ladiges 1991a; Ladiges *et al.* 1992; Nelson and Ladiges 1996; Morrone and Carpenter 1994). The general area cladogram for areas of similarity should give the phylogenetic relationships between the broad geographic areas defined by *Thamnochortus*. More detailed relationships should be indicated in the general area cladograms of narrow areas of endemism defined by the concentric ring method.

The procedure to determine area cladograms for areas of similarity and narrow areas of endemism is the same. Taxon-area cladograms were constructed using the topology of the *Thamnochortus* cladogram with areas of similarity and narrow areas of endemism as biogeographic units in the respective analyses. All possible paralogy-free sub trees (Nelson and Ladiges 1996) were determined for each terminal clade, i.e. *T.dumosus* clade, *T.rigidus* clade, *T.stokoei* clade, *T.sporadicus* clade, *T.pellucidus* clade, *T.erectus* clade and *T.pluristachyus* clade.

In resolving the paralogy free sub-trees assumption 2 (Nelsen and Platnick 1981) was applied. Unlike assumption 0 and 1, assumption 2 allows for dispersal and extinction in the case of widespread taxa, missing areas or redundant distributions, reducing the probability of ambiguous or misleading results (Nelsen and Platnick 1981; Nelson and Ladiges 1991b; Morrone and Crisci 1995). The resultant set of informative area trees is coded to create a data matrix for parsimony analysis, with an all-zero outgroup (x) (Nelson and Platnick 1991a) added. The result of the parsimony analysis is a general area statement.

BIOGEOGRAPHICAL AND ECOLOGICAL SPECIATION PATTERNS

Distributional correlates of speciation were investigated by overlaying the distributions of species within each clade. This is similar to the creation of ancestral species maps (Wiley 1980; Anderberg 1986), but differs in that distribution of basal species does not necessarily encompass that of other species in the clade.

Similarities and differences in distribution patterns within clades were compared and considered in terms of areas of differentiation and selection pressures. The ecology of the distribution area and the differences in ecological profiles of species were included in the evaluation and diagrams representing the ecological profile of species within terminal clades were constructed. The result was an assessment of relative influences of geography and ecology on the speciation patterns observed in each clade.

RESULTS

PHENETIC ANALYSIS OF THE SPECIES COMPLEX

Species groups are referred to using the name of the species which predominates in the group.

Principle Component Analysis

In the PCA analysis (Fig 2), specimens representing the five species group separately, although there are some misplaced individuals i.e. 88b, 38pl and 56sc. The *T. bachmanii* cluster is the most distinct of the species clusters.

The greatest contribution to axis 1 comes from female flower length (Table 6), the texture

Table 6. The contribution of each character to the PCA of the species complex, with the largest contributing characters in bold.

Characters	Axis 1	Axis 2	Axis 3
diameter culm base	0.14672	**0.64169**	-0.27693
diameter culm apex	0.44568	0.56285	0.00118
female flower length	**-0.89105**	0.05983	0.23547
female flower length/breadth	0.30170	-0.21869	0.24907
female flower odd outer tepal length	-0.75676	-0.24517	0.13014
female flower odd outer tepal width	-0.72972	-0.11879	0.15269
female flower length/odd outer tepal length	-0.16406	-0.29074	0.29569
female flower pedicel length	-0.83282	0.33574	0.22110
ratio length of flower to length of pedicel	0.54085	-0.52817	-0.07762
outer tepal margin texture	**-0.90119**	0.13362	-0.13627
outer tepal core texture	-0.84437	0.12830	-0.13342
colour outer tepals	-0.60046	0.30236	-0.12876
female bract texture	-0.29116	-0.43062	**-0.57301**
female spathes prominent	-0.72286	0.03185	0.15839
female bract margin hyaline	0.32958	-0.32991	**-0.53380**
female side tepals small or large wings	-0.66401	-0.43319	-0.11114
female side tepals visible or not	**-0.86689**	0.17115	-0.22354
female bract colour	0.39602	0.21524	**0.62949**
female inflorescence shape	-0.65603	-0.44565	0.17938
female side tepal apex	-0.71543	-0.05090	-0.15483
female spikelet number	-0.29060	**-0.62384**	0.22472
culms ridged	-0.07806	**0.81497**	-0.21253
male inflorescence shape	0.26148	0.31050	-0.17929
culm rugulose	-0.74377	0.29493	-0.07608
sterile branches absent or present	0.00540	-0.19653	-0.15680

of the outer tepal margin and whether the female side tepals are visible behind the bracts or not. Diameter of the culm base, the number of female spikelets and the presence of ridges on the culm are the greatest contributors to Axis 2. Axis 3 predominantly represents female bracts, the core texture, the texture of the margin and the colour.

Cluster analysis

Species Groupings

The results of the UPGMA cluster analysis (Fig. 3) are largely congruent with those of the PCA analysis; however the *T.platypteris* specimens are divided into two groups in the cluster analysis and there are discrepancies in the placing of specimen 62st, 88b, 56sc, 36sc, 15sc and 37sc.

T.stokoei 62 is separated as an outlier to the entire species complex (Fig 3). *T.stokoei* 62 differs from the main group of *T.stokoei* specimens by the length of the odd outer tepal and pedicel. The length of the odd outer tepal is considerably smaller than those of the other species. In the PCA analysis *T.stokoei* is placed between the groups of *T.bachmanii*, *T.stokoei* and *T.schlechteri* specimens.

The next major division at a similarity value of 1.602 separates the *T.platypteris*, *T.comptonii*, *T.scabridus* group from the *T.bachmanii*, *T.schlechteri*, *T.stokoei*.

T.schlechteri and *T.stokoei* separate from *T.bachmanii* at a similarity value of 1.256. *T.schlechteri* and *T.stokoei* are differentiated at a similarity level of 1.2 (Fig 3). The specimen 88b lies in the *T.stokoei* cluster. The specimen *T.bachmanii*88 is included in the *T.stokoei* group and not in the *T.bachmanii* group because of its solitary flower spikelet and larger flowers..

The *T.platypteris* cluster is not sub-divided into groups comparable with current species boundaries. The first group is composed of *T.platypteris* specimens 26pl, 30pl, 24pl, 35pl, 23pl, and 22pl. *T.platypteris* specimen 38pl is closely allied to the next major division which consists of three closely related sub-divisions. The first of these sub-divisions is composed of *T.comptonii* specimens. Three *T.comptonii* specimens 12c, 13c and 14c are found in the next sub-division. In addition to these three specimens, this second sub-division is composed of *T.platypteris* specimens, 21pl, 32pl, 33pl, 34pl, 29pl, 31pl, 25pl and 27pl. The final subdivision is composed of two groups of *T.scabridus* specimens. *T.scabridus* specimens, 57sc, 53sc, 51sc, 54sc, 50sc, 39sc and 40sc group together. Associated with this group is a smaller one containing specimens 52sc, 37sc, 15sc and 36sc. At the base of the entire group is 56sc which was placed in the *T.comptonii* group in the PCA analysis.

Key characters

The details of characters for each cluster are given in Appendix 3. Measurements have been averaged across each group. All states of qualitative characters found in a cluster are presented and where more than one state occurred, the state which is most common in each cluster is in bold type. The differences between the *T.bachmanii*, *T.stokoei*, *T.schlechteri* group of specimens and the *T.platypteris*, *T.scabridus*, *T.comptonii* group is summarised in Table 7. More detail on these characters can be found in Appendix 3 .

Table 7. The characters distinguishing the *T.platypteris*, *T.scabridus*, *T.comptonii* group from the *T.bachmanii*, *T.stokoei*, *T.schlechteri* group in the UPGMA analysis.

Character	*T.platypteris* group	*T.bachmanii* group
texture of female flower outer tepal margin and core	mainly chartaceous to membranous	coriaceous
female outer tepal colour	cream/tan/red brown	cream/tan
female flower side tepal position relative to bracts	visible behind bracts	not visible, except in two specimens of *T.bachmanii*
Female flower length	long (5.17-7.37mm)	short (3.07-5.08mm)
Pedicel length	long (0.82-2.37mm)	short (0.32-0.87mm)

Within the *T.bachmanii*, *T.schlechteri*, *T.stokoei* group, *T.bachmanii* differs from *T.stokoei* and *T.schlechteri* by having stouter culms with grooves, more spikelets per culm and flowers which are smaller. The shape of *T.bachmanii* female spikelets is more cylindrical-oblong than the v-shaped spikelets of *T.stokoei* and *T.schlechteri*. *T.schlechteri* has longer flowers with a wider odd outer tepal and longer pedicels than *T.stokoei*. However, apart from a single specimen, *T.stokoei* had wider wings than *T.schlechteri*. Few specimens of *T.stokoei* had the prominent spathes of *T.schlechteri*.

T.platypteris 1 specimens (22pl, 23pl, 35pl, 24pl, 30pl and 26pl) have considerably longer flowers and pedicels than other specimens in the *T.platypteris*, *T.scabridus*, *T.comptonii* group. The margins of female bracts, in the *T.platypteris* 1 group, are not hyaline.

The flowers of the *T.comptonii* (10c, 11c, 16c, 17c, 20c, 18c and 19c) cluster have short pedicels compared to the other specimens in the *T.platypteris*, *T.stokoei*, *T.comptonii* group. The outer tepal texture of the female flowers tends towards coriaceous with the predominating colour being cream rather than tan or red brown. There are only a few specimens of the *T.comptonii* group which have prominent spathes, 10c (the type specimen for *T.comptonii*), 11c and 16c.

T.platypteris 2 specimens (21pl, 32pl, 33pl, 34pl, 29pl, 31pl, 25pl and 27pl) have flowers and pedicels which are only slightly shorter than those of the first *T.platypteris* group and these are still longer than flowers in all other specimens. Like the first *T.platypteris* group, this cluster has more inflorescences than the specimens of *T.comptonii* and *T.schlechteri*, which tend to be solitary or paired. The two *T.platypteris* clusters differ in the texture of the outer tepals margins (coriaceous in *T.platypteris* 1, chartaceous in *T.platypteris* 2) and female bracts (coriaceous in *T.platypteris* 1 tending towards chartaceous-membranous in *T.platypteris* 2). The main distinction between the two groups is the lack of the hyaline margin on the female bract, which distinguished the first *T.platypteris* group from all other specimens in the *T.platypteris*, *T.stokoei*, *T.comptonii* cluster.

The distinguishing features of the *T.scabridus* cluster are the relatively long odd outer tepal and the tan female bracts. Like *T.platypteris* the group has prominent spathes, but there are only one or two spikelets per culm, not many.

Distribution of groups and odd specimens

T.bachmanii ranges from Paarl in the south to the northern end of the Olifants River Valley, Karoopoort in the east across to Hopefield on the west coast. There is a northern enclave of the species centred on the Khamiesberg region down to the west coast at Hondeklipbaai (Fig. 4).

T.bachmanii 88 is grouped with *T.stokoei* (Fig 2,3) but it's locality lies within the distribution of *T.bachmanii* specimens outside the known distribution of *T.stokoei* (Fig. 5). The region covered by *T.stokoei specimens* is the south-western mountains of the Overberg. The locality of *T.stokoei* 62 is within the range of *T.stokoei*. The *T.schlechteri* group is located in the dry inland mountains of the Cedarberg and Koue Bokkeveld, to the north of the Overberg region (Fig. 6).

The specimens of the *T.comptonii* cluster are located in the central and southern Cedarberg area with a single specimen, *T.comptonii* 20, occurring in the Karoo, near Laingsberg (Fig. 7). *T.platypteris* localities are predominantly north of the Cedarberg region in the Van Rhynsdorp-Nieuwoudtville area (Fig. 8). There are records of *T.platypteris* specimens from the northern Cedarberg, namely *T.platypteris* 28, from North east of the Pakhuis pass, and 36, which is linked with the *T.scabridus* specimens.

There is no difference in the localities of the first and second group of *T.platypteris* specimens. The three *T.comptonii* specimens (12c, 13c and 14c) that are grouped with the second cluster of *T.platypteris* specimens are all found south and east of the northern distribution of *T.platypteris* specimens. *T.comptonii*12 is from Karoopoort, 13 from the Karoo, Laingsberg and 14 from Rosendal in the Koue Bokkeveld.

The small distinct group of *T.scabridus* specimens (15sc, 36sc, 37sc, 52sc) come from the central Cedarberg, northern Cedarberg, Van Rhyns pass and Karoopoort (Koue Bokkeveld), respectively. The remaining *T.scabridus* specimens were collected from the Koue Bokkeveld-Swartruggens region (Fig. 9) with one collection, *T.scabridus* 53 from Tweedside, Laingsberg. *T.scabridus* 56 is located in the Baviaanskloof.

CLADISTIC RESULTS

Character delimitation

Quantitative characters delimitation

The detailed results of the morphometric analysis are presented and reviewed within the description of morphometric characters (see Appendix 1).

Cladistic analysis

Two trees (tree length of 268; consistency index of 0.25; retention index of 0.54) resulted from the unweighted PAUP analysis (Fig. 10a and 10b). The two trees differ only in the arrangement of the *T.arenarius-T.sporadicus* clade. In the first tree (Fig. 10a) *T.gracilis* is the sister taxon to *T.arenarius* and *T.lucens*, and *T.obtusus* and *T.sporadicus* form a species pair. In the second tree (Fig. 10b) *T.obtusus* is placed above *T.gracilis* as sister lineage to *T.arenarius* and *T.lucens*, followed by *T.sporadicus* and then *T.gracilis*. In the consensus tree the *T.sporadicus* clade collapses in a polytomy.

Character consistency

The CI of each character was calculated over the two fundamental trees. The graph (Fig 11) indicates those characters that have a different consistency index for the two trees and present the minimum, maximum and average ci values for these characters. The characters which have different consistency indices across the two trees are height, appearance of sterile branches relative to flowering, origin of the sterile branches, colour of the female bracts, shape of the female flower outer tepal apex and male bract shape.

Three characters, apart from those apomorphies distinguishing *Thamnochortus* from *Rhodocoma*, have consistency indices of 1. These characters are female bract texture, tip of female bract recurved or not and position of epidermal cell wall thickening. Nine characters have consistency indices of 0.5. These characters are culm texture, sheath length relative to internode length, presence or absence of fertile branches, female spikelet shape, female bract shape, female flower shape, decurrent tepal bases notched or not, male spikelets not as wide as long or not and male spikelet length.

Those characters in the 0.3 to 0.4 consistency index category are origin of sterile branches (the ci varies on the two cladograms), female spathes prominent or not, basal bracts of female as long as spikelet or not, female bract awn distinct or not, female outer tepals winged or keeled, the position of the subsidiary cells relative to guard cells and the size of parenchyma cells relative to epidermal cells.

The five remaining characters which have variable consistency indices have consistency indices between 0.2 and 0.3. In total there are 21 characters in this ci category. These characters are culm diameter, height, sheath core texture, appearance of sterile branches relative to flowering, nature of the rhizome, number of female spikelets, female bract length, colour of the female bracts, presence or absence of a distinct central vein on the female bracts, female flower length, side tepals visible either side of bract or not, female outer tepal apex rounded or not, nut shape, male spikelet lorate or not, male spikelet box-like or not, relative length of basal bracts of male spikelets, male bract length, male flower length, position of stomata, patterns of guard cell cuticle, epidermal cell width and sclerenchyma ridges.

The remaining nine characters all have consistency indices below 0.2. These characters are culm base decumbent or not, the texture of the female bract margin, female tepal texture, female flower outer tepal apex, male outer tepal specialisations, male tepal rigidity, number of parenchyma layers and thickness of the sclerenchyma walls.

The character of post fire survival habit has a ci of 0.11 on these cladograms (Character 51).

Clades and Characters

By convention clades are named by the basal-most species.

The entire *T.dumosus-T.amoena* clade has sterile branches present post flowering (Fig 10a). This character state is also found in *T.gracilis*, *T.sporadicus*, *T.punctatus*, *T.ellipticus* and *T.muirii*. The female bracts of the *T.dumosus-T.amoena* clade have distinct central veins. This character is also observed in *T.comptonii*, *T.arenarius*, *T.gracilis* and the *T.karooica-T.spicigerus* pair.

The *T.dumosus* clade has chartaceous sheaths, however, these are also a feature of *T.comptonii* and *T.papyraceus*. The sheaths of the *T.amoena* clade are coriaceous. This is the common texture in *Thamnochortus*, but the *T.bachmanii* clade is the only other clade where all species have coriaceous sheaths. Within the *T.dumosus* clade and *T.amoena* clade are two species pairs, *T.acuminatus-T.fruticosus* and *T.cinereus-T.rigidus*, which are distinguished in having hairy culms. The *T.acuminatus-T.fruticosus* pair are unique in *Thamnochortus* in having epidermal thickening on the outer wall of the epidermis. The *T.acuminatus-T.fruticosus* pair also have female sheaths as long as the inflorescence. This is not a unique synapomorphy as female sheaths as long as the inflorescence also occur in *T.papyraceus*.

The *T.stokoei* clade is characterised by v-shaped inflorescences, but this feature is also found in *T.acuminatus* of the *T.dumosus* clade. The basal bracts of the female spikelet are virtually as long as the spikelet in the *T.stokoei* clade, and in *T.acuminatus* and *T.levynsieae*. The *T.papyraceus* clade has prominent female spathes. This feature is also found in *T.ellipticus*, *T.muirii* and *T.paniculatus*. The *T.comptonii* clade has male spikelets which are less than 10mm in length. Male spikelets below 10mm are also found in the *T.muirii-T.paniculatus* pair. The *T.platypteris* group consistently have three or less female inflorescences per spikelet. The only other species which are restricted in the number of spikelets per culm are *T.acuminatus* and *T.ellipticus*.

T.scabridus and *T.schlechteri* and *T.stokoei* have female spikelets which are as wide as long.

Species included in the *T.amoena-T.dumosus* and *T.stokoei* clades share a unique character; chartaceous female bracts.

The *T.gracilis-T.obtusus* clade, with the exception of *T.gracilis*, has sterile branches predominantly from the base of the culms which are present while flowering. Two other species which share this combination of sterile branch characters are *T.pellucidus* and *T.dumosus*. The *T.gracilis* clade, along with *T.obtusus* and *T.punctatus*, have linear lanceolate bracts on the female spikelet. In all species of the *T.gracilis* clade, these female bracts are less than 8mm long (also in *T.obtusus*, *T.bachmanii* and *T.pluristachyus*).

T.punctatus, *T.insignis* and *T.bachmanii* have lorate male inflorescences, a feature which recurs in the *T.karooica-T.spicigerus* pair and in *T.fraternus*. All of these species, and *T.erectus*, have male spikelets which have a box-like shape.

The entire *T.acuminatus-T.bachmanii* clade, with the exception of *T.dumosus*, have winged outer tepals in the female flower. Wings also occur in the *T.spicigerus* clade and in *T.pluristachyus.*

Female flowers of the *T.pellucidus* clade have keeled outer tepals. Keeled tepals of the female flowers are also present in the *T.paniculatus* clade, *T.dumosus*, *T.pulcher*, *T.nutans* and *T.levynsieae*. The *T.glaber* clade has narrow oblong female flowers which are also found in *T.fraternus* and *T.muirii*. The nuts of the *T.glaber* clade are ovate, not round. Ovate nuts are also found in *T.fruticosus*, *T.pulcher* and *T.paniculatus*.

Between the *T.pellucidus* clade and the *T.pluristachyus* clade lie *T.pulcher* and *T.nutans*. Together with *T.dumosus* these species have distinct female bract awns.

The *T.erectus-T.pluristachyus* clade contains two clades within it, the *T.erectus* and *T.pluristachyus* clades. The entire *T.erectus-T.pluristachyus* clade has culms over 1,5cm in diameter, although there are some exceptions in *T.fraternus*, *T.muirii* and *T.paniculatus* where specimens have culms thinner than 1.5cm. Other species with thick culms are *T.cinereus*, *T.insignis* and *T.glaber*. The male bracts of the *T.erectus-T.pluristachyus* clade are less than

6mm long. The *T.bachmanii* clade also has male bracts smaller than 6mm, as does *T.scabridus* clade, *T.ellipticus* and *T.levynsieae*.

The *T.erectus* clade has culms in excess of 1m tall. *T.insignis* is the only species outside the group which has such tall culms. Female side tepals are visible in this clade, as they are in the *T.acuminatus-T.fruticosus* pair and the *T.stokoei* clade, *T.schlechteri* being an exception.

The *T.pluristachyus* clade is uniquely defined by recurved female bract apices. The inner edge of the outer female tepals is rounded, a state which is also in *T.glaber* and scattered through the *T.bachmanii* clade occurring in the *T.arenarius-T.lucens pair*, *T.obtusus* and *T.insignis*.

T.levynsieae is basal in the genus *Thamnochortus*.

Testing cladogram

Bootstrap analysis

The bootstrap results (Fig. 12) show that the majority of clades were poorly supported, with bootstrap values between 20-50%.

Deletion of problem taxa

Reiterative deletion of *T.bachmanii*, *T.insignis* and *T.punctatus*, singly and in combinations, had varying effects on cladogram structure and the consistency index. Removal of *T.insignis* caused little change in topology, placing *T.punctatus* in the polytomy of *T.gracilis*, *T.sporadicus* and *T.obtusus*, in the consensus tree of three trees. The treelength was reduced to 252 steps and the consistency index increased to 0.27. The consensus tree had 271 steps and a consistency index of 0.25. Deletion of *T.insignis* and *T.bachmanii* did not increase the consistency index further, but treelength increased to 256. However, there was considerable change in topology. Relationships within the *T.gracilis* clade were resolved as follows. *T.obtusus* was sister species to *T.sporadicus*, *T.punctatus* was the sister species to *T.obtusus-T.sporadicus*, *T.gracilis* basal to *T.obtusus-T.punctatus*, *T.lucens* basal to *T.obtusus-T.gracilis* and *T.arenarius* basal to *T.obtusus-T.lucens*. This rearranged *T.gracilis* clade was placed basal to the *T.erectus-T.pluristachyus* clade. Within the *T.stokoei* clade, *T.platypteris* and *T.comptonii* form a polytomy.

Removing all three species changes the cladogram topology considerably, decreases the treelength to 227 steps and increases the consistency index to 0.3. *T.nutans* and *T.levynsieae* are basal in the *Thamnochortus* group, *T.spicigerus* clade forms a polytomy with the *T.fraternus* and *T.muirii*. The *T.glaber* clade is contained in a large polytomy with *T.gracilis*, *T.arenarius*, *T.lucens*, *T.obtusus*, *T.pellucidus* and *T.sporadicus*. The *T.stokoei* clade is placed in the same polytomy. *T.dumosus* and *T.pulcher* are grouped with the *T.stokoei* clade. The *T.dumosus-T.amoena* clade remains without *T.dumosus*.

The highest consistency index, 0.31, and lowest treelength, 219, was obtained by removing *T.bachmanii* and *T.punctatus*. Apart from the *T.spicigerus* clade the terminal groups remained intact but there was a basal polytomy of clades including all species from the *T.bachmanii* clade to *T.levynsieae*. *T.insignis* and *T.erectus* formed part of this polytomy, with *T.karooica* and *T.spicigerus* remaining together as a species pair.

Finally, removal of *T.punctatus* and *T.insignis*, altered the topology considerably. The *T.bachmanii* clade, without *T.obtusus* and *T.sporadicus*, and including *T.dumosus*, was placed below the *T.dumosus-T.amoena* clade. The *T.stokoei* clade was still intact but as a sister lineage to *T.papyraceus*, with *T.obtusus* and *T.sporadicus*, and the *T.pellucidus* clade basal. The *T.erectus-T.pluristachyus* clade remained intact.

This analysis confirmed that the topology below the level of the terminal clades lacked integrity. In terms of bootstrap values, the reiterative analyses indicated that clades with a bootstrap value of 20% were robust, although species associations with a bootstrap greater than 10% showed a tendency to remain together.

COMPARATIVE BIOLOGY AND EVOLUTION

Non-phylogenetic analyses

The Mann-Whitney U tests comparing all values of resprouters to those of seeders, without the influence of history, show no significant difference between resprouters and seeders in terms of geographical area, height and number of flowers per culm. Similarly, there was no significant difference in area occupied by winged or keeled species. The chi-squared test indicated that there was no significant relationship between female outer tepal development and fire survival strategy (Table 8) (P=0.073).

Table 8. Chi-square contingency table indicating the numbers of species for each permutation.

	seeder	resprouter
wings	14	9
keels	6	5

Phylogenetic analyses

Non-directional evolutionary analyses

The comparison between seeder and resprouter sister clades (Fig 13) using the Wilcoxon paired t-test determined that the variables were statistically different at the P=0.05 level (Table 9).

Table 9. Summary of statistical results of the historical comparison of seeders and resprouters in terms of height, numbers of seeds per culm and size of distribution area. * indicates the greater value. Deatails of data presented in Table 10-13.

	Seeder	Resprouter	Sig. Level
No. of species			NS
Plant height		*	0.031
No. flowers/culm			NS
Distribution		*	0.036

There is no significant difference in the number of species found in each sister seeding and resprouting lineages (Table 10).

Number of species per lineage

Table 10. Indicating the number of species in each seeding and resprouting lineage.

Resprouting lineage	No. of species		Seeding lineage
T.fruticosus	1	1	*T.acuminatus*
T.cinereus	1	1	*T.rigidus*
T.scabridus	1	1	*T.schlechteri*
T.arenarius-T.sporadicus	5	1	*T.punctatus*
T.ellipticus-T.glaber	3	1	*T.pellucidus*
T.erectus	1	2	*T.karooica-T.spicigerus*

Height differences in fire survival habit

Resprouters are generally taller than seeders except in *T. erectus* and *T. karooica-T.spicigerus* clade where the average maximum height for each lineage was the same (Table 11).

Table 11. Maximum Height values for each seeder and resprouter lineage.

Resprouter lineage	Average Maximum Height (cm)		Seeder lineage
T.fruticosus	60	30	*T.acuminatus*
T.cinereus	120	100	*T.rigidus*
T.scabridus	50	30	*T.schlechteri*
T.arenarius-T.sporadicus	62	60	*T.punctatus*
T.ellipticus-T.glaber	85	40	T.pellucidus
T. erectus	150	150	*T.karooica-T.spicigerus*

Reproductive output of seeders and resprouters

Absence of a significant difference, using a Wilcoxon paired t-test, between seeders and resprouters in the maximum and minimum number of flowers per culm (Table 9) was unexpected considering that for maximum reproductive output, in all cases but one resprouters had more flowers per culm than seeders, while in minimum reproductive output all but two seeders produce less flowers than resprouters. In maximum output the exception is the *T.erectus-T.spicigerus* clade where the two seeders have proportionally more flowers than *T.erectus* the resprouter (Table 12a). In minimum output the exceptions are *T.ellipticus-T.pellucidus* and *T.erectus-T.spicigerus* clades (Table 12b).

Table 12a. The maximum number of flowers per culm.

Resprouter lineage	Average Maximum Number of flowers per culm		Seeder lineage
T.fruticosus	240	135	*T.acuminatus*
T.cinereus	2112	500	*T.rigidus*
T.scabridus	40	20	*T.schlechteri*
T.arenarius-T.sporadicus	412	350	*T.punctatus*
T.ellipticus-T.glaber	188	144	*T.pellucidus*
T. erectus	368	1311	*T.karooica-T.spicigerus*

Table 12b. The minimum number of flowers per culm.

Resprouter lineage	Average Minimum Number of flowers per culm		Seeder lineage
T.fruticosus	42	16	*T.acuminatus*
T.cinereus	132	15	*T.rigidus*
T.scabridus	14	1	*T.schlechteri*
T.arenarius-T.sporadicus	30	18	*T.punctatus*
T.ellipticus-T.glaber	33	36	*T.pellucidus*
T. erectus	7	211	*T.karooica-T.spicigerus*

However, there is considerable variation in number of spikelets and number of flowers in the majority of species (Table 12c). A consequence of this variation is that there is considerable overlap in the ranges of sister lineages (Fig. 14). Only the *T.cinereus-T.rigidus* and the *T.erectus-T.spicigerus* lineages have recognisable differences in the ranges of the sister seeding and resprouting lineages. In these lineages the greatest difference is found in the maximum number of seeds.

Table 12c. Range in number of spikelets and number of flowers per spikelet for each species.

Species	No. spikelets	No.flowers/spikelet	Range in flower production
T. acuminatus	1-3	16-45	16-135
T. amoena	4-6	20-40	80-240
T. arenarius	7-24	16-40	112-960
T. bachmanii	5-8	14-42	70-336
T. cinereus	6-44	22-48	132-2112
T. comptonii	1-2	20-22	20-44
T. dumosus	2-4	5-20	10-80
T. ellipticus	1-3	20-26	20-78
T. erectus	7-23	1-16	7-368
T. fraternus	6-20	6-19	36-380
T. fruticosus	3-6	14-40	42-240
T. glaber	3-8	14-36	42-288
T. gracilis	4-20	8-14	32-280
T. guthrieae	3-6	10-16	30-96
T. insignis	11-23	8-20	88-460
T. karooica	5-27	22-46	110-1242
T. levynsieae	2-10	12-14	24-140
T. lucens	2-8	10-50	20-400
T. muirii	2-20	16-40	32-800
T. nutans	3-15	8-22	24-330
T. obtusus	1-5	4-14	4-70
T. paniculatus	2-3	1-14	2-42
T. papyraceus	2-3	12-40	24-120
T. pellucidus	3-8	12-18	36-144
T. platypteris	1-4	4-16	4-64
T. pluristachyus	10-60	12-26	120-1560
T. pulcher	2-5	14-28	28-140
T. punctatus	3-7	6-50	18-350
T. rigidus	5-20	3-25	15-500
T. scabridus	1-2	14-20	14-40
T. schlechteri	1-2	1-10	1-20
T. spicigerus	13-23	24-60	312-1380
T. sporadicus	2-4	10-20	20-80
T. stokoei	1-2	9-30	9-60

Distribution area of seeders and resprouters

Resprouters consistently covered a larger area than their sister seeding clades, except in the *T.scabridus-T.schlechteri* pair where the distribution area of the resprouter was smaller by a single grid square (Table 13).

Table 13. The sizes of the distribution are measured in number of 1/4° grid squares occupied by the lineage.

Resprouter lineage	Maximum Number of grid squares covered		Seeder lineage
T.fruticosus	31	5	*T.acuminatus*
T.cinereus	32	9	*T.rigidus*
T.scabridus	5	6	*T.schlechteri*
T.arenarius-T.sporadicus	76	10	*T.punctatus*
T.ellipticus-T.glaber	22	6	*T.pellucidus*
T.erectus	26	16	*T.karooica-T.spicigerus*

Distribution area of winged and keeled lineages

It is possible that development of the wing may have, independently of fire survival strategy, influenced dispersal ability and hence biogeographic distribution. However, there is no significant difference in number of grid squares covered by winged and keeled lineages (Table 14).

Table 14. Comparison of the total number of 1/4° grid squares covered by winged and keeled lineages.

Winged lineage	No. 1/4° grid squares.		Keeled lineage
T. acuminatus-T. bachmanii	251	28	*T. erectus-T.spicigerus*
T. ellipticus-T. pellucidus	42	27	*T.fraternus-T.pluristachyus*

The lack of a significant result in the phylogenetic comparison of these two habits may well be due to the small sample size and large variation in the size of distribution area in the winged category.

Directional evolutionary analyses

Evolutionary association of outer tepal specialization and fire survival habit

In testing the association of wings with the seeding habit, and that of keels with the resprouting habit, the number of gains and losses of wings and keels respectively differed depending on which state was assigned to the equivocal branch on the tree displaying the dependent character (Fig. 15). These values were the same for both of resolved trees (Table 15).

Table 15: The number of gains and losses of keels and wings in *Thamnochortus* when the equivocal branch is assigned the different states in both cladograms.

Equivocal branch state.	Evolution of Wings		Evolution of Keels	
	gains	losses	gains	losses
wing state	2	2	3	2
keel state	3	1	2	3

Similarly, each permutation produced a slightly different probability. However, the probability of the random evolution of wings is low in most cases (Table 16a), but not to the point where there is a significant association with the evolution of the reseeding habit. In contrast, the probability of the keels evolving randomly on the cladogram was consistently low enough to make an association between keels and the resprouting habit significantly probable below the 1% level (Table 16b).

Table 16a: The probability of wings evolving randomly on both phylogenetic trees for the four permutations of character state distribution on the equivocal branches in the respective characters.

Specialization of female outer tepals.	Evolution of fire survival habit.	
	seeding state	resprouting state
Fig. 10a		
winged state	0.3192	0.1809
keeled state	0.2505	0.160
Fig. 10b		
winged state	0.3176	0.1800
keeled state	0.2473	0.1581

Table 16b: The probability of keels evolving randomly on both phylogenetic trees for the four permutations of character state distribution on the equivocal branches in the respective characters.

Specialization of female outer tepals.	Evolution of fire survival habit.	
	seeding state	resprouting state
Fig. 10a		
winged state	0.0012	0.0053
keeled state	0.0012	0.0053
Fig. 10b		
winged state	0.0013	0.0056
keeled state	0.0013	0.0056

Edaphic specificity in seeder and resprouting habits

Superficially, seeders appear to be associated with the relatively richer soils of coastal sands and limestone (Table 17). However, comparing substrates of sister seeding and resprouting lineages (Table 18) indicates that there is no definite pattern associated with fire survival habit.

Table 17. The proportion of seeding and resprouting species of *Thamnochortus* on different substrates.

	TMS	Coastal sands	Limestone
number of species	26	4	4
%resprouters	53	0	0
%seeders	46	100	100

Table 18. Seeding and resprouting lineages and the respective substrates. TMS refers to Table mountain sandstone and CS refers to coastal sands.

Resprouting lineage	Soil type		Seeding lineage
T.fruticosus	TMS	TMS	*T.acuminatus*
T.cinereus	TMS	TMS	*T.rigidus*
T.scabridus	TMS	TMS	*T.schlechteri*
T.arenarius-T.sporadicus	TMS	CS	*T.punctatus*
T.ellipticus-T.glaber	TMS	TMS	*T.pellucidus*
T.erectus	TMS	TMS/CS	*T.karooica-T.spicigerus*

There is a single seeding lineage, *T.punctatus*, associated exclusively with coastal sands (Table 18). The sister seeding lineage to *T.erectus* is split between TMS and coastal sands with *T.karooica* found on TMS derived soils and *T.spicigerus* occurring on coastal sands. The *T.erectus* lineage is the sister lineage to the limestone clade, *T.pluristachyus*. The entire limestone clade consists of seeding species.

ECOLOGICAL ANALYSES

Habitat specificity

Describing species as being habitat specific or generalists (Table 19) according to altitudinal and rainfall criteria presented some difficulties. Rainfall across species distributions varied less than the specified 500mm, while altitudinal range varied little in certain species and by as much as 1000m in others. Thus, in terms of soil texture, type, drainage and rainfall all species were habitat specific, but in some species there was considerable variation in altitude, usually restricted to above or below a certain point. Species recorded as generalists are thus not true habitat generalists merely distributed across a broader range of altitudes. However, it should be made clear that species considered to be low altitude rarely go above 1000m, while species which are high altitude seldom occur below 1500m.

Table 19: Species of *Thamnochortus* divided according to the categories of the eight types of endemism. `Wide' and `Narrow' describe the geographic distribution of the species. The species are either habitat specific or general and are common or rare within their habitats.

	wide		narrow	
	common	rare	common	rare
general	*T.lucens* *T.fruticosus*	*T.cinereus*	*T.schlechteri* *T.stokoei* *T.sporadicus* *T.nutans* *T.levynsieae* *T.guthrieae* *T.gracilis* *T.arenarius* *T.pulcher*	*T.acuminatus*
specific	*T.bachmanii* *T.karooica* *T.insignis* *T.erectus* *T.obtusus* *T.spicigerus* *T.pluristachyus* *T.muirii*	*T.fraternus* *T.glaber* *T.rigidus*	*T.scabridus* *T.platypteris* *T.comptonii* *T.punctatus* *T.pellucidus* *T.papyraceus* *T.paniculatus*	*T.dumosus* *T.amoena* *T.ellipticus*

PCA analysis of ecological factors

Graphical representation places the high altitude species, *T.papyraceus*, *T.stokoei*, *T.schlechteri* and *T.comptonii* together (Fig. 16), while the low altitude limestone species, *T.fraternus*, *T.muirii*, *T.paniculatus* and *T.pluristachyus* are associated on the extreme right of the x axis. Except for *T.stokoei*, which occurs at higher altitudes, all species occurring in or near the marshy habitats group at the extreme positive end of the y axis. Those species found in low to mid altitudes are dispersed in the centre group of the PCA but there does not seem to be a distinct gap between them.

Component 1 is largely representative of maximum altitude and soil type, with a strong influence from winter rainfall and minimum altitude (Table 20; Fig 16). This is not surprising as these factors are indirectly related. The group of limestone species is small, occurring at low altitudes in an area that receives predominantly winter to year-round rainfall. The binary coding of the character soil type, sandstone or limestone, and the relatively small size of the group circumscribed by it, could have resulted in inadvertent weighting of the character and related character associations.

Moisture forms a large part of components 2 and 3 with total rainfall and habitat drainage having the strongest influence in component 2 along with minimum altitude. Most of the species occurring in areas which may be seasonally marshy, with the exception of *T.glaber*, occur in winter rainfall areas with relatively high year round rainfall. Component 3 is entirely moisture related, the greatest contribution coming from habitat drainage, then total average rainfall and finally winter rainfall.

Table 20. The relative contribution of each ecological factor to the eigenvectors used in constructing the ecological PCA projection.

Ecological factor	Axis 1	Axis 2	Axis 3
total average rainfall	-0.21563	**0.60306**	**0.54459**
proportion of winter rainfall	-0.62581	0.20318	**0.48105**
soil type	**0.73827**	-0.26639	0.24853
maximum altitude	**-0.76273**	-0.16788	-0.25043
minimum altitude	**-0.63730**	**-0.50157**	-0.07725
drainage	0.00856	**0.71893**	**-0.61305**

Fire regeneration mode, plotted onto the PCA of the ecological associations, indicates a separation of seeders and resprouters on the y axis (Fig. 17). This pattern indicates that resprouters tend to occur in the wetter areas of higher rainfall.

Habitat information gathered from herbarium specimens and field observations, excluding rainfall, was compiled to give a general habitat profile of each species (Table 21). The pattern of species preference for wet and dry habitats has been plotted on the cladogram (Fig. 18).

Table 21: Ecological profiles of the thirty-four species of *Thamnochortus*.

Soil Moisture	Soil Type				Altitude (m)
	Limestone	Sandstone			
		sandy	sandy-gravel	gravel-rock	
Damp		*T.glaber* *T.obtusus*			<300
		T.dumosus *T.fruticosus* *T.sporadicus*			300-1000
		T.cinereus			1000-1500
				T.stokoei	>1500
Dry	*T.pluristachyus* *T.muirii* *T.fraternus* *T.paniculatus*	*T.erectus* *T.spicigerus* *T.insignis* *T.punctatus* *T.pellucidus*			<300
		T.scabridus	*T.lucens* *T.arenarius* *T.guthrieae* *T.ellipticus* *T.amoena* *T.platypteris* *T.bachmanii* *T.gracilis*		300-1000
		T.acuminatus	*T.karooica* *T.comptonii*	*T.rigidus* *T.nutans* *T.levynsieae* *T.pulcher*	1000-1500
				T.schlechteri *T.papyraceus*	>1500

BIOGEOGRAPHICAL ANALYSES

Grid Diversity

The grid squares with the highest concentration of species (10-13 species) are found on Cape Peninsula and on the Soetanysberg, near Cape Agulhas. The Hottentots Holland-Franschoek mountains into the Riviersonderend range have slightly lower concentrations of species (8-9 species) (Fig. 19). Smaller concentrations of species are found in the Cedarberg-Bokkeveld region, along the Langeberg-Outeniqua and the south coast from Potberg to the Gouritz river mouth. The rest of the western Cape has a species richness of 1-3 species per 1/4° grid square.

Areas of endemism

Areas of similarity

Four areas with a similar species composition were located at a similarity level of approximately 0.05. At higher levels of similarity five smaller sub-areas are detected; three in area C and two in area D (Fig. 20).

Four areas of similarity

The six grids of area A are in the Cedarberg and on the West coast flats, defining a dry, west coast-northern Cedarberg association (Fig. 21). The second area, B, incorporates grids from the dry inland areas of the Koue Bokkeveld, Karoo and Klein Swartberg. South of these areas lies C and D. Area C includes the Cape Peninsula, the Cape flats and southerly part of the west coast, across the Hottentots Holland-Du Toits Kloof mountains to the Riversonderend range and the adjacent south coast. Area D includes the southern Cape from Cape Agulhas to Knysna and the adjacent coastal mountains. Nineteen species are endemic to an area of similarity (Table 22). The remaining fifteen species occur in two or three of the four areas of similarity.

Table 22. Distribution of species with respect to the four areas of similarity.

Species	A	B	C	D
T.acuminatus	+	+		
T.amoena				+
T.arenarius			+	
T.bachmanii	+	+	+	
T.cinereus			+	+
T.comptonii	+			
T.dumosus			+	+
T.ellipticus				+
T.erectus			+	+
T.fraternus			+	+
T.fruticosus		+	+	
T.glaber				+
T.gracilis			+	+
T.guthrieae			+	+
T.insignis				+
T.karooica				+
T.levyniseae	+		+	+
T.lucens			+	+
T.muirii				+
T.nutans			+	
T.obtusus			+	+
T.paniculatus				+
T.papyraceus		+		
T.pellucidus			+	+
T.platypteris	+			
T.pluristachyus				+
T.pulcher			+	+
T.punctatus	+		+	
T.rigidus		+		
T.scabridus		+		
T.schlechteri		+		
T.spicigerus			+	
T.sporadicus			+	
T.stokoei			+	

Sub-areas of Area C and D

Sub-group C1 includes the Peninsula and the Cape Flats lying between Table Bay and Hottentots' Holland mountains. C2 is the small block of coastal mountains which include the Hottentots Holland and Koelberg. Sub-group C3 covers a larger area of mountains from the Tulbagh River Valley in the north, across the Riviersonderend mountains to the Bredasdorpberg in the south. Except for the grid square 3421AB, the grid squares in D1 are concentrated on the Bredasdorp flats, west of the Bree river. The other group, D2 is an amalgamation of the grid squares east of the Breede river, extending beyond the Gouritz river and including those of the Langeberg (Fig 21).

Parsimony analysis

The consensus tree produced in the parsimony analysis indicated seven possible areas of endemism (Fig 22). Area A is composed of two grid squares situated in the Cedarberg region. Area B is situated in the middle of the West Coast flats, while area C lies in the adjacent mountain range extending across the Olifants river valley to the Hex River Mountains. South of C in the Du Toitskloof-Riviersonderend mountains lies area D. Further east in the Langeberg is area E, with area F incorporating the adjacent southern coastal flats. Area G delimits the Cape Peninsula and the adjacent Cape Flats region.

Two of the areas (B and C) do not contain any endemic species (Table 23). In each case, the grouping of grids is the result of the grid squares having an identical complement of fairly widespread species. Of the remaining five groups, A, D, E, F and G, only G fulfils Morrone and Crisci's criteria, having two or more species endemic to the area and occurring in more than one grid square. The endemics in area G are *T.levynsieae* and *T.nutans*. These species are restricted to two grid squares within area G, the Table Mountain Chain. Thus, defining the boundaries of the areas of endemism using the methods and criteria of Morrone and Crisci (1995) defines a single area of endemism in the entire Cape Floristic Region, the Table Mountain Chain, excluding several other regions rich in endemics.

Table 23. Species occurring in each area identified according to Morrone's method as an area of endemism. Species endemic to the specified areas are indicated by *.

A	B	C	D	E	F	G
T.acuminatus	T.bachmanii	T.bachmanii	T.cinereus	T.cinereus	T.insignis	T.bachmanii
*T.comptonii	T.lucens	T.lucens	T.gracilis	*T.ellipticus	T.muirii	T.erectus
T.platypteris	T.punctatus	T.sporadicus	T.lucens	T.karooica	*T.pluristachyus	T.fruticosus
			T.pulcher	*T.amoena	T.paniculatus	T.gracilis
			T.sporadicus		T.obtusus	T.obtusus
			*T.stokoei		T.fraternus	T.pulcher
					T.pulcher	T.punctatus
					T.guthrieae	T.spicigerus
					T.erectus	T.sporadicus
					T.pellucidus	*T.nutans
						T.lucens
						*T.levynsieae
						T.guthrieae
						T.arenarius

Concentric ring map method

The overlay of species distributions (Fig. 23) pin-points areas of endemism corresponding to parsimony areas A, D, E, F and G and illustrates the overlap of distributions between the endemic areas.

In the Cedarberg and Koue Bokkeveld region, which corresponds to area A in the parsimony method, there are effectively two centres of endemism: the Cedarberg area with *T.comptonii* endemic and *T.acuminatus*. The distribution range of *T.acuminatus* overlaps with the Koue Bokkeveld area which has two endemics, *T.schlechteri* and *T.scabridus*.

The south-western mountains (area D of the parsimony method) are fairly central relative to the other areas of endemism. There is considerable overlap of species distributions from both area G, the Cape Peninsula, and are F, the southern coastal flats in the mountains of area D. *T.arenarius* and *T.spicigerus* overlap from area G while *T.pellucidus* and *T.dumosus* overlap area D and F. There are two species endemic to the Riviersonderend, Hottentots-Holland range of area D, *T.stokoei* and *T.pulcher*.

The Langeberg centre, area E in the parsimony analysis, is supported by three species, *T.karooica, T.ellipticus* and *T.amoena*. The distribution of *T.karooica* extends across the Gouritz River valley to the Outeniqua range.

The adjacent south coast flats is another area of endemism, corresponding to area F. On the map of distributions (Fig. 23) the area of overlap is smaller and more coastal than that circumscribed for area F. The eastern most boundaries of *T.pluristachyus* and *T.paniculatus* overlap with the distributions of *T.pellucidus* and *T.dumosus*. *T.pellucidus* and *T.dumosus* range from the Overberg to Cape Agulhas. In the Overberg region the distributions overlap with the Riviersonderend, Hottentot-Holland region of endemism.

The Cape Peninsula represents the most strongly supported area of endemism, area G. *T.nutans* and *T.levynsieae* are both endemic to the Table Mountain chain. *T.punctatus* occurs on low altitude areas of the Cape Peninsula with outlying populations extending up the west coast to the Malmesbury area. *T.spicigerus* has a similar distribution but it is restricted to coastal dunes. There is an outlying specimen of *T.spicigerus* adjacent to the Overberg centre of endemism.

T.arenarius is another species whose distribution overlaps with the Cape Peninsula area of endemism and that of the Overberg region.

A single species, *T.papyraceus*, is endemic to the high altitude region of the Klein Swartberg.

Species with similar geographical distribution patterns

The initial differentiation in this phenogram (Fig. 24), at a similarity level of 0.003, corresponds to the dry northern area (A and B; Fig. 21) and the Cape Peninsula-South coast region (C and D; Fig. 21).

The first group, *T.acuminatus-T.papyraceus*, is a dry arid coast and inland mountain group, including species from the west coast inland to the Cedarberg-Koue Bokkeveld and across the Karoo to the Klein Swartberg (Fig. 25).

The second group, *T. amoena-T.stokoei* includes those species from the Cape Peninsula, Overberg, Riviersonderend, Agulhas and south coast flats and adjacent mountain ranges. This group divides into two at a similarity level of 0.007 (Fig. 24) forming the *T.amoena-T.glaber* group, from the Langeberg and Tsitsikama ranges (D; Fig 21), and *T.arenarius-T.stokoei* group, from the Cape Peninsula, Agulhas and South coast flats (Fig. 25).

T.glaber is an anomaly in the Langeberg group as it has a coastal distribution, ranging from Knysna eastwards to the Dwessa region in the eastern Cape.

The first division, at similarity value of 0.016, in the Cape Peninsula-South coast flats section, *T.arenarius-T.stokoei*, separates *T.stokoei* from the rest of the group. The position of *T.stokoei* is an anomaly. This is a species with a distribution restricted to the Riversonderend mountains. It may have been placed with the Cape-Peninsula-Overberg group or with those species occuring on the south coast flats or in adjacent mountain ranges. It is possible that the combination of the position of the grid relative to the geographical topology and collection gaps placed the documented distribution of the species between the two divisions.

The second major division (similarity value 0.047) distinguishes the group of species on the south coast flats from the *T.arenarius-T.erectus* group, which has a distribution ranging from the Cape

Peninsula across the Overberg mountains to Cape Agulhas. Within this Cape Peninsula- Overberg group there are further subdivisions; the first group identifying the ubiquitous species, *T.arenarius-T.dumosus*, whose distributions cover the entire Cape Peninsula-Overberg region and the second group separating those species with restricted distributions within the Cape Peninsula-Overberg region, theTable Mountain Chain endemics, *T.nutans* and *T.levynsieae*, and those species found on the Cape Flats, *T.obtusus-T.spicigerus.*

Area cladograms

Areas of similarity

Five informative paralogy free sub-trees (Table 24) were identified from the taxon-area cladogram of *Thamnochortus* (Fig 26a) which used the four defined areas of similarity as biogeographic units.

Table 24. The five informative paralogy free sub-trees from the taxon-area cladogram using areas of similarity as biogeographic units.

Clades	Informative sub-trees
T.dumosus	(D,(C,B)) and (D,(C,A))
T.amoena	(D,(C,B))
T.stokoei	(C,(B,A))
T.sporadicus	(D,(A,C))
T.pellucidus	No informative sub-trees
T.erectus	No informative sub-trees
T.pluristachyus	No informative sub-trees

The general area cladogram (Fig. 26b), resulting from the combination of these trees, groups the dry areas of the Cedarberg, West coast (area A) and the Koue Bokkeveld, Karoo, Klein Swartberg (area B) together. Area C, which includes Cape Peninsula, Cape Flats as far north as Malmesbury, south western mountains south to Agulhas and north to Olifants river, is the sister area to the dry areas. The Langeberg centre and south coast region are basal in the cladogram.

Narrow areas of endemism

Twelve informative paralogy free sub-trees (Table 25) were found on the taxon-area cladogram of *Thamnochortus* which used narrow areas of endemism as biogeographic units (Fig 27a).

Table 25. The twelve informative paralogy free sub-trees from the taxon area cladogram using narrow areas of endemism as biogeographic units.

Clades	Informative sub-trees
T.dumosus	(F,(D,A)) and (D,(G,A)) and (F,(G,A))
T.amoena	(E,(D,A))
T.stokoei	(D,I,A))
T.sporadicus	(G,(F,D)) and (G,(F,D))
T.pellucidus	(H,(D,E)) and (H,(F,E)) and (H,(G,E))
T.erectus	(D,(E,G)) and (F,(E,G))
T.pluristachyus	No informative sub-trees

The general area cladogram, resulting from a combination of the informative trees in a three area analysis, lacks resolution (Fig. 27b). The Klein Swartberg (area I), locality of a single species- *T.papyraceus*, is basal to the polytomy which includes all other endemic areas. The general cladogram for areas of endemism is thus uninformative on relationships between areas of endemism.

The lack of resolution in the cladogram is due to the overlapping distributions of *Thamnochortus* species, which did not allow the identification of discrete areas of endemism. Species occurred in more than one area of endemism confounding the historical pattern of area relationships.

BIOGEOGRAPHICAL AND ECOLOGICAL SPECIATION PATTERNS

The maps and ecological diagrams illustrate that within each clade, species distribution is related to different features, predominantly rainfall and altitude.

Within the *T.acuminatus-T.rigidus* clade (Fig. 28), the *T.dumosus* clade and *T.amoena* clade reflect similar ecological patterns. *T.acuminatus* experiences a drier climate in the Cedarberg than *T.fruticosus* or *T.dumosus* do in the southern, more mesic region. Both *T.fruticosus* and *T.dumosus* are found in damper habitats (Fig. 29a). Similarly, *T.cinereus* and *T. rigidus* lie along different mountain ranges, although there is some overlap in the Karoopoort region. *T.rigidus*, is located along the comparatively more arid Klein Swartberg mountain range while *T.cinereus* is found in the coastal more mesic Langeberg range. The sister species to *T.cinereus* and *T.rigidus* is *T.amoena* whose distribution range overlaps with that of *T.cinereus* in the Langeberg.

The two species are distinct in terms of altitude, with *T.amoena* occurring at lower altitudes (Fig. 29b).

The *T.stokoei* clade exhibits a similar pattern with respect to the north-south rainfall gradient (Fig. 30). The *T.comptonii* clade is located in the dry northern Cedarberg, Koue Bokkeveld and Klein Swartberg region, while *T.stokoei*, is found in the wetter Riviersonderend mountains. The sister species *T.scabridus* and *T.schlechteri* share the same distribution and are only separated in terms of substrate and altitude (Fig. 31). *T.scabridus* is commonly found in deep sand which may be aeolian in origin while *T.schlechteri* is found at higher altitude in gravelly rocky soil. A small population of the sister species *T.platypteris* lies adjacent and marginally overlapping with this distribution. *T.comptonii* lies between this pocket and the main locality of *T.platypteris* in the northern Cedarberg, overlapping with this northern distribution. *T. comptonii* occurs at higher altitude than *T.platypteris* (Fig. 31). The sister species to this clade, *T.papyraceus* and *T.stokoei*, are geographically separate from the species complex clade. *T.papyraceus* occurs in the Klein Swartberg while *T.stokoei* is found in the Riviersonderend mountains.

The distribution of species within the *T.bachmanii* clade differs from the previous clades in that there is considerable geographical overlap. Within this clade is the *T.arenarius-T.sporadicus* polytomy. The distribution of *T.arenarius*, *T.gracilis* and *T.obtusus* are virtually entirely contained with the distribution ranges of the more wide spread species, *T.sporadicus* and *T.lucens* (Fig. 32). Each of the species in this polytomy is found on the Cape Peninsula but are ecologically distinguished by substrate, or altitude or flowering time (Fig. 33).

T.obtusus and *T.sporadicus* both favour seasonally damp sandy substrate, but *T.obtusus* tends to be restricted to below 300m while *T.sporadicus* is found between 1000 to 1500m. *T.gracilis* occurs at the same altitude as *T.sporadicus* but in dry sandy-gravel. *T.arenarius* and *T.lucens* are sister species occurring in the same substrate, sandy-gravel at the same altitude (300-1000m). *T.lucens* is the more widespread species with the distribution of *T.arenarius* being virtually entirely contained within that of *T.lucens* (Fig. 32). Specimens and observations indicate that *T.lucens* flowers in both spring and autumn. *T.arenarius*, however, flowers only in late autumn, after the autumn flowering of *T.lucens* and prior to the spring flowering (Fig. 33).

The sister species to the *T.sporadicus* clade is *T.punctatus*. The distribution of this species extends from the Cape Peninsula north to just inland of Saldanha, overlapping considerably with the distributions of the species in the polytomy (Fig. 34). In terms of substrate, *T.punctatus* is distinct from all the polytomy species, occurring in dry sandy soil (Fig 35). Bordering on the south-eastern most enclave of the *T.obtusus* and *T.lucens* distribution lies *T.insignis*. The distribution of this species has been extended to the east and west as a result of cultivation. The boundaries of the original distribution are marked on the map. *T.bachmanii* is sister species to the entire clade. The distribution of this species overlaps broadly with that of *T.punctatus* and the two wide spread species belonging to the polytomy, *T.lucens* and *T.sporadicus*. However, unlike the other species in the clade, *T.bachmanii* does not occur on the Cape Peninsula and it has a distribution range far greater than any other species in the clade, extending northwards up the west coast (Fig. 34).

The members of the *T.pellucidus* clade are geographically distinct (Fig. 36). *T.guthrieae* distribution extends from the Cape Peninsula to the Bredasdorp flats inland to the Paarl Mountains. The sister taxon, *T.ellipticus*, is endemic to the Langeberg. These species cover an altitudinal range of 300 to 1000m and grow in similar substrate conditions (Fig. 37). *T.glaber*, the sister taxon, has a widespread, patchy coastal distribution occurring in seasonally damp, sandy soils from the Knysna area eastwards into the Transkei. The sister species to the clade *T.pellucidus*, also has a coastal distribution, occurring in the dry sandy soil of the Bredasdorp flats. The distribution range of *T.pellucidus* lies within that of *T.guthrieae*, but the two species are separated altitudinally (Fig. 37).

The *T.erectus-T.pluristachyus* clade has two smaller clades circumscribed within it. Ecologically these two clades are distinguished on the basis of soil type. The *T.erectus* clade occurs on coastal sands and Table Mountain Group sandstone, while the species of the *T.pluristachyus* clade are restricted to growing on, or immediately adjacent to, limestone pavement. The distribution areas of the two clades is very similar, predominantly south-coast, *T.karooica* is an exception. Each clade has been represented on a different map.

T.erectus has a disjunct distribution, occuring on the Cape Peninsula and along the south coast to Knysna (Fig. 38). This taxon is the sister to the *T.karooica-T.spicigerus* pair. Like *T.erectus*, *T.spicigerus* is a coastal species. The distribution of *T.spicigerus* lies from the Cape Peninsula up to the Langebaan area, overlapping with the distribution of *T.erectus* in the Cape Peninsula area. *T.erectus* favours more acid coastal sands and Table Mountain Group sandstone while *T.spicigerus* occurs on sandy coastal soils. The species also differ in flowering time. *T.erectus* flowers in spring and *T.spicigerus* in autumn (Fig. 39). *T.karooica*, the sister species of *T.spicigerus* has a distinct karoid distribution.

The species in the limestone clade, *T.pluristachyus* clade, have very similar distributions and altitudes and there is considerable overlap in the distribution ranges (Fig. 40). Species are predominantly distinguished ecologically and biologically (Fig. 41). *T.muirii* has the most easterly distribution in the group and, at the western boundary, *T.muirii* and the sister species *T.paniculatus* co-occur. Both species flower in spring but at slightly different times, first *T.muirii* and then *T.paniculatus*. Field observations indicate that the species do not grow in close proximity to one another either, *T.muirii* preferring shallow soil on limestone while *T.paniculatus* grows in, amoung and adjacent to limestone outcrops. The area of overlap of these two species marks the eastern boundary of *T. fraternus*, which extends to the Cape Peninsula on and adjacent to limestone soils. *T.fraternus* flowers in autumn. *T.pluristachyus* co-occurs with both *T.paniculatus* and *T.muirii*. There is a slight difference in flowering time, *T. pluristachyus* flowers in early spring. Populations of *T.pluristachyus* have been seen side by side with populations of *T.paniculatus*, but the former is restricted to the limestone outcrops.

DISCUSSION

THE SPECIES COMPLEX

Associations of specimens

In both the PCA (Fig. 2) and the cluster analysis (Fig. 3) most specimens are associated into groups matching the currently recognised species; for convenience they are named as the species..

The PCA analysis (Fig. 2) illustrates the large amount of variation found within, rather than between species, particularly the *T.scabridus*, *T.comptonii*, *T.stokoei* and *T.schlechteri* associations. The many sub-groups in the cluster analysis (Fig. 3) may also be due to the variation in characters and presence of intermediate forms. However, the hierarchical nature of a clustering algorithm such as UPGMA may force unnatural groupings (James and McCulloch 1990) which do not reflect the true pattern of similarities between groups (Sneath and Sokal 1973). The anomalies in specimen associations present only in the phenogram may thus be a function of the clustering method.

Characters of groups

In the PCA (Fig. 2) characters based on female flowers make the greatest contribution to axis 1. Axis 2 represents plant robustness while axis 3 is largely composed of female bract characters.

Character variation within clusters is high and few characters are consistent within groups (Appendix 2). The resolution of *T.platypteris* specimens into two groups in the UPGMA analysis (Fig. 3) is an example of this variation. The flowers of the first group of *T.platypteris* are the largest in the species complex and this is the only group which lacks the hyaline margin on the female bracts. In contrast, the second group has slightly smaller flowers, although they are still larger than those of other specimens, and hyaline margins on the female bracts. The specimens of the two clusters are not geographically distinct. This morphological variation is a feature of *Thamnochortus* and may be an indicator of genetic plasticity and ecological malleability (Wiens 1995). If this is true, then many morphological features of *Thamnochortus* are traits, and thus unsuitable for inclusion in cladistic analysis (Nixon and Wheeler 1990).

Biogeography and ecology of groups

Geographically the distributions of the groups in the species complex are not all completely disjunct. *T.bachmanii and T.stokoei* have adjacent distributions (Fig. 4 and 5) as do *T.scabridus* and *T.schlechteri* (Fig. 6 and 9), while the locality of some specimens in the *T.platypteris* clusters (Fig. 8) are situated within the distribution areas of *T.comptonii* (Fig. 7), *T.schlechteri* (Fig. 6) and *T.scabridus* (Fig. 9).

T.bachmanii specimens occur at fairly low altitudes (Table 23) in sandy-gravelly habitats. Adjacent to the southern group of *T.bachmanii* specimens lies the south western mountains where *T.stokoei* specimens tend to be found at high altitude in damp gravelly-rocky substrates. *T.schlechteri* specimens are collected from the Koue Bokkeveld region at a similar altitude to that of *T.stokoei*, but in a much drier substrate.

The distribution of the *T.platypteris* clusters overlaps with *T.comptonii* localities in the northern Cedarberg and with *T.scabridus* and *T.schlechteri* in the Koue Bokkeveld region. There is no ecological or geographical distinction between the two *T.platypteris* clusters. *T.comptonii* is distinct from *T.platypteris*, occurring at a much higher altitude (Table 23). Similarly, *T.schlechteri* specimens in the Koue Bokkeveld are ecologically distinct from *T.platypteris*, occurring at higher altitudes. *T.scabridus* is found at the same altitudes as *T.platypteris* but grows in distinct substrate, sandy blow-outs rather than gravelly sand.

Recognition of species

The pattern observed in the field was indicative of closely related groups shifting across ecological gradients. The question was, which species should be recognised for cladistic analysis? *T.bachmanii*, *T.stokoei* and *T.schlechteri* specimens form discrete if closely related groups, with two exceptions. *T.bachmanii*88 which groups morphologically with *T.stokoei* because of the solitary spikelets but is geographically within the distribution of *T.bachmanii*, and *T.stokoei*62 which is a morphological outlier to the entire species complex due to the length of the odd outer tepal in the female flower, but which lies within the distribution of *T.stokoei*.

The relationships between the *T.platypteris*, *T.comptonii* and *T.scabridus* specimens based on morphology are far more complex. The specimens of *T.platypteris* are separated into main two groups in the cluster analysis. This pattern is not repeated in the PCA analysis and there does not appear to be any geographical or ecological difference in the two groups of specimens. In the cluster analysis, based on morphology, one of the groups, *T.platypteris*2, is embedded in a group with the *T.comptonii* and *T.scabridus* specimens. The other group *T.platypteris*1 is particularly similar to the *T.comptonii*, *T.platypteris*2, *T.scabridus* group. Geographically *T.scabridus* is distinct but localities for specimens of *T.platypteris* and *T.comptonii* overlap; however *T.comptonii* and *T.platypteris* specimens are distinct in altitude and substrate.

The complexity of the patterns does not resolve the species boundaries. It does, however, illustrate the variation in characters found in *Thamnochortus*. Considering the extent of the variation it was decided to err on the side of caution and recognise each species separately rather than including *T.platypteris*, *T.comptonii* and *T.scabridus* in one species and having many polymorphic characters in the cladistic matrix. The species delimitations of Linder (1985) and Pillans (1928; 1945) were used recognising *T.bachmanii*, *T.stokoei*, *T.schlechteri*, *T.platypteris*, *T.comptonii* and *T.scabridus*.

CLADISTICS

Cladogram structure

The cladogram is very well resolved (Fig 10a and b), with lack of resolution only in the *T.sporadicus* clade. By conventional methods the support for this topology is weak.

Testing the cladogram

Bootstrap support for the major nodes, apart from *T.acuminatus-T.stokoei*, is generally over 50%. However, one clade in particular, *T.bachmanii* clade, is very weakly supported in the bootstrap analysis. The *T.gracilis-T.obtusus* clade has a bootstrap value of 10.32%. While this value is not high, it is understandable in the light of the variation in characters within the genus *Thamnochortus*. However, with the inclusion of the sister species *T.insignis* and *T.bachmanii* the bootstrap values drop to 1% and 2% respectively. This is particularly poor support and affects the bootstrap values on the rest of the cladogram (Fig. 12).

These low bootstrap values are probably related to the malleable relationship which these two species have with this clade. Given that there are synapomorphies supporting the placing of these species in other clades, e.g. male spikelets lorate joining *T.punctatus*, *T.insignis*, *T.bachmanii*, *T.karooica*, *T.spicigerus* and *T.fraternus*; *T.insignis* and *T.erectus* share the apomorphy of subsidiary cells which overtop the guard cells, it is possible that placing them in this group would improve the bootstrap values. However, removing the three sister species to the polytomy clade in different combinations, did not alter the terminal group arrangements to any great degree, although in some cases the basal nodes from *T.arenarius-T.levynsieae* collapse to form a polytomy.

The low bootstrap values are consistent with the low consistency index and absence of unique synapomorphies, however they do not reflect the resolution of the terminal clades determined during the reiterative deletion of the problem taxa, *T.bachmanii*, *T.insignis* and *T.punctatus*. Poor bootstrap values may be due to few characters or lack of character congruence (Sanderson 1989). The latter explanation applies to *Thamnochortus*.

Consistency in characters

Features in *Thamnochortus* exhibit a great deal of variation in some respects and little in others. For example, continuity between different states meant that in four characters a species was coded as `either/or' for the character states. The intermediate forms hindered the delimitation of states, thus variation was not consistently extreme to allow for definitive character state delimitation.

The majority of characters in *Thamnochortus* had what may be considered a very low consistency index, between 0.3 and 0.4 (Fig. 11). The low consistency indices is related to high levels of homoplasy (Sober 1988). Several studies have indicated a link between homoplasy and the size of the data matrix (Chappill 1989; Sanderson and Donoghue 1989; Klassen *et al.* 1991). Klassen *et al.* (1991) graphically portrayed the relationship between the number of taxa, characters and the consistency index for random data; for data sets of between 30 to 35 taxa and 50 characters a consistency index of between 0.1 and 0.15 could be expected. Furthermore, relating the number of taxa to the consistency index using data from published literature, Klassen *et al.* (1991), illustrated that for data sets of between 30 to 40 taxa a consistency index of between 0.1 and 0.3 can be expected. Thus, the ci values for the cladogram, and characters, of *Thamnochortus* may be related to the size of the data matrix. Data from other studies support this hypothesis, for example, a study in the Leguminosae with a data matrix of similar size (37 taxa and 81 characters) had a consistency index of 0.256 (Ridder-Numan 1995).

Synapomorphic Characters

The *T.stokoei* clade is the only group where the female bracts are chartaceous (ci= 1; Appendix 1). Similarly the bootstrap value for this clade is high, 59.91% (Fig. 12). The two clades within the *T.stokoei* clade do not have any unique synapomorphies and this is reflected in the respective bootstrap values. The *T.acuminatus-T.fruticosus* pair are the only species to have epidermal thickening exclusively on the outer walls. The bootstrap value for this pair is 62%.

The only other two groups with unique synapomorphic characters are within the *T.obtusus* clade and *T.plurisachyus* clade. *T.arenarius*, *T.lucens* and *T.obtusus* are the only species to have female bracts 8mm long. The bootstrap value in support of this clade does reflect the support of a unique synapomorphy because of the lack of resolution in the relationship between *T.gracilis*, *T.obtusus* and *T.sporadicus*. The female bract apices of the *T.pluristachyus* clade are distinct in that they are recurved. Given this apomorphy it is surprising that the bootstrap value is 32.71%.

Although there is a dearth of unique synapomorphies in *Thamnochortus*, character distributions are relatively restricted. For example, a v-shaped female spikelet is found in the *T.comptonii-T.stokoei* clade and only *T.acuminatus* has a similar shaped inflorescence. Female flowers narrow oblong or not, defines two neat groups, *T.ellipticus-T.glaber* and *T.fraternus-T.paniculatus*. Other characters which follow this pattern are described in the results. It is the interaction of characters with restricted patterns which defines the clades.

The ci values of the cladograms (Fig. 10a and 10b) are certainly affected by the many homoplasious characters (Sober 1988). The degree of homoplasy is not only determined by the inherent nature of the characters; the size of the data matrix, particularly the number of taxa, also has a large impact on homoplasy levels (Chappill 1989; Klassen *et al.* 1991; Sanderson and Donoghue 1989). Few of the major nodes are supported by unique synapomorphies. The relatively poor character support for the clades is reflected in the values of the bootstrap analysis. Despite the lack of synapomorphic characters and poor bootstrap values, the consistency index for the cladogram is comparable to that for data sets of similar size (Sanderson and Donoghue 1989; Klassen *et al.* 1991). Furthermore, evidence from the reiterative deletion of problem taxa indicate that the resolution of the terminal clades, i.e *T.dumosus*, *T.amoena*, *T.stokoei*, *T.pellucidus*, *T.erectus* and *T.pluristachyus* clades, is robust although the support for the more basal nodes is ambiguous. Since these are the clades of interest in comparative biology and historical biogeography analysis, the topology of the cladograms (Fig 10a and 10b) was considered a suitable basis for further analysis.

COMPARATIVE BIOLOGY AND EVOLUTION

Phylogenetic assessment of biological features of *Thamnochortus*

Evolution of seeding and resprouting condition

It cannot be determined whether resprouting or seeding is the ancestral condition. The species most basal within *Thamnochortus*, *T.levynsieae*, is a resprouter. However, the basal position of this node is not secure. Furthermore, lack of resolution regarding fire survival habit within the next clade, *T.erectus-T.pluristachyus*, and within the outgroup means that the ancestral node is not resolved in terms of fire survival strategy (Fig. 13). For this reason it is unclear whether the resprouting condition was ancestral, lost and reappeared, or alternatively, whether reseeding is ancestral and resprouting habit has evolved several times. Thus, reseeding could be a relictual condition (Frumhoff and Kern Reeve 1994).

Contrast in height between seeders and resprouters

Plants in the resprouting species of *Thamnochortus* are generally taller than the sister seeding clades (Table 11). This is in contrast to the present hypothesis (le Maitre and Midgley 1992), the multi-stemmed growth-form and necessary allocation of resources to a lignotuber reduces the opportunity for sustained height growth in the lignotuberous resprouters of fynbos. Thus, they are often overtopped by taller seeders.

In *Thamnochortus* both seeding and resprouting species are multi stemmed and have similar rhizome morphology: thus, the rationale of le Maitre and Midgley (1992) regarding seeders and resprouters is not wholly applicable to *Thamnochortus*.

A comparison of height between seeders and resprouters in *Rhodocoma*, using the data of Linder and Vlok (1991), indicates that seeders are generally taller than resprouters. In the first lineage the seeder *R.arida* (1.5-3m) is generally taller than the resprouter *R.fruticosa* (0.4-0.8m). In the second lineage the seeder lineage contains two species, *R.gigantea* and *R.gracilis*, which are 3m and 0.5-1m respectively. The sister resprouting lineage is 1m high. Thus, within the *Restionaceae*, between genera of similar growth forms, there is no consistent pattern.

Comparison of reproductive output in seeders and resprouters

Seeders and resprouters in *Thamnochortus* produce similar quantities of seed, except for *T.cinereus-T.rigidus* and *T.erectus-T.spicigerus* (Table 12a,b,c and Fig. 14). Similar results have been found in non-phylogenetic comparisons of chaparral shrubs (Keeley 1977) and *Banksia* (Zammit and Westoby 1987). However, studies on the legume *Bossiaea* (Hansen *et al.* 1991) and the restiad *Lygnia barbata* (Bell and Pate 1993) indicated that seeders have a higher reproductive output.

In studies of *Bossiaea*, Hansen *et al.* (1991) showed that seeders produced more flowers than sprouters. Reproductive costs were lower for seeders as the flowers were considerably smaller than those of resprouters. The ratio of ovules to carpel in seeders was less than that of resprouters, however the final seed numbers per ovule were comparable due to poor survivorship in ovules of resprouters. Final reproductive output was greater in seeders than in resprouter because of the higher numbers of flowers. Less detailed studies of Bell and Pate (1993) indicated that a seeder morphotype of *Lygnia barbata* produced more male and female spikelets per culm than resprouter morphotypes.

The source of conflicting results may lie in the notable absence of phylogenetic comparisons in the cited evaluations. Historical constraints on reproductive output in different clades may result in underestimated or overestimated reproductive output for seeder and resprouter species. Incorporating the evolutionary factor may illustrate a poor connection between reproductive output and fire survival habit, such as in *Thamnochortus*. Alternatively, it is possible that the range data used in *Thamnochortus* did not accurately represent the reproductive output of species, resulting in a misleading impression of the reproductive output of seeding and resprouting lineages in *Thamnochortus*.

Relationship between distribution area and fire survival habit

Seeding lineages of *Thamnochortus* are more restricted in their distribution area than resprouting lineages (Table 13). This reinforces similar findings of non-phylogenetic studies on Proteaceae, i.e. *Banksia* (Lamont and Markey 1995), *Leucospermum* (Rourke 1972), *Protea* (Rourke 1980) and *Mimetes* (Rourke 1984).

The size of a distribution area is the result of the ability to persist in the landscape or dispersal ability (Howe and Smallwood 1982; Lamont and Markey 1995). Resprouting lineages may be more persistent in the landscape because plants are not necessarily eliminated by fires (Keeley 1986). Subsequently, even though populations of resprouters may grow more slowly than those of seeders, they may be relatively more stable. In contrast, the boundaries of seeding populations may be subject to greater change in response to fire, restricting the possibility of extended distribution over time (Cowling *et al.* 1992).

In fynbos legumes distribution appears to be largely related to habitat specificity (Schutte *et al.* 1995). Both seeding and resprouting habitat specificists have localized distributions; while habitat generalists have significantly wider distributions. However, most fynbos legume seeders are habitat specific, even those which are generalists are geographically restricted. Thus, the general pattern in distribution size may be similar to that of *Thamnochortus* although it is partially masked by the differentiation into habitat specialists and generalists. *Thamnochortus* species are all habitat specific (Table 19) and so distribution patterns are not confounded by the complications of differential habitat specificity.

Association between fire survival habit and female outer tepal specialization

In *Thamnochortus* winged outer female tepals were derived independently of fire survival habit and not as a direct result of the evolution of a reseeding habit (Table 16a). However, the probability of wings evolving randomly was low, implying that there may be an indirect or masked connection between wings and seeding habit. The evolution of keels appears to be closely associated with a switch to resprouting habit (Table 16b). This does not imply exclusivity. In the group of *Thamnochortus* species that have keeled female outer tepals (Fig. 15), there are equal numbers of seeders and resprouters, while nine resprouting species have winged female outer tepals. The association between the evolution of wings and seeding, keels and resprouting is not based on the statistics of individual numbers of species which have the various combinations, but is an assessment of the correlation of evolutionary events.

The proposal that the evolution of winged tepals are associated with seeding habit and keeled tepals with the resprouting habit is an extension of the hypothesis of Zammit and Westoby (1987). The study on seeding and resprouting *Banksia* shrubs concentrated on seed release, seed germination, seedling establishment and survivorship. The results suggested that selection processes led to more pronounced adaptations for the reduction of seedling mortality in seeders than in resprouters. Winged tepals, in species of *Thamnochortus*, may increase dispersal distances, possibly increasing gene flow and colonizing potential (Howe and Smallwood 1982; Johnson 1992) and reducing predation pressures (le Maitre and Midgley 1992). Thus, winged tepals may be an adaptation in seeding species reducing the probability of seedling mortality (Howe and Smallwood 1982). The reduction of keels associated with the resprouting habit may be a result of differential resource allocations commonly associated with resprouters and seeders (Hansen *et al.* 1991).

However, the connection between winged tepals and the seeding habit is tenuous and the lack of information on resource allocation, germination rates and seedling establishment restricts the argument to speculation. Further investigation in these areas may uncover the relative advantages and disadvantages of wings and keels, ultimately determining the extent of a connection between fire survival habit and the specialization of the female outer tepal.

Resprouters do not appear to be at a competitive disadvantage in terms of the number of flowers or presence of wings. Sprouters generally have similar numbers of flowers to seeders and, in certain cases, resprouting species have the dispersal advantage of winged seeds. In addition, there is the possibility that sprouters persist in the landscape. This needs to be confirmed by assessing the stability of resprouting vs seeding populations in the landscape. However, there is the possibility that seeding is a plesiomorphic condition with the resprouting habit arising in several independent evolutionary events. Thus, it is necessary to evaluate probable evolutionary pressures which would promote the evolution of the resprouting condition.

Influential factors in the evolution of fire survival habits

Key differences pertaining to fire survival habit, such as shoot growth (Hansen *et al.* 1991) and location of starch reserves (Pate *et al.* 1990; Pate *et al.* 1991), are not known in *Thamnochortus* and the mechanism of resprouting is poorly understood. In the majority of seeding-resprouting comparisons, the exceptions being the Myrtaceae (Pate *et al.* 1990) and certain of the Restionaceae (Pate *et al.* 1991), carbohydrate reserves were found to be higher in rhizomes or roots of resprouters than in seeders. Pate *et al.* (1991) suggested that in those species of resprouter which lacked starch reserves, carbohydrates degraded from wall reserves may act as an energy source in post-fire regeneration. It appears that similar patterns of reserve storage may be found in *Thamnochortus*, but the data are currently not available to test these hypotheses.

Hypotheses regarding ecological evolutionary pressures

Soil nutrients

There are similar percentages of seeding and resprouting species on nutrient poor Table Mountain Group sandstone (Table 17). Coastal sands have a higher proportion of seeders to resprouters while only seeding species are found on limestone soils. Coastal sands and limestone soils are more fertile than Table Mountain Group sandstone (Cowling *et al.* 1994). Thus, in *Thamnochortus* seeders appear to dominate on the more nutrient rich soils. However, recent evidence indicates that there are limitations to the edaphic resources on limestone as the pockets of limestone soils are usually small and easily depleted (Mustart *et al.* 1994).

Species found on coastal sands are in two clades. *T.bachmanii*, *T.punctatus* and *T.insignis* are all basal to the resprouting *T.arenarius-T.sporadicus* clade, while *T.spicigerus* is in the *T.erectus* clade (Fig. 10a). Thus it is not possible to test the sister lineage comparisons statistically as there are only two independent contrasts of seeders and resprouters on different soils (Table 18). *Thamnochortus* species found on limestone are all in the *T.pluristachyus* clade (Fig. 10a). All of the species in this clade are seeders. This may be significant as every other clade in *Thamnochortus* has resprouters but it is not possible to test statistically as there is only one limestone clade.

In the literature there are two conflicting hypotheses with regard to soil nutrients and distribution patterns of seeders and sprouters. Le Maitre and Midgley (1992) suggested that, since the cost of nutrient allocation to seeds is higher compared to maintenance of dormant buds in resprouters, one would expect seeders to occur on nutrient rich soils. This does not account for the maintenance of starch and nutrient reserves in the resprouter. However, Lamont and Markey (1995) and Keeley (1986) found that resprouters occurred more frequently on more fertile soils, with seeders being restricted to nutrient poor soils. These studies did not use phylogenies for the basis of comparisons. In *Thamnochortus* the proportions of seeders and resprouters on different substrates (Table 17) indicates that the seeding habit is associated with nutrient rich soils; however the comparison between seeding and resprouting lineages was uninformative, due to few replications within the genus.

The presence of a single limestone clade, *T.pluristachyus,* in the genus suggest that factors other than seeding or resprouting determine the evolution of substrate specificity; however the absence in dry habitats. The lack of accurate assessment of habitat drainage and soil texture for each species limits the comparison. Detailed information on soil type, texture and moisture content of habitats is needed to test these hypotheses.

Relatively high number of seeding species are usually associated with areas of reliable high rainfall (le Maitre and Midgley 1992; Lamont and Markey 1995; Schutte et al. 1995), or high moisture content, e.g river banks and marshes (Schutte et al. 1995). However, other studies indicate that resprouters are replaced by seeders at more xeric sites (Keeley 1986). Furthermore, incorporating species interaction, it is possible that if resprouters were present in an area, higher rainfall would encourage quicker regeneration in a post-fire environment (le Maitre and Midgley 1992).

The present lack of clarity in a pattern of association between fire survival habit and rainfall in *Thamnochortus* makes it difficult to relate the evolution of the resprouting habit to a shift in rainfall patterns. There is evidence of such a shift in the Miocene, which led to the aridification of Namaqualand (Linder et al. 1992). This change in rainfall patterns is thought to have affected speciation events in *Microloma* (Bruyns and Linder 1991) and may have impacted those of *Thamnochortus*.

Habitat specificity and fire survival habits

Resprouters may be more environmentally resilient than seeders (Lamont and Markey 1995) and thus not habitat restricted, being able to occur in many different climatic and edaphic conditions. It has already been shown that resprouters are considerably more widespread than their sister seeders, however all species in *Thamnochortus* appear to occupy a narrow range of habitats (Table 19). There is variation in altitudinal range but this only occurs in some species and even then there are restrictions to higher or lower altitudes within species.

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Grid diversity - Species richness

The Cape Peninsula, with thirteen species, is the area with the highest number of species of *Thamnochortus* (Fig. 19). The only area with similar numbers is the coastal flats near Cape Agulhas. The Overberg region, incorporating the Hottentots Holland and Riviersonderend mountains, represents the next area of species richness followed by the Cedarberg and Langeberg-Outeniqua regions which have similar numbers of *Thamnochortus* species.

This pattern is similar to that documented by Oliver *et al.* (1983) and Weimarck (1941), areas rich in *Thamnochortus* species (Fig. 19) are generally species rich (Oliver *et al.* 1983). However, Oliver *et al.* (1983) showed that the Overberg region has the highest overall plant diversity whereas, while the Cape Peninsula is the region of species richness for *Thamnochortus*.

Phytogeographic areas defined by *Thamnochortus*

Areas of similarity

The demarcation of biogeographic areas through the grouping of grid squares with similar species located four main areas A: dry west coast-northern Cedarberg association, B: dry inland Koue Bokkeveld, Karoo and Klein Swartberg, C: the Cape Peninsula and flats across the south western mountains to Riviersonderendberg including the adjacent south coast flats, and D: the south coast flats east of Cape Agulhas inland including the mesic south coast mountains (Fig. 20 and 21). The large Cape Peninsula-Riviersonderend region, area C, has 3 sub areas, C1: southerly west coast and Cape Peninsula, C2: coastal south western mountains and C3: inland south western mountains and Riviersonderend. The south coastal flats, part of area D, has two sub-groups; D1, found between Cape Agulhas and the Bree river and D2 which includes the coastal flats on the eastern side of the Breede river and the Langeberg mountain range (Fig. 20 and 21). The four areas were defined by species with similar distributions, i.e occurring in the same grid squares. Over half the species (nineteen; Table 22) are endemic to one of the four areas, thus, with the understanding that there are many varied definitions for endemism, it is possible to consider these areas of similarity broadly defined areas of endemism (Platnick 1991).

Phytogeographic areas in fynbos

Equivalents to areas A, B, C and D can be found in both Weimarck (1941) and Oliver *et al.* (1983), but the boundaries of the corresponding areas are different. Similarly, the limits of certain sub-centres differ as do the associations of some sub-centres with specific biogeographic divisions. Area A corresponds roughly with the North-western centre of Weimarck (1941) and Oliver *et al.* (1983), except that it excludes the Koue Bokkeveld, now part of area B, and includes elements of the West Coast Flats, equivalent to a south-western sub-centre (Weimarck 1941; Oliver *et al.* 1983). In addition to the Koue Bokkeveld region, area B includes the Karoo Mountain centre of Weimarck (1941). Oliver *et al.* (1983) did not distinguish a separate dry inland centre. The Koue Bokkeveld region falls into the North western centre while the Swartberg mountains are included in the southern centre. Area C is considerably smaller than it's counterpart, the south-western centre (Weimarck 1941). The sub-divisions within it, however, correspond favourably with those recognised by Oliver *et al.* (1983) that were considered equivalent to Weimarck's (1941) sub-centres.

Adjacent to the Cape Peninsula sub-section lie the Cape Flats, which are analogous to the west coastal centre of Oliver *et al.* (1983). However, the northern boundary of this area in *Thamnochortus* is further south than in previous studies. The area referred to as the Overberg by Oliver *et al.* (1983) is split into two groups in *Thamnochortus* (C2 and C3), with the most coastal mountains being distinguished from the inland mountains. The Bredasdorp sub-centre, included in the south-western centre of Weimarck (1941) and Oliver *et al.* (1983), is correlated to area D in *Thamnochortus* (D1). Apart from this, the rest of area D corresponds well with the southern area of Oliver *et al.* (1983). Weimarck (1941) divided this southern region into three, distinguishing the Langeberg and adjacent coastal flats, Outeniqua and adjacent coastal flats and south-eastern centres. In *Thamnochortus*, the subdivisions within the area D correspond to Weimarcks Langeberg centre, which included limestone outcrops on the adjacent coastal flats, (D2) and south coast area (D1). The lack of differentiation, from west to east, across the southern centre may be due to the decrease in number of *Thamnochortus* species along this gradient, leaving only one species, *T.glaber*, occurring in Weimarck's south-eastern centre.

Narrow areas of endemism

Strict adherence to the parsimony method located just one area of endemism, G; the Table Mountain chain on the Cape Peninsula. This was the only area to fulfil the requirements specified by Morrone and Crisci (1995). Areas B and C have no endemic species (Table 23) while the number and distribution of endemics in areas A, D, E, and F (Fig. 22: Table 23) do not fulfil the criteria of the parsimony method specified by Morrone and Crisci (1995).

In the concentric ring method, however, areas corresponding to A, D, E, F and G are found (Fig. 23). Area A corresponds to the centre of endemism found in the Cedarberg and Koue Bokkeveld region. Area D in the south-western mountain chain has two species endemic to it, *T.stokoei* and *T.pulcher*, and shares other species with areas F and G. Area E is equivalent to the Langeberg centre of endemism, while area F is homologous to the adjacent south coast flats. Finally, area G corresponds to the Cape Peninsula and adjacent south coast flats. Mapping the distribution of species using the concentric ring method reinforces the areas of endemism which were located in

Morrone's (1994) method but rejected according to the standards set by Morrone and Crisci (1995).

In the arid Cedarberg- Koue Bokkeveld region (area A) there are four species with overlapping distributions (Fig. 23). The endemic *T.comptonii*, and *T.acuminatus* are found in the northern Cedarberg. The southerly distribution of *T.acuminatus* coincides with two other species which have distributions restricted to the Koue Bokkeveld area, *T.schlechteri* and *T.scabridus*. There are, in effect, two areas of endemism linked by the distribution of *T.acuminatus*.

Overlapping distributions are a particular feature of area of endemism D situated in the south western mountains. The southern part of the distribution of the endemic *T.stokoei* overlaps with the northern most distribution of the endemic *T.pulcher*. Two species from the Cape Peninsula centre (area G), *T.arenarius* and *T.spicigerus*, overlap with the distribution of *T.pulcher* as do two species from the south coast flats (area F), *T.pellucidus* and *T.dumosus*.

The Langeberg centre, area E, is one of the better supported areas of endemism (Fig. 23), with endemics *T.ellipticus*, *T.amoena* and *T.karooica*. *T.karooica* is the more wide ranging species of the three occurring in the Langeberg and crossing the Gouritz river valley into the Outeniqua mountains.

The southern coastal flats, area F, lie adjacent to the mountains where area of endemism E is found (Fig. 23). The map of concentric rings locates the region of greatest overlap along the coast. The species distributions defining this region are *T.insignis*, *T.paniculatus* and *T.pluristachyus*.

Although area G fulfils the criteria of Morrone and Crisci (1995) with two species endemic to the area, these species, *T.nutans* and *T.levynsieae* only occur in two of the five grid squares forming G. The remaining species have outlying populations to the north of the Cape Peninsula, up the west coast, while others overlap with the distributions of species in area D. Three examples of distributions coinciding are visible on Fig. 23. *T.spicigerus* occurs on the Cape Peninsula, on sand dunes up the west coast to Langebaan and along the south to Betty's Bay. *T.punctatus* overlaps with the Cape Peninsula distribution and occurs inland of the west coast. *T.arenarius* is found on the Cape Peninsula mountains and the south-western mountains of area D.

The patterns of distribution of *Thamnochortus* species support the hypothesis that narrowly endemic species are not randomly distributed in the Cape Floristic Region, but are clumped creating centres of endemism. The concentric ring method locates five areas of endemism for *Thamnochortus*. These areas are the Cedarberg-Koue Bokkeveld mountains, the Langeberg centre, the south coast flats, the south-western mountain range of the Hottentots Holland-Riviersonderend mountains and the Cape Peninsula. The tiled pattern in the distribution of *Thamnochortus* species (Fig. 23) results in similarities in the general species composition between areas of endemism, and prevents the classification of endemic areas in the manner suggested by Morrone and Crisci (1995), i.e. using sympatric borders of endemic species. The conflict between pattern and methods are just two of the shortcomings in the Morrone (1994) method.

Methodological problems in determining areas of endemism

Constraints of Morrone's endemism criteria

In *Thamnochortus* the distribution of species is seldom entirely sympatric. Only *T.levynsieae* and *T.nutans*, restricted to the mountains of the Cape Peninsula, occur in the same grid squares and no where else. In all other cases of endemic species, although they were restricted to a particular area, the distributions of endemics in the area are not sympatric. Instead a tile effect is observed, for example on the south coast, (Fig. 22), with the distributions of endemics overlapping with one another but not coinciding completely. The literature indicates that the lack of congruence in distribution boundaries is a feature of some fynbos endemics (Linder *et al.* 1992). The lack of sympatry in distributions prohibit species, which are endemic to the region, from being classified as endemics in the context of the areas identified using Morrone's (1994) method.

Constraints of the grid method

Limitations of methods which use grid squares as basic units in biogeographical analyses are firstly, how to compensate for the bias of collection, secondly how to determine the optimal size of the grid squares, and finally the lack of recognition that the grid square method gives to vastly different habitats within the same grid square.

Constraints of poor collections of species, or in certain areas, may influence results through incorrect assignation of grids, or alternatively by grids being omitted from endemic areas. Methods which assign species to poorly collected grid squares (Pearson and Juliano 1994), based on assumptions regarding the known distribution, weaken the predictions that are made.

Big grid squares reduce the noise caused by many smaller, but empty grid squares, particularly given the bias of massive collection in certain accessible areas and a dearth of specimens from others. The disadvantage of larger grid squares is a decrease in the resolution in the study, especially considering the environmental heterogeneity which may occur in a large grid square. If differentiation between habitats is ignored, the method is restricted to the definition of geographical areas of endemism. Species endemic to different environments found within a single grid square are not differentiated.

In *Thamnochortus* there are cases where a broad distinction in ecological profile (i.e. montane vs coastal flats) is important in determining areas of endemism. The first is the case of endemic region D and *T.pulchers'* distribution extending into blocks allocated to areas F and G because of the placing of the grid squares relative to mountain ranges. The second case concerns *T.muirii*, an endemic of flats in area F, co-occurring, in terms of grid square, with *T,karooica*, an endemic of mountains in area E.

Species with similar geographic distribution pattern

The phytogeographical species groups of *Thamnochortus* can be described as a predominantly arid species group, from the Cedarberg-Koue Bokkelveld region, and a mesic group which extends from the Cape Peninsula in the south-west across as far as Dwessa in the east and inland to the Langeberg range (Fig. 24). In the group of mesic species there are further subdivisions; in the south-west there are those species common to the Cape Peninsula-Overberg region, including the species endemic to the Cape Peninsula mountains and those endemic to the Cape Flats, moving eastwards the group of species occuring on the south coast flats is distinguished as are those species found in the Langeberg-Outeniqua mountains (Fig. 25).

These areas corespond, in part, to the phytogeographical groups described by Weimarck (1941). The arid group of species from the Cedarberg, Koue Bokkeveld, Klein Swartberg localities are within the north-west and Karoo endem-centres of Weimarck (1941).

The associations within the mesic group of *Thamnochortus* species are generally more restricted in distribution than those described by Weimarck (1941); however, there are similarities and certain groups of *Thamnochortus* lie within the core area of an endem-centre. For example, those *Thamnochortus* species in the Langeberg group, with the exception of *T.glaber*, are montane.

Weimarck (1941) included both montane and coastal lowland species in the group of Langeberg endemics, with the specification that the lowland species or biotypes were generally restricted to limestone, and in the broader group Langeberg-south western species. *T.glaber*, the exception in the Langeberg group of *Thamnochortus*, is not a limestone endemic. This is the only species of *Thamnochortus*, which is found in the area defined by the south-eastern group of Weimarck (1941).

The distribution of the southern group of species, described by Weimarck (1941) as lying between the south-western centre and south-estern centre, corresponds to the southern coastal group in *Thamnochortus.* Similarly, the area defined by the south-western endemics of Weimarck (1941) coincides with the distribution of the Cape Peninsula-Agulhas group of *Thamnochortus*. The Cape Peninsula centre, which lies within this region, is analogous to that of Weimarck (1941); however a separate group of Cape Flats endemics has previously not been recognised.

The general pattern of phytogeographical groups in *Thamnochortus* correspondes to that described by Weimarck (1941); however distributions of species groups in *Thamnochortus* appear more contained a feature which may be prescribed to analysis within a single genus and the comparatively few number species, 34 *Thamnochortus* to Weimarck's 464 species from different Cape genera.

Area cladogram

The first distinction in the resolved area cladogram of phytogeographic areas (Fig. 26a) is between the summer (area D) and winter rainfall regions (C, A and B). Within the winter rainfall group there is further differentiation into arid (A and B) and mesic regions (C). A similar differentiation in summer and winter rainfall is found in *Leucadendron* (Williams 1983) and *Disperis* (Manning and Linder 1992) and patterns within *Disperis* (Manning and Linder 1992) support the distinction between arid and mesic regions in the winter rainfall group. Although the presence of these boundaries has been acknowledged in the past (Weimarck 1941; Rourke 1980; Manning and Linder 1992), the analysis of *Thamnochortus* is the first to place the events in historical context.

The decrease in reliable summer rainfall in the Western Cape and the aridification of Namaqualand were the result of a increase in the upwelling of the Benguela current approximately 6.2 to 5.5 million years ago. The regularity of upwelling events was related to a drop in sea level caused by *al.* 1995). It is suggested that geographical speciation is directly linked with large scale environmental changes, while ecological speciation is more dependent on the local extinction of populations, for example, due to fire and smaller scale environmental changes.

The alteration in rainfall in the Miocene and the aridification of Namaqualand appear to have impacted speciation in *Thamnochortus*. There is differentiation into an summer (all-year) rainfall group and winter (summer drought) rainfall group. In the winter rainfall group there is differentiation into mesic and arid region group (Fig. 26a). There is, however, considerable overlap of species between areas, particularly between the summer rainfall and mesic winter rainfall areas (Fig. 23). Sister lineages are usually distinct in terms of summer-winter rainfall regions (e.g. *T.ellipticus* and *T.guthrieae*, *T.spicigerus* and *T.karooica*) or mesic-arid winter rainfall areas (e.g. *T.acuminatus* and *T.fruticosus*, *T.comptonii* clade and *T.stokoei*).

Where there is overlap of closely related species, for example in the *T.pluristachyus* limestone clade, ecological differentiation occurs particularly in flowering time and substrate texture, i.e. sand, gravel or rock.

CONCLUSION

It is uncertain whether the reseeding or resprouting habit is basal in *Thamnochortus*, but within the robust terminal clades it is clear that the extant resprouting species evolved from seeding ancestors. A broad assessment of the relative advantages of the fire survival strategies indicates that resprouters are at a greater advantage, being taller and more widely dispersed. Thus, seeding appears to be a relictual feature. The persistence of seeding is difficult to explain given equal number of species per resprouting and seeding lineage and the advantages evident in the biological profile of the resprouting habit.

The assessment of the interaction of fire survival habit and outer tepal specialization indicates a certain amount of evolutionary constraint. While the evolution of wings and seeders may be related, the probability of this is not statistically significant. In contrast there was a strong probability that the reduction of wings to keels was directly related to the evolution of resprouting.

The connection between fire survival habit, outer tepal specialization and speciation events was not clear. However, given evidence of historical constraints in these characters and the variation in traits and characters, which is a feature of *Thamnochortus*, it is proposed that biological features heavily influenced the evolutionary potential and direction in response to key environmental events and ecological conditions.

The differentiation pattern on general area cladogram of areas of similarity indicates that the change in rainfall patterns in the Miocene may have acted as a large scale vicariant event promoting speciation in *Thamnochortus*. Differentiation into areas of similarity is similar to the phytogeographic areas determined for other genera, however *Thamnochortus* provides the first evidence for a sequence of differentiation. Habitat profiles of sister lineages give evidence of ecological radiation. Where sister species have overlapping distributions flowering time and preference for substrate texture most commonly define different ecological niches.

In the comparative evaluation of speciation patterns in *Thamnochortus*, changes in rainfall patterns in the Miocene and differentiation into ecological niches appear to be the predominant

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APPENDIX 1 Character descriptions

Characters are central to cladistic study and thus it is critical that proper consideration be given to character description and character state delimitation (Pimentel and Riggins 1987). The necessity of including specific explanation with regard to character delimitation has been expressed fairly recently (Stevens 1991), but the benefits of this procedure have already been recognised and accepted.

1. Plant culms diameter - less than 1.8mm, greater than 1.8mm.

Culm diameter varies a great deal in *Thamnochortus*. There is a group of species in which the majority of individuals have culms with particularly large diameters - robust culms. In contrast there is a group with particularly spindly culms. While the extremes are obvious there is a gradation from spindly to a group where the culms are neither large nor spindly. It is difficult to define the spindly and intermediate groups separately (Fig. 42), those species which ad culms of diameters smaller and greater than 1.8mm were coded as 0/1.

The majority of the species with limited ranges in culm diameter are found below 1.5mm. All species below this interval are considered spindly. At 1,8mm there is a `dip' (Almeida and Bisby (1984) in the graph. At this point only those species which have ranges extending to 2mm and beyond overlap. Robust culms have therefore been defined as where the measurement range of culm diameter extends beyond 1,8mm. Evidence of the gradation between the spindly and intermediate groups lies in the number of species that are coded as equivocal.

2. Height - less than 0.6m, 0.6m to 1.00m, greater than 1.00m. (unordered)

In the field the differences between the extremes are obvious. In Fig. 43, however, three groups are apparent. Those species less than 0.6m, the short group, those species between 0.6m and 1.00m and finally those greater than 1.00m tall, the tall group.

Culm surface - sulcate or not (excluded).

Sulcate grooves are present in several species after drying. The nature of the grooves appeared to depend on the age of the culm that had been selected for pressing and on the age of the specimen. *T. bachmanii* is the only species which consistently exhibited clear grooves in fresh material.

Culm surface - rugulose or not (excluded).

In some species, including those which have sulcate culms, the culms become ridged during drying. Due to the lack of consistency in ruguloseness within species and the possibility that it could be an artefact of drying it was excluded.

3. Culm texture - smooth or hairy.

Hairy constitutes a velvety cover on the culms as illustrated by Cutler (1969). In the absence of these hairs the culms are referred to as glabrous, although they may have other markings. The length of the hairs appears to vary from species to species, *T. acuminatus* having the shortest.

4. Culm base -erect or slightly decumbent.

In *Thamnochortus* there are two predominant habits. The first describes those species where the arrangement of the culms give the plant a V shape, it is common in these forms to find a tightly caespitose rhizome. The second habit describes those species which have sprawling or more U shaped plants. On the whole the V shaped group has culms which are straight and do not bend at the base, in the U shaped group it is common for the culms to be slightly bent at the base just after the point of origin on the rhizome. The term slightly decumbent refers to the culms which bend at the base.

5. Sheath length - as long as internode or not.

Certain species, particularly in the chartaceous bract group, were found to have sheaths which extended the length of the internode. In other species the sheaths were usually shorter than half the internode and in many cases decayed with age.

6. Sheath core texture - chartaceous, coriaceous, cartilaginous. (unordered)

The sheath texture varies between species mainly from cartilaginous through to papery. Sheath core texture refers to the texture of the central portion of the sheath ignoring the margins. The texture of the sheath in virtually all the species become less sturdy as one approaches the margins of the sheath. In addition, the proportion of each state present in the sheath also differs between species but in no apparently describable pattern. Sheath persistence and decay varies between species. In some species the margin of the sheath decays, in others approximately half the sheath decays while the lower half remains convolute around the culm, in still other species the sheath splits rather than decays so that the sheath remains as frayed remnants. The nature of the decay of the sheath is probably linked to the texture, and pattern of textures, in the sheath.

7. Sterile branches -absent, present during flowering, present post flowering. (unordered)

Many *Thamnochortus* species do not have any sterile branches apart from during the seedling or resprouting stage of development. Two groups can be recognised amoung those species which do have sterile branches; firstly one where the sterile branches are present continually before, during and after flowering and secondly one where the sterile branches develop on the culm once it has finished flowering. The position of the sterile branches is dealt with as a separate character.

Sterile branches - stout or slender (excluded).

Examining the sterile branches present in certain species, there appeared to be a difference in the width of the branchlets. Due to the nature of the sterile branches it was not possible to measure the difference with callipers or a ruler. Attempts were made to sledge microtome some of the branches and measure the diameter under a microscope but only one species, *T. punctatus* sectioned successfully. The character was not deemed important enough to warrant further study.

8. Sterile branches - from the base or from the culm.

Sterile branches originate either from the rhizome, or from the nodes on the culm. In some species, such as *T. arenarius* and *T. gracilis*, they arise from both. Generally the sterile branches originating in the nodes only arise on the previous years culms.

9. Fertile branches - present or not.

Only two species have fertile branches *T. levynsieae* and *T. gracilis*. On a purely observational level these two species are not similar in appearance. It is very likely that this feature evolved twice in *Thamnochortus.*

10. Rhizome - habitually short to absent, varying in length, habitually long. (unordered)

In species which have characteristically short rhizome the bases of the culms are very close together and virtually no rhizome can be distinguished between them. Some species vary from being tightly caespitose to having distinguishable rhizomes of varying lengths. In these cases the relative length of the rhizome appears to depend on the nature of the substrate. Variation in rhizome length may occur on the same plant. There are, however, a few species which have a consistently long rhizome.

Female inflorescence.

11. Female spathes - prominent or not.

In most cases the female spathes decay, or are as tall as, or shorter than the bracts. In a few species, however, the spikelets are flanked by one or two spathes which extend beyond the spikelet. Most of the species which have these prominent spathes form a small group within the chartaceous bract group. There are two exceptions; *T. ellipticus* and *T. muirii*.

Female spikelets.

The female spikelets of *Thamnochortus* vary in number and shape. It is generally the arrangement and size of the bracts which determine the shape of the spikelet.

12. Female spikelet number - one to three or four to many.

A small group of species have only a few spikelets per inflorescence. Those species which have many spikelets per inflorescence seldom have less than four at flowering time.

13. Female spikelet shape - v-shaped or cylindrical.

Species generally have one of two definable spikelet shapes. The first of these is the v-shaped group (Fig. 44a). The shape of these spikelets may be emphasised by the presence of one or two spathes. The second group, the cylindrical spikelet, encompasses the vast majority of the species (Fig. 44b). Prior to flowering the spikelets of this group are elliptical in shape. During flowering, when the bracts have opened, they often have an elongate oblong shape. This is the predominant shape for this group, however, there are slight differences and variations, such as in the robustness of the spikelet. These irregularities make it difficult to describe sub-groups with any confidence so the character states were defined as v-shaped and not v-shaped.

Female bracts.

Bracts vary in size, shape, texture and colour. Texture and colour are variable within the bract, specifically in the margins and core of the bract. The apices of the bracts are also variable in shape and the presence of awns.

14. Relative length of basal bract to spikelet -virtually as long as the spikelet or not.

In the majority of species the lower bract covers only a portion of the bract above (Fig. 44b). In a few species the basal bract almost entirely covers, not only the bract in the row immediately above it but most of the next bract as well and the basal bract may be almost as long as the entire spikelet (Fig. 44a). The spikelet then appears to have a flattish apex rather than a conical one.

15. Female bract length - range less than 8mm, between 8mm and 15mm or greater than 15mm. (unordered)

The species were coded as having bracts long or short and measurements were made to accurately define the two states. The morphometric data, presented in Fig. 45, indicated two intervals. The first at 8mm and the second at 15mm. This resulted in a multistate character, states defined as above.

16. Female core bract texture - chartaceous to membranous and not chartaceous to membranous.

The bract texture of *Thamnochortus* has two variables: the texture of the central portion of the bract and the size of the hyaline margin. This character deals with the former variable. Central bract texture varies from the chartaceous membranous type through coriaceous to cartilaginous. Only one or two species are cartilaginous, the rest are either coriaceous or chartaceous to membranous. The character coded in three states did not contribute to the resolution of the cladogram. Since the chartaceous-membranous species formed a distinct group the states were defined as chartaceous membranous or not.

17. Female bract margin - not hyaline, narrow hyaline, wide hyaline. (unordered)

This is the second of the two bract texture variables. Amoung those species which have a hyaline margin there is variation in the width of the margin relative to the rest of the bract. The three states are distinct and easy to identify.

18. Female bract shape - linear lanceolate to an acuminate point or not.

The predominant variation in the female bract shape is in the width and the relative position of the widest part of the bract. This character defines a particular group of species that not only have a bract which is slightly narrower than the more common lanceolate bract (Fig. 44c), but that also has an acuminate point at the apex of the bract (Fig. 44d). This is the same type of bract shape defined in the male bract shape character but it circumscribes a different group of species.

19. Female core bract colour - cream, tan, red-brown, dark brown. (unordered)

The female bracts are often bicoloured with the central core region usually being darker than the margins. The bracts characteristically vary in colour with age. This character defines the core colour into four states. The colours are distinct, although there is a slight gradation through tan towards the darker red brown colour.

20. Female bract tip - recurved/splayed or not.

At flowering time the bracts of the female spikelet open exposing the flower. In most cases the bracts simply open retaining their form (Fig. 44a), but in a few species the bract becomes recurved or arched away from the axis of the spikelet (Fig. 44b).

21. Female bract awn - distinct or not.

Only three species of *Thamnochortus* have distinct awns on the female bracts, *T. pulcher*, *T. nutans* and *T. dumosus* (Fig. 44e). In two of these species, *T. nutans*, and *T. pulcher*, the awn is emphasised by the decay of the apical margins of the bract. In other species bracts have the acuminate apices or the apex is acute but tending towards blunt.

22. Female bract central vein - distinct or not.

In several species the central vein in the female bract is distinct. Two extreme examples of this are found in *T. dumosus* and *T. karooica* which have cartilaginous veins, while the rest of the bract is coriaceous to chartaceous. In the rest of the species there is no prominent vain on the female bracts.

<u>Female flowers</u>.

Size, and in particular length varies between the species, and in some cases there is considerable variation within species. The female flower structure in *Thamnochortus* is two whorls of three tepals each with those of the outer whorl more or less modified. The outer lateral tepals are flattened into keels or wings, while the odd outer tepal is smaller and similar in shape to the inner tepals. The shape of the tepals, shape of the tepal apices and the texture of the tepals varies between species. After pollination the ovary of *Thamnochortus* expands and the outer wall hardens and darkens in colour. In expanding the ovary often changes shape and differences in the shape of the nuts are apparent between species.

23. Female flower length - range less than 6mm or exceeding 6mm.

There is an obvious difference between the small flowers (below 3.5mm) and the large flowers (above 6mm), however, there is a gradient in flower size from the smaller class into the larger middle class (Fig 46). This gradient makes it difficult to determine a boundary denoting the difference between small and large. At the upper length of the scale there is a definite interval at 6mm with only three species crossing the 6mm interval.

24. Female flower shape - narrow oblong or not.

The general female flower shape in the species of this genus varies from oblong or urn shaped to round. The group which is best defined by this character, however, has a particular oblong shape not characteristic of any other species in *Thamnochortus* (Fig. 44i,j and k). While there is slight variation within the group, in each case the shape can be recognised as differing from the round female flower found in the rest of the genus (Fig. 44f,g and h). The flower is characteristically narrower than long. The outer tepals are keeled and except for the flower of *T. fraternus*, close tightly over the rest of the flower. The base of the outer tepals are paler than the upper portion (two thirds) and in most characteristic cases form a v down to the base of the pedicel.

25. Female side tepals - as others, keeled or winged.

The states keeled or winged describe groups within *Thamnochortus*, the third state differentiates the outgroup *Rhodocoma*. In *Rhodocoma* the six tepals, inner and outer whorls, are not differentiated or specialized. The side tepals appear the same as the other tepals. In *Thamnochortus* tepals are specialised either as keels or wings. A keel is narrower than the wings (relative to the size of the flower) and coriaceous to cartilaginous in texture. Occasionally the outer edge of the keel may be coriaceous to membranous. The wing is described as a broadly developed lateral tepal (relative to the size of the flower) which tends to be more chartaceous to membranous in texture.

26. Female outer tepal texture - chartaceous to coriaceous, coriaceous to cartilaginous

Wings and keels of the female flowers of *Thamnochortus* are either cartilaginous or chartaceous. However, the entire tepal is seldom the same texture. In predominantly chartaceous tepals the part of the tepal closest to the centre of the flower may be more coriaceous. In predominantly cartilaginous tepals the outer rim of the tepal is usually more flexible tending towards a coriaceous texture. Thus, two categories are defined the first where the outer edge of the tepal is chartaceous with a coriaceous inner core and secondly tepals which have harder tepal texture with the rim being coriaceous.

27. Side tepals - clearly visible either side of bract or not.

Certain of the winged species have female flowers with broad wings and or spikelets with narrow bracts. This leads to the situation where the side tepals are visible either side of the bracts. In almost all cases where this happens both lateral tepals are visible, however, in *T. erectus* it is normally only one lateral tepal that is occasionally visible. *T. erectus* was still coded as having side tepals visible.

28. Female side tepals - mucronate/cuspidate points or not.

The upper portion of the female side tepals vary in several respects. The terminal apex may form a sharp acuminate point (Fig. 44f), be rounded (Fig. 44h), or come to a blunt ending (Fig. 44g) (the outer curved portion forming an approximately 90 degree angle with the inner edge). Only two species, *T. acuminatus* and *T. stokoei*, have acuminate points at the apex of the outer tepals, however, this does not occur consistently within the species, other specimens having rounded apices with mucronate or cuspidate points. There does not appear to be a connection between the shape of the outer tepal apex and the presence of a point, as several other species have mucronate or cuspidate points on the outer tepal.

29. Side tepal apex - rounded or not.

The different apex shapes present in the side tepals of *Thamnochortus* have been described in the previous character (mucronate cuspidate points). The rounded side tepal apex is distinctive and the most consistent of shapes (Fig. 44h).

30. Decurrent base of side tepal - notched or not.

The bases of all the tepals attach below the unilocular ovary to the pedicel. In some of the species the base of the outer tepals elongates slightly and forms a small rib which is attached to the pedicel. The base of the tepals usually lie close together with no gap i.e. the pedicel cannot be seen. In two species, however, *T. fraternus* and *T. paniculatus* the base of the outer tepals pull away from each other slightly and this creates a notched appearance (Fig. 44i).

31. Nut shape -round, ovate, elliptical or rectangular.

The differences in shape between the round ovate and elliptical nuts are few and it is often difficult to distinguish between these three states. The rectangular shape, however, (Fig. 44p q and r) is particularly distinct. The nuts are longer than wide and the corners have a squarish appearance leading to a rectangular rather than elliptical shape. Because of the difficulty of distinguishing the round, ovate and elliptical forms (Fig 44 l, m, n, o and p) only two states were defined. The first state describes those species with a slightly rounder shape and the second state defines those species which have a clearly rectangular nut.

Male inflorescence

Male spikelet shape.

The shape of the male spikelets is determined by the length to breadth ratio of the spikelet and the arrangement of the bracts. Three different characters have been coded for male bract shape. Two are associated with the length to breadth ratio's and one with the arrangements of the bracts.

32. Male spikelet shape - lorate or not.

The male spikelets have several different shapes which can be defined loosely as elliptical, v-shaped, lorate (Fig 44 s, t and u). Of all these groups the lorate is the most consistent, for this reason it was distinguished from the rest of the shape types.

33. Male spikelet shape - as wide as long or not.

Amoung the assemblage loosely defined as small v-shaped, is a group of three species that are as wide as long. The width measurement in all species was taken across the widest part of the bract. In the case of these three species the broadest part was across the top of the spikelet because of the V-shaped nature of the spikelet (Fig. 44s).

34. Male spikelet shape - box-like or not.

Bract arrangement affects the appearance of the male spikelets. In the groups which have been loosely described as V-shaped and elliptical the spikelet appear smooth overall as the basal bracts are in many cases distinctly longer than the apical bracts, although they need not necessarily overtop them or cover them. In other species, predominantly the ones which have lorate male spikelets, the bracts are ordered in an opposite decussate arrangement. This gives the spikelets a box-like appearance which can be obscured by pressing (Fig. 44u).

35. Male spikelet - less than 10mm or greater than 10mm.

There is a scale of size in the male spikelets with certain species appearing to be considerably larger than others. In Fig. 46, however, the wide variation in spikelet size within species can be seen. Nevertheless, there is a point at which species with smaller spikelets can be distinguished from those with the larger spikelets, 10mm.

36. Male bract shape - linear-lanceolate to an acuminate point or not.

The majority of the bracts are elliptical to lanceolate in shape with the apices varying from obtuse to acute and acuminate. While several of the bracts are linear-lanceolate not all of them have an acuminate tip (Fig. 44v, w and x). Using this character state was meant to define a small group of species which had this particular combination of bract shape and apex.

37. Basal bracts - virtually as long as spikelet or not.

In most male spikelets the basal bracts cover a half to three-quarters the length of the bract above (Fig. 44t and u). In a small group of species, however, the basal bract cover the bracts which lie above it and the apices of all the bracts lie on the same line (Fig. 44s). This gives the top of the spikelet a flattish appearance.

38. Male bract length - range less than 6mm, 6mm to 10mm, greater than 10mm.

Bract size variation was determined from the basal bracts in the spikelet as in some species bract size varies up the length of the spikelet. Although there is extensive variation there are only two species which have ranges that cross 6mm (Fig. 48). This point circumscribes the group with smaller bracts. There is little variation in the bract size of the species in this group. Those species which fall into the group with bracts from 6mm to 10mm on the whole have greater variation in their ranges. However, they are all smaller than 10mm. In fact there are only two species that have ranges greater than 10mm.

39. Male flower size - less than 3mm, between 3 and 4mm and greater than 4mm (unordered).

The male flowers are all elliptical in shape, but some are larger than others. In Fig. 49 it was possible to determine two breaks. The first at 3mm and the second at 4mm.

40. Male outer tepals - conduplicate or keeled.

The outer tepals of the male flowers are folded and enclose the inner tepals and anthers. If the ridge caused by the folding of the outer tepal is the same texture as the rest of the tepal, the tepal was considered conduplicate. If the ridge was reinforced, (i.e. of a harder texture) and in some cases flattened, the tepal is considered to be keeled.

41. Tepal texture - both tepals the same texture, outer tepal more rigid.

The majority of species have outer tepals that are much harder than the inner tepals; either coriaceous or cartilaginous outer tepals and generally membranous inner tepals. In some species, however, the texture of the inner and outer tepals is the same, usually both membranous.

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42. Stomatal position - sunk, superficial or raised (unordered).

There are three variations in stomatal structure and position with respect to the epidermis. The first category describes those species where the guard cell lies below the outer surface of the epidermis, sunk. Secondly there are those species where the guard cells lies flush with the epidermal surface, superficial. Finally there are two species, *T. fruiticosus* (Fig. 50d) and *T. cinereus*, that have guard cells raised above the epidermis. Any species in which the guard cells lay even slightly lower than the surface of the epidermal cells were classified as having stomata which were sunk (Fig. 50b,f).

43. Development of guard cell cuticle - flat, slightly raised, raised. (unordered).

The cuticle above the guard cell varied a great deal with respect to thickness and pattern. Patterns, such as undulating surface or extra lips on the outer or inner corners, were not consistent throughout the replicate specimens and were not included as a character. The thickness of the cuticle of the guard cell was consistent within species. There are two extremes, deep cuticles (Fig. 50b,f ; raised), and very flat or thin cuticles (Fig. 50a,c,d,e). Between these extremes lies a third group. This distinguished as those species with cuticles that belong to neither of these groups. The cuticles are not flat (thin), nor are they particularly thick (deep).

44. Position of subsidiary cells relative to guard cells -above guard cells or not.

In the majority of species the upper surface of the subsidiary cells lies below that of the guard cell. In *T. erectus* and *T. insignis*, however, the subsidiary cells overtop the guard cells (Fig. 50c).

45. Position of thickening on epidermal walls - anticlinal walls thickened or outer wall only thickened.

T.acuminatus and *T.fruticosus* (Fig. 50a,d) consistently had thickening of the epidermal walls restricted to the outer wall. The epidermal walls of the remaining species are thickened on both the anticlinal and outer walls.

46. Epidermal cell size - narrow or wide.

The width of the epidermal cells was determined using a eye piece micrometer. Below 0.05mm the epidermal cells were considered narrow and above this they were considered wide.

Chlorenchyma cells - narrow or wide (excluded).

In *Thamnochortus* there are two layers of chlorenchyma cells which are equal in length or the lower layer may be narrower. The width of the cells appeared to vary between species. Closer inspection of replicate specimens showed, however, there is no consistent pattern to the width of the parenchyma rows within species. For this reason there was no further investigation to identify limits of character states.

47. Number of Parenchyma layers - less than 2 and equal to 2, or greater than 2.

This character is consistent within species with the majority of species having one to two layers of parenchyma between the chlorenchyma and the sclerenchyma (Fig. b,d,e). The second smaller group of species three or more layers (Fig. 50c,f).

48. Parenchyma cell size relative to epidermal cell size -parenchyma smaller or larger than epidermal cells.

In each culm section the size of the parenchyma cells varied. Relative to the size of the epidermal cells there is are two definite patterns; firstly, where all parenchyma cells are smaller than the epidermal cells and secondly (Fig. 50a,d), where the parenchyma cells are larger than the epidermal cells.

49. Sclerenchyma thickening - thick or thin walls.

The thick (Fig. 50c,e) and thin walls (Fig. 50a) of the sclerenchyma were easy to identify and classify into two different states.

Sclerenchyma layer - number of rows; less than 5, between 5 and 9, greater then 9 (excluded). The number of layers of sclerenchyma varied between species. However, while it is possible to identify those species that have a thicker band of sclerenchyma from those which have a thin band of sclerenchyma, the character is not consistent in some species (Table 26) and was thus excluded.

50. Outer circumference of sclerenchyma - distinct ridges intruding into the parenchyma, small ridges, no ridges.

The outer circumference of the sclerenchyma band may be ridged or smooth. The ridges are not always opposite a vascular bundle, but the two may coincide. Ridges may be regular and definite (Fig.f) obviously intruding into the parenchyma layers. In a smaller number of species the ridges are irregular and bulge-like rather than intrusive (Fig. 50e). Few species have no ridges (Fig. d)

Table 26. Comparison of the results from the two replicate specimens of each species.

Species	Replicate 1	Replicate 2
T. acuminatus	4 - 6	9 - 12
T. amoena		8 - 10
T. arenarius	4 - 6	7 - 8
T. bachmanii	7 - 8	6 - 7
T. cinereus	15 - 19	12 - 13
T. comptonii	5 - 7	7 - 9
T. dumosus	5 - 8	6 - 9
T. ellipticus	8 - 11	
T. erectus	4 - 6	6 - 8
T. fraternus	6 - 8	3 - 4
T. fruticosus	7 - 10	7 - 9
T. glaber	12 - 15	7 - 8
T. gracilis		7
T. guthrieae	4 - 6	9
T. insignis	10 -16	11 - 12
T. karooica	9 - 11	7 - 8
T. levynsieae	3 - 5	5
T. lucens	7 - 9	8 - 9
T. muirii	7 - 10	7
T. nutans	6 - 8	5
T. obtusus	7 - 9	6 - 9
T. paniculatus	8 - 13	5 - 7
T. papyraceus	4 - 8	5 - 7
T. pellucidus	6 - 8	5 - 8
T. platypteris	6 - 9	5 - 6
T. pluristachyus	4 - 6	5 - 6
T. pulcher	7 - 10	6 - 8
T. punctatus	8 - 12	7 - 8
T. rigidus	13 - 15	10
T. scabridus	5 - 6	8
T. schlechteri	6 - 8	4 - 5
T. spicigerus	9 - 10	8
T. sporadicus	5 - 8	9
T. stokoei	6 - 7	6 - 9

51. Post fire survival strategy - resprouter or seeder.

Post fire survival habit was determined through field observations in post fire environments. Resprouting refers to those species in which the adults survived fire and coppiced, seeding refers to those species in which adults were killed by fire and regeneration was from seed. This character was used in comparative analyses and was not included in the initial cladistic analysis which determined the topology of the tree.

52. Number of locules in the ovary - more than one or one.

All *Thamnochortus* species have a single locule in the ovary. The *Rhodocoma* species of the outgroup have three locules per ovary.

53. Number of styles - more than one or one.

All *Thamnochortus* species have a single style. The *Rhodocoma* species of the outgroup have three styles per ovary.

54. Fruit -seeds or nuts.

After fertilisation the ovules of *Rhodocoma* are released as seeds from the three locules which split open. The ovule of *Thamnochortus* remains within the locule forming a nut which is dispersed with the tepals still attached.

Appendix 2. The data matrix of 54 characters described in Appendix 1. State numbers correspond to the order of listing in Appendix 1.

	C1	C2	C3	C4	C5	C6	C7	C8	C9	C10	C11	C12	C13	C14	C15	C16	C17	C18	C19	C20	C21	C22	C23	C24	C25	C26	C27
Rhanda	1	2	0	1	0	1	0	?	0	1	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0
Rhgigantea	1	2	0	0	0	1	2	0	0	1	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0
Rfruticosus	0	0/1	0	0	0	1	0	?	0	1	0	0	0	0	0	0	1	0	3	0	0	0	0	0	0	1	0
T.acuminatus	0/1	0	1	1	1	2	1	0	0	0	0	1	1	1	2	1	2	0	2	0	0	1	1	0	2	1	1
T.amoena	0/1	1	0	1	0	1	1	0	0	0	0	0	0	0	2	1	2	0	0	0	0	1	1	0	2	1	0
T.arenarius	0	0/1	0	1	0	1	2	1	0	1	0	0	0	0	0	0	2	1	1	0	0	1	0	0	2	0	0
T.bachmanii	0	1	0	0	0	1	0	?	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	2	1	0
T.cinereus	1	1	1	1	0	1	1	0	0	1	0	0	0	0	1/2	1	2	0	2	0	0	1	0	0	2	1	0
T.comptonii	0	0	0	1	0	2	0	?	0	1	1	0	1	1	1/2	1	2	0	0	0	0	1	0	0	2	1	1
T.dumosus	0	0	0	1	0	2	1	1	0	0	0	0	0	0	0/1	1	2	0	1	0	1	1	0	0	1	1	0
T.ellipticus	0	0	0	0	0	0	1	0	0	1	1	1	0	0	1	0	1	0	2	0	0	0	0/1	1	1	0	0
T.erectus	1	2	0	0	0	1	0	?	0	1	0	0	0	0	0/1	0	0	0	1	0	0	0	0	0	2	1	1
T.fruticosus	0/1	0	1	0	1	2	1	0	0	2	0	0	0	0	1	1	1	0	2	0	0	1	0/1	0	2	1	1
T.fraternus	0/1	1	0	1	0	1	0	?	0	0	0	0	0	0	1	0	0	0	2	1	0	0	0	1	1	1	0
T.glaber	1	0	0	1	0	1	2	0	0	1	0	0	0	0	2	0	2	0	2	0	0	0	0	1	1	0	0
T.gracilis	0/1	1	0	1	0	1	1	0	1	2	0	0	0	0	0	0	1	1	1	0	0	1	0	0	2	0	0
T.guthrieae	0	0	0	0	0	0	2	0	0	1	0	0	0	0	1	0	1	0	2	0	0	0	0	1	1	0	0
T.insignis	1	2	0	0	0	1	0	?	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	2	1	0
T.karooica	1	2	0	1	0	1	0	?	0	1	0	0	0	0	1	0	2	0	1	0	0	1	0	0	2	0	1
T.levynsieae	0/1	1	0	1	0	1	0	?	1	2	0	0	0	1	1	0	0	0	3	0	0	0	0	0	1	0	0
T.lucens	0	1	0	1	0	1	2	1	0	1	0	0	0	0	0/1	0	1	1	1	0	0	0	0	0	2	0	0
T.muirii	0/1	1/2	0	1	0	1	1	0	0	0	1	0	0	0	0/1	0	0	0	2	1	0	0	0	1	1	1	0
T.nutans	0/1	0	0	1	0	1	0	?	0	1	0	0	0	0	1	0	0	0	3	0	1	0	0	0	1	1	0
T.obtusus	0	0	0	1	0	1	2	1	0	2	0	0	0	0	0	0	1	1	2	0	0	0	0	0	2	1	0
T.paniculatus	0/1	1	0	1	0	1	0	?	0	0	1	0	0	0	1	0	0	0	2	1	0	0	0	1	1	1	0
T.papyraceus	0	0	0	0	1	2	0	?	0	0	1	1	1	1	1	1	2	0	0	0	0	0	1	0	2	0	1
T.pellucidus	0	0	0	0	0	1	2	1	0	0	0	0	0	0	1	0	2	0	1	0	0	0	0	0	1	0	0
T.platypteris	0	0	0	0	0	0	0	?	0	1	1	1	1	1	1	1	2	0	2	0	0	0	1	0	2	1	1
T.pluristachyus	1	1	0	1	0	0	0	?	0	0	0	0	0	0	0	0	1	0	2	1	0	0	0	0	2	1	0
T.pulcher	0	0	0	0	0	0	0	?	0	0	0	0	0	0	1	0	0	0	3	0	1	0	1	0	1	1	0
T.punctatus	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0/1	0	1	1	1	0	0	0	0	0	2	1	0
T.rigidus	0/1	1	1	1	0	1	1	0	0	0	0	0	0	0	0/1	1	2	0	2	0	0	1	0	0	2	1	0
T.scabridus	0	0	0	0	0	0	0	?	0	1	1	1	1	1	0/1	1	1	0	1	0	0	0	0/1	0	2	1	1
T.schlechteri	0	0	0	1	0	0	0	?	0	1	1	1	1	1	0/1	1	1	0	2	0	0	0	0	0	2	1	0
T.spicigerus	1	2	0	0	0	1	0	?	0	1	0	0	0	0	0/1	0	0	0	3	0	0	1	0	0	2	0	1
T.sporadicus	0	0	0	0	0	1	1	1	0	2	0	0	0	0	1	0	2	0	2	0	0	0	0	0	2	0	0
T.stokoei	0	0	0	0	0	0	0	?	0	0	0	1	1	1	1	1	2	0	1	0	0	0	0	0	2	1	1

Appendix 2. cont.

	C28	C29	C30	C31	C32	C33	C34	C35	C36	C37	C38	C39	C40	C41	C42	C43	C44	C45	C46	C47	C48	C49	C50	C51	C52	C53	C54
Rharida	0	0	0	?	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	1	0	0	0
Rhgigantea	0	0	0	?	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0
Rfruticosus	0	0	0	?	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0
T.acuminatus	1	0	0	0	0	0	0	1	0	1	2	1/2	1	1	1	0	0	1	1	0	1	1	2	1	1	1	1
T.amoena	1	0	0	0	0	0	0	1	0	0	1	2	1	1	1	0	0	0	0	0	1	0	0	1	1	1	1
T.arenarius	0	1	0	0	0	0	0	1	1	0	0	1	0	1	0	2	0	0	0	1	0	1	0	0	1	1	1
T.bachmanii	1	0	0	0	1	0	1	0/1	0	0	0	1/2	0	1	1	0	0	0	0	0	0	0	0	1	1	1	1
T.cinereus	0	0	0	0	0	0	0	1	0	0	1	1	1	1	2	1	0	0	0	0	0	0	0	0	1	1	1
T.comptonii	1	0	0	0	0	0	0	0	0	0	0	1	0	1	1	1	0	0	0	0	0	0	2	1	1	1	1
T.dumosus	0	0	0	0	0	0	0	1	1	0	0/1	0/1	1	1	1	0	0	0	1	0	0	0	2	1	1	1	1
T.ellipticus	1	0	0	1	0	0	0	1	0	0	0	1	1	1	1	0	0	0	0	1	0	0	0	0	1	1	1
T.erectus	1	0	0	0	0	0	1	0/1	0	0	0	0	0	1	1	1	1	0	0	1	0	1	0	0	1	1	1
T.fruticosus	0	0	0	1	0	0	0	1	1	0	0/1	1	1	1	2	0	0	1	1	0	1	0	1	0	1	1	1
T.fraternus	1	1	1	0	1	0	1	1	0	0	0	0	1	1	1	1	0	0	0	0	0	1	0	1	1	1	1
T.glaber	1	1	0	1	0	0	0	1	1	0	1	1/2	1	0	1	0	0	0	1	0	1	0	0	0	1	1	1
T.gracilis	0	0	0	0	0	0	0	0/1	1	0	0	0	1	0	1	1	0	0	0	0	0	0	1	0	1	1	1
T.guthrieae	1	0	0	1	0	0	0	1	0	0	1	1	1	1	1	0	0	0	0	0	0	0	0	0	1	1	1
T.insignis	0	1	0	0	1	0	1	0/1	0	0	0	0	0	0	1	1	1	0	0	0	0	0	1	1	1	1	1
T.karooica	1	0	0	0	1	0	1	1	0	0	0	1	1	1	0	2	0	0	0	0	0	1	0	1	1	1	1
T.levynsieae	0	0	0	0	0	0	0	0/1	0	0	0	0	1	0	0	0	0	0	0	1	0	1	0	0	1	1	1
T.lucens	1	1	0	0	0	0	0	1	1	0	0	0	1	1	1	0	0	0	0	0	0	0	1	0	1	1	1
T.muirii	1	1	0	0	0	0	0	0	0	0	0	1	1	1	1	0	0	0	1	0	0	0	1	1	1	1	1
T.nutans	0	0	0	0	0	0	0	1	1	0	1	1	1	1	1	1	0	0	0	1	0	1	0	0	1	1	1
T.obtusus	1	1	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	1	0	0	0	1	0	1	1	1
T.paniculatus	1	1	1	1	0	0	0	0	0	0	0	0	1	1	1	0	0	0	1	1	0	0	1	1	1	1	1
T.papyraceus	1	0	0	0	0	0	0	1	0	0	1	2	1	1	1	2	0	0	0	0	0	1	0	1	1	1	1
T.pellucidus	0	0	0	0	0	0	0	1	0	0	0/1	1	1	1	1	0	0	0	0	0	0	0	0	1	1	1	1
T.platypteris	1	0	0	0	0	0	0	0	0	0	0	0/1	1	1	1	1	0	0	0	0	0	0	0	1	1	1	1
T.pluristachyus	1	1	0	0	0	0	0	1	0	0	0	0	1	0	1	1	0	0	0	0	0	1	0	1	1	1	1
T.pulcher	0	0	0	1	0	0	0	1	0	0	2	2	1	0	1	0	0	0	0	0	0	0	2	1	1	1	1
T.punctatus	0	0	0	0	1	0	1	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	1	1	1	1
T.rigidus	0	0	0	0	0	0	0	1	0	0	1	1	0	1	0	0	0	0	0	0	0	0	0	1	1	1	1
T.scabridus	1	0	0	0	0	1	0	0	0	0	0	0	0	0	1	1	0	0	1	0	0	1	0	0	1	1	1
T.schlechteri	1	0	0	0	0	1	0	0	0	1	1	1	1	1	1	1	0	0	0	1	0	1	1	1	1	1	1
T.spicigerus	1	0	0	0	1	0	1	1	0	0	0	0	1	1	0	2	0	0	0	1	0	1	0	1	1	1	1
T.sporadicus	1	0	0	0	0	0	0	1	0	0	0	1/2	0	0	1	1	0	0	0	0	0	0	1	0	1	1	1
T.stokoei	0	0	0	0	0	1	0	0/1	0	1	1	1	1	1	1	0	0	0	0	0	0	0	1	1	1	1	1

Appendix 3a: Detail of qualitative characters supporting major groups and specimens in the species complex.

	female outer tepal					
	outer margin texture	texture	colour	visible	apex	wings/keels
T.comptonii	0/1	0/1	0/1	1	0/1	2
*T.platypteris*2	1/2	1/2	0/1/2	1	0/1	2
T.scabridus	1/2	1/2	0/1	1	0/1	2
*T.platypteris*38	1	1	0	1	1	2
*T.platypteris*1	1/2	1	0/1/2	1	0/1	2
T.schlechteri	0	0	0	0	0	1
T.stokoei	0	0	0/1	0	0	1/2
T.bachmanii	0	0	0/1	0/1	0	1/2
*T.stokoei*62	0	0	0	0	0	2

Appendix 3a. Continued..

	female spathes, infloresence, bracts & spikelets					
	spathes	bract texture	bract margin texture	bract colour	inflorescence shape	spiklet number
T.comptonii	0/1	1	1	1/2	0/1	0/1
*T.platypteris*2	1	0/1	1	1/2	1	0/1
T.scabridus	1	0/1	1	1/2	1	0/1
*T.platypteris*38	0	0	1	2	0	1
*T.platypteris*1	1	0/1	0	2	1	0/1
T.schlechteri	1	0	0/1	2	1	1
T.stokoei	0/1	0/1	1	1/2	0/1	0/1
T.bachmanii	0/1	0/1	1	1/2	0	0
*T.stokoei*62	1	0	1	2	1	1

Appendix 3a. Continued

	male infloresence	sterile branches	culm texture	
	infloresence shape		rugulose	sulcate
T.comptonii	0	0	1	0/1
*T.platypteris*2	0	0/1	1	0/1
T.scabridus	0	0/1	0/1	0/1
*T.platypteris*38			0	0
*T.platypteris*1	0	0	1	1
T.schlechteri	0	0	0	0
T.stokoei	0	0/1	0	0
T.bachmanii	0/1	0/1	0	1
*T.stokoei*62	0	0	0	0

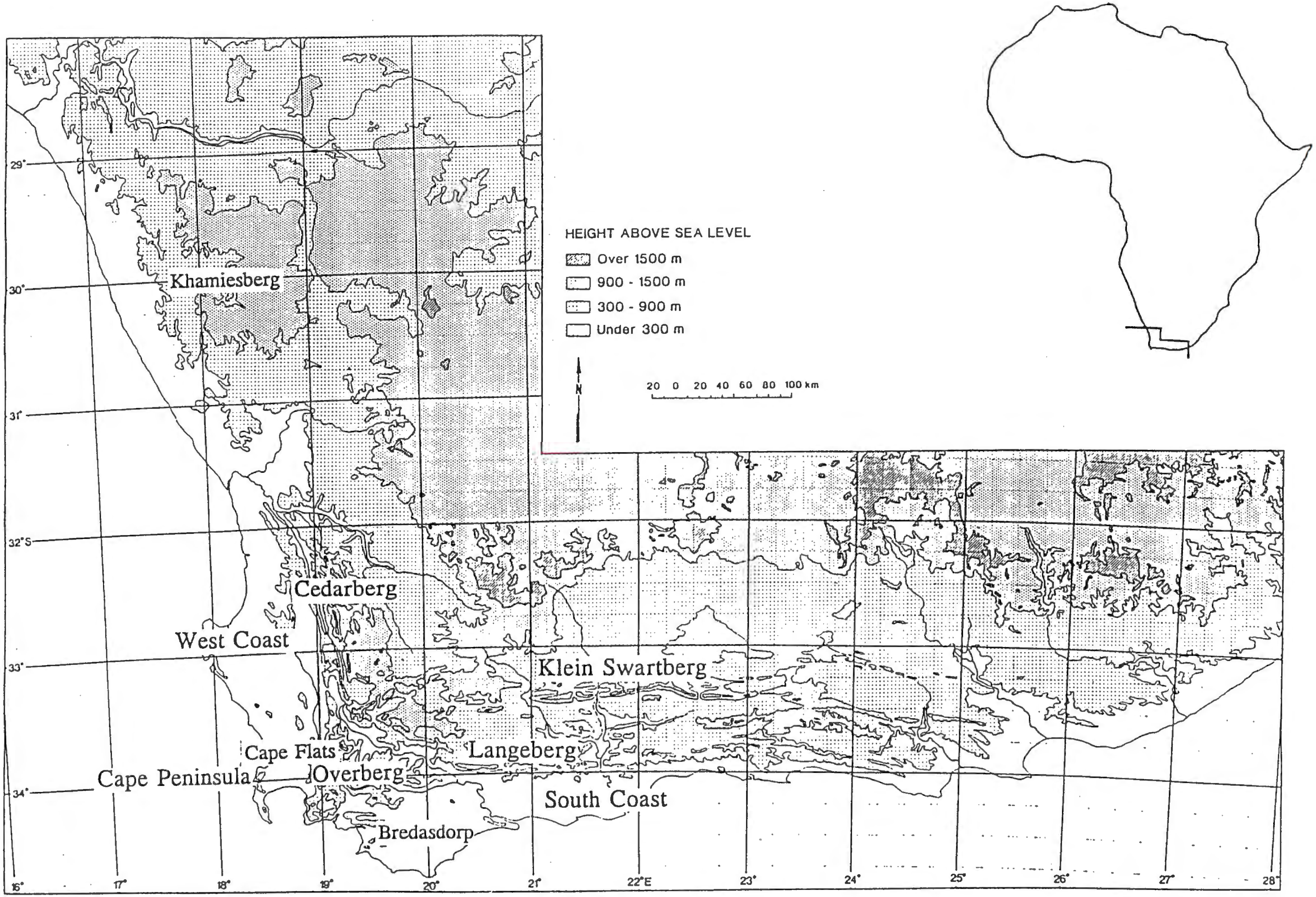

Fig. 1. A map of the Cape Floristic region. Areas referred to in the thesis are labelled.

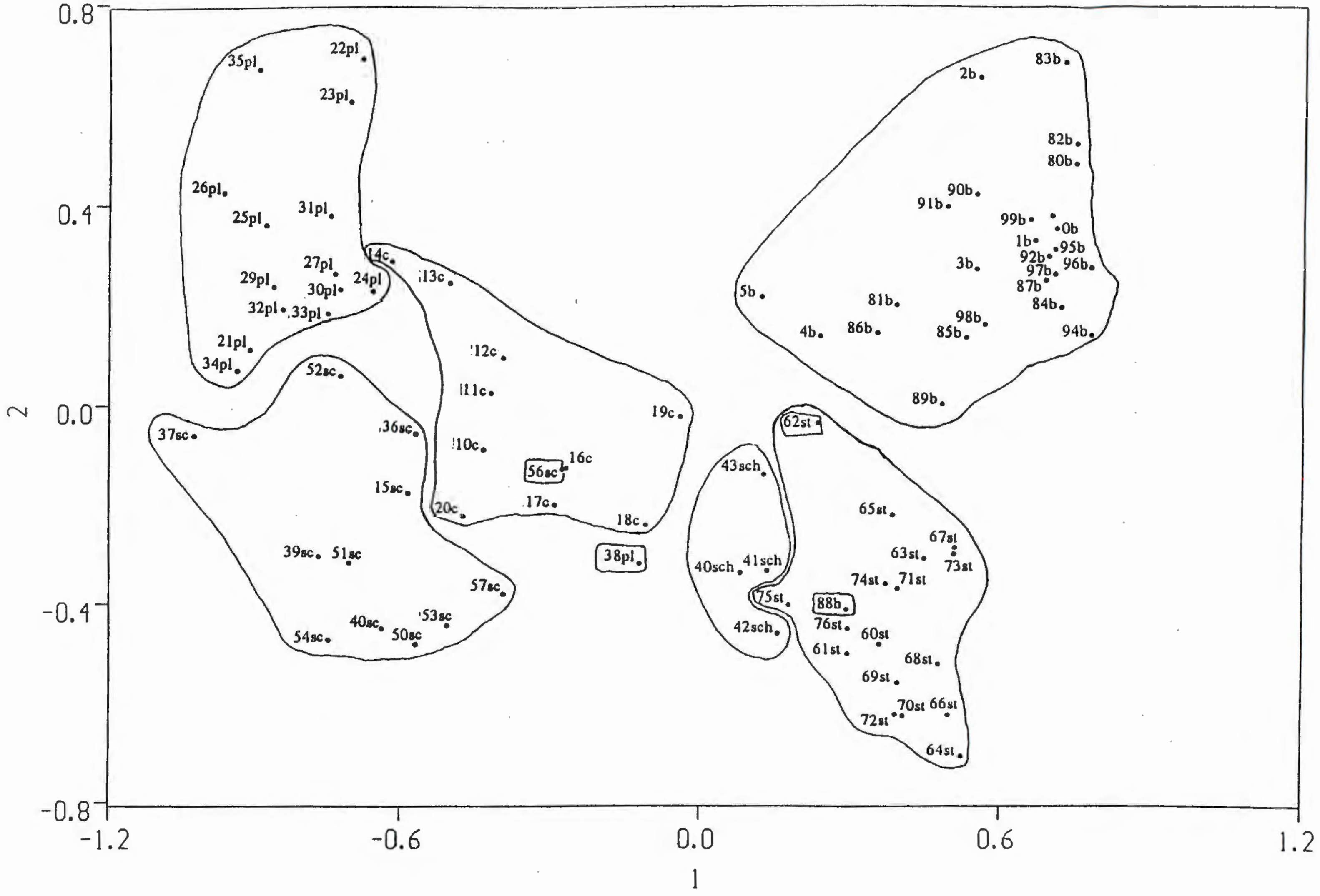

Fig. 2. The PCA pattern of the *Thamnochortus* species complex. Individual specimens are labeled numerically. The letters indicate the species groups: c = *T.comptonii*; pl = *T.platypteris*; sc = *T.scabridus*; sch = *T.schlechteri*; st = *T.stokoei* and b = *T.bachmanii*.

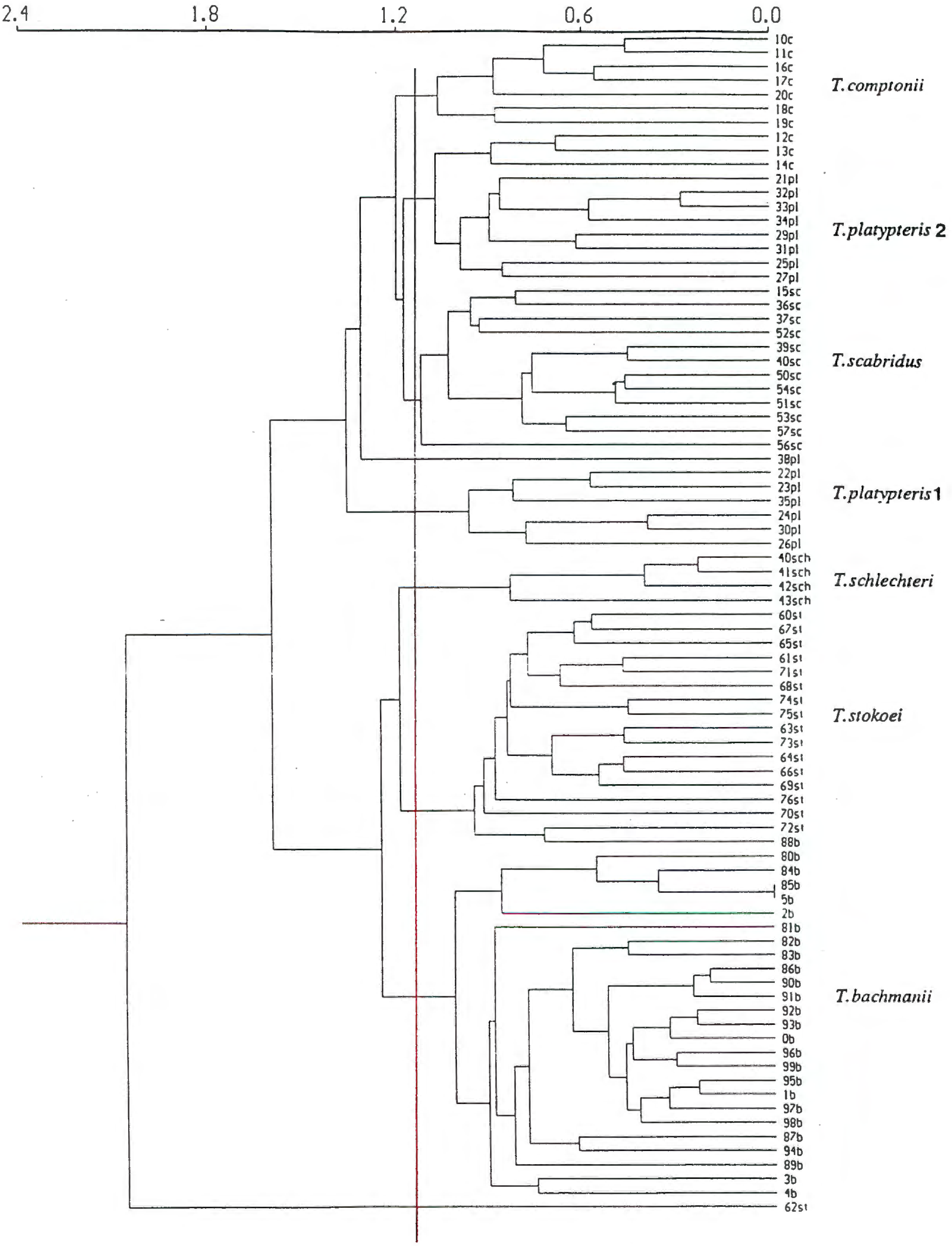

Fig. 3. The phenogram of the *Thamnochortus* species complex. Individual specimens are labeled numberically. Species: c = *T.comptonii*; pl = *T.platypteris*; sc = *T.scabridus*; sch = *T.schlechteri*; st = *T.stokoei* and b = *T.bachmanii*.

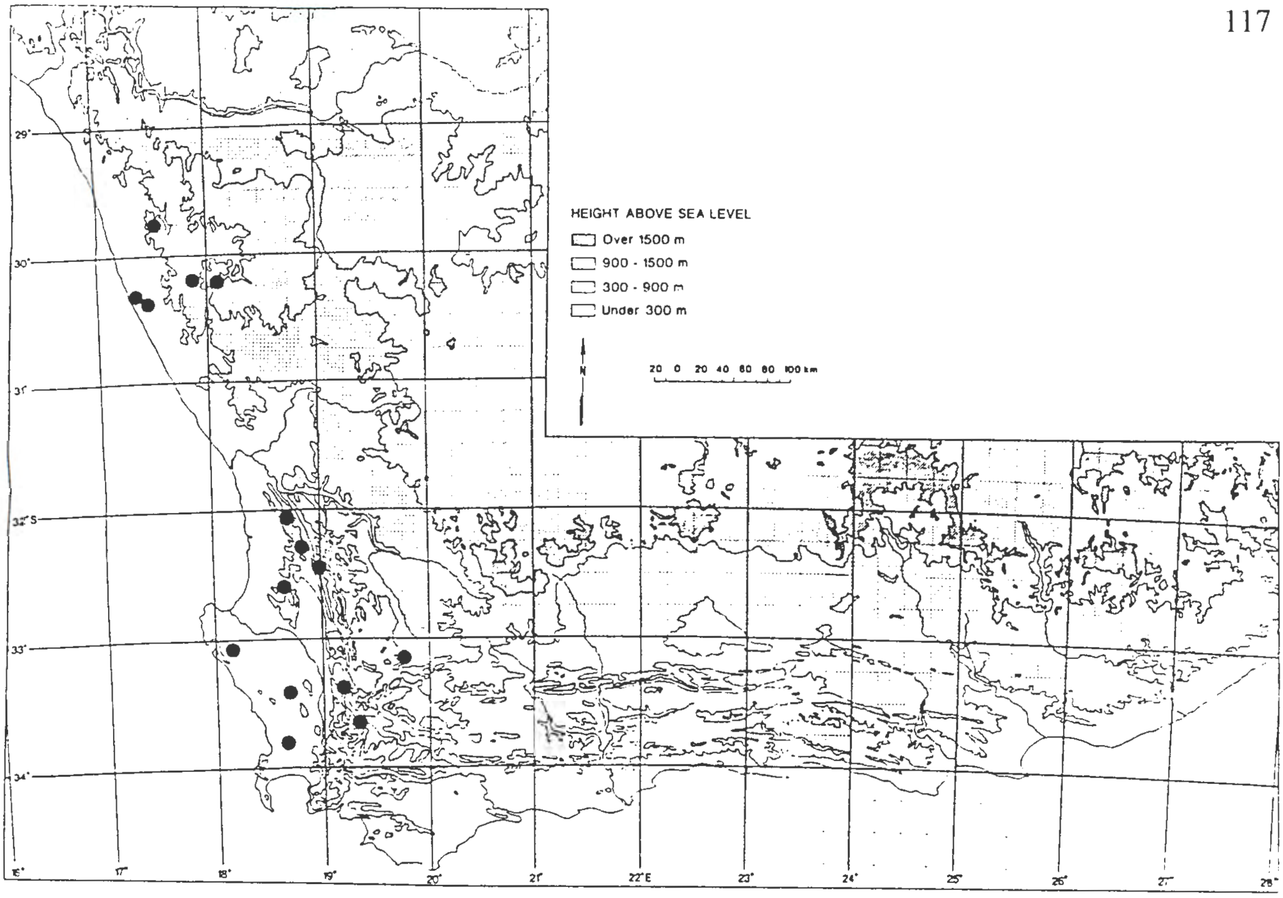

Fig. 4. The distribution of *T.bachmanii*.

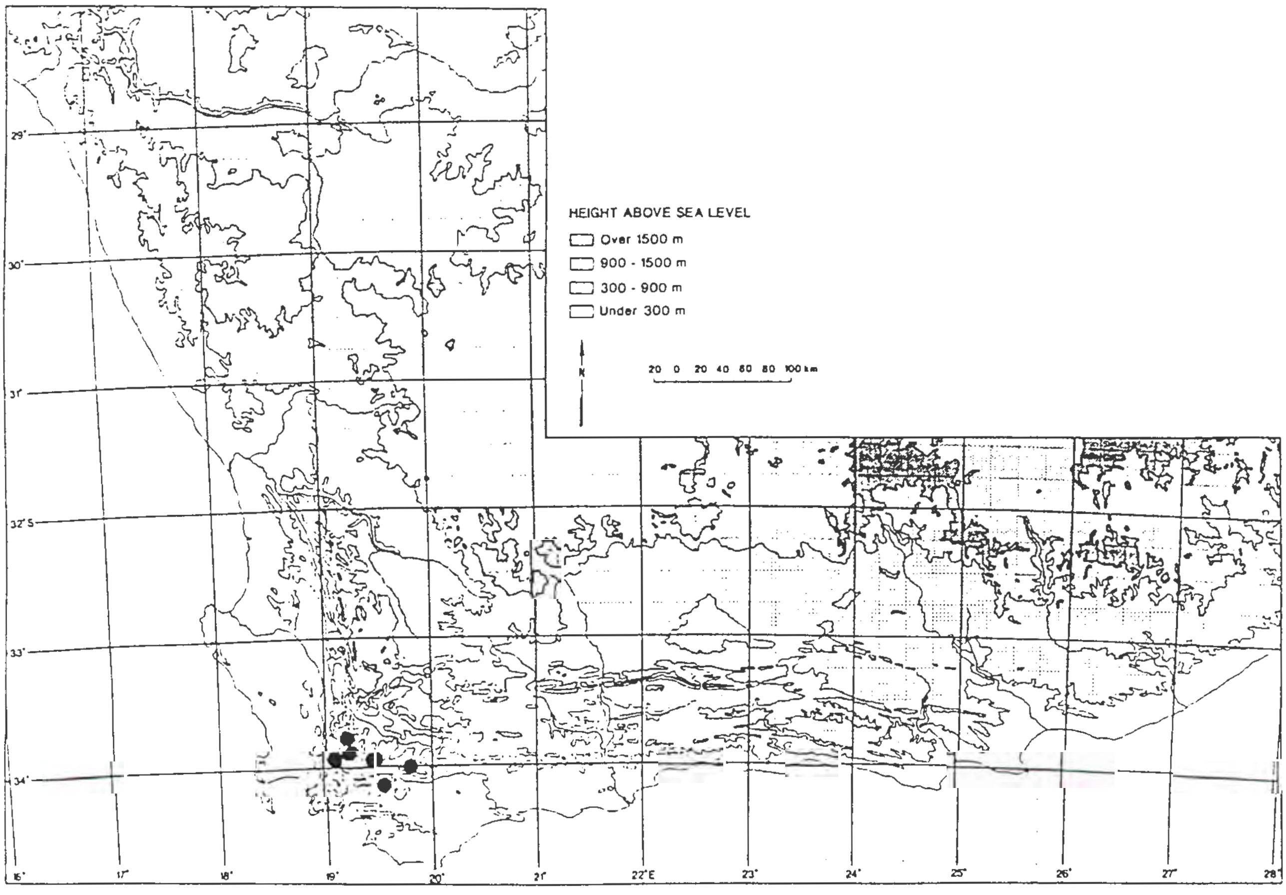

Fig. 5. The distribution of *T.stokoei*.

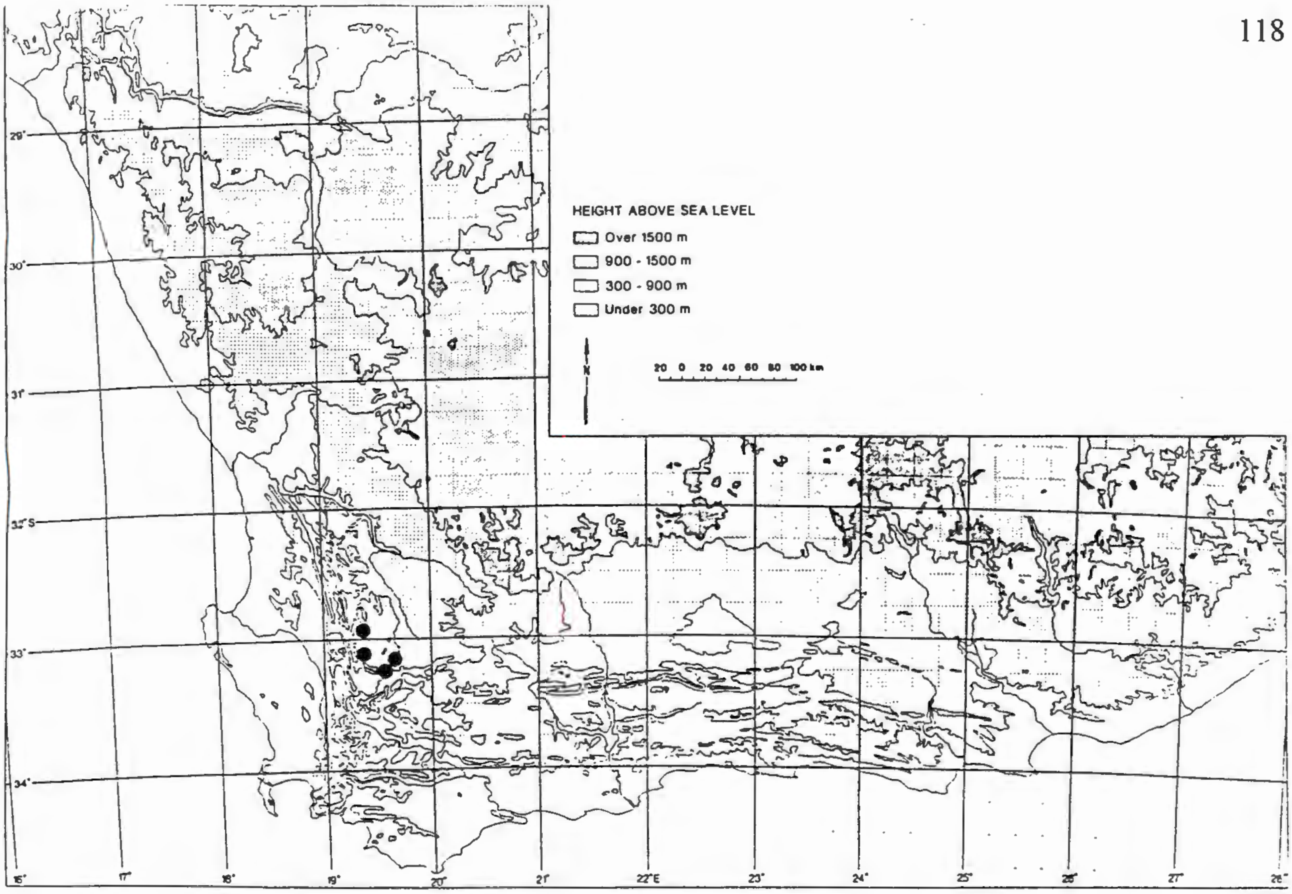

Fig. 6. The distribution of *T.schlechteri*.

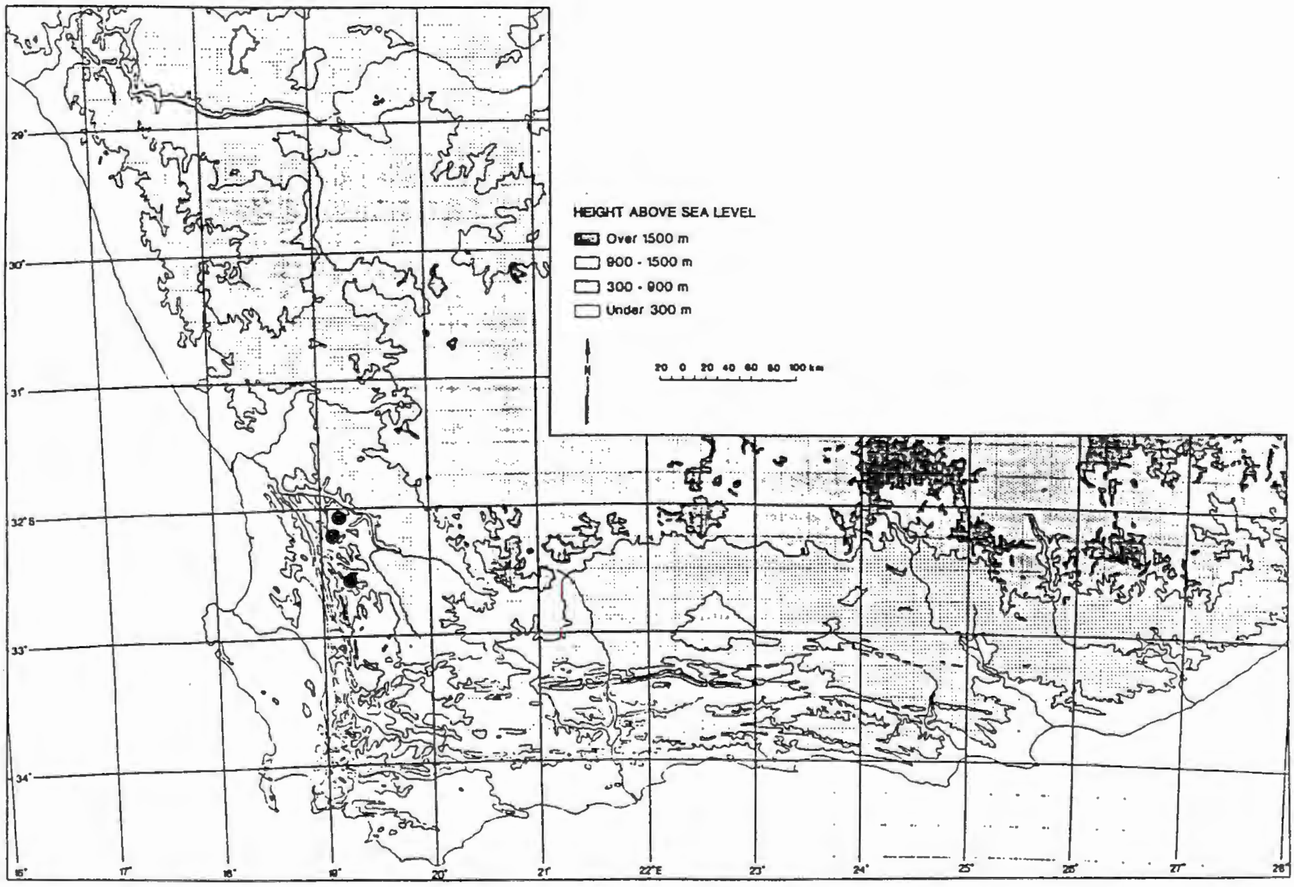

Fig. 7. The distribution of *T.comptonii*.

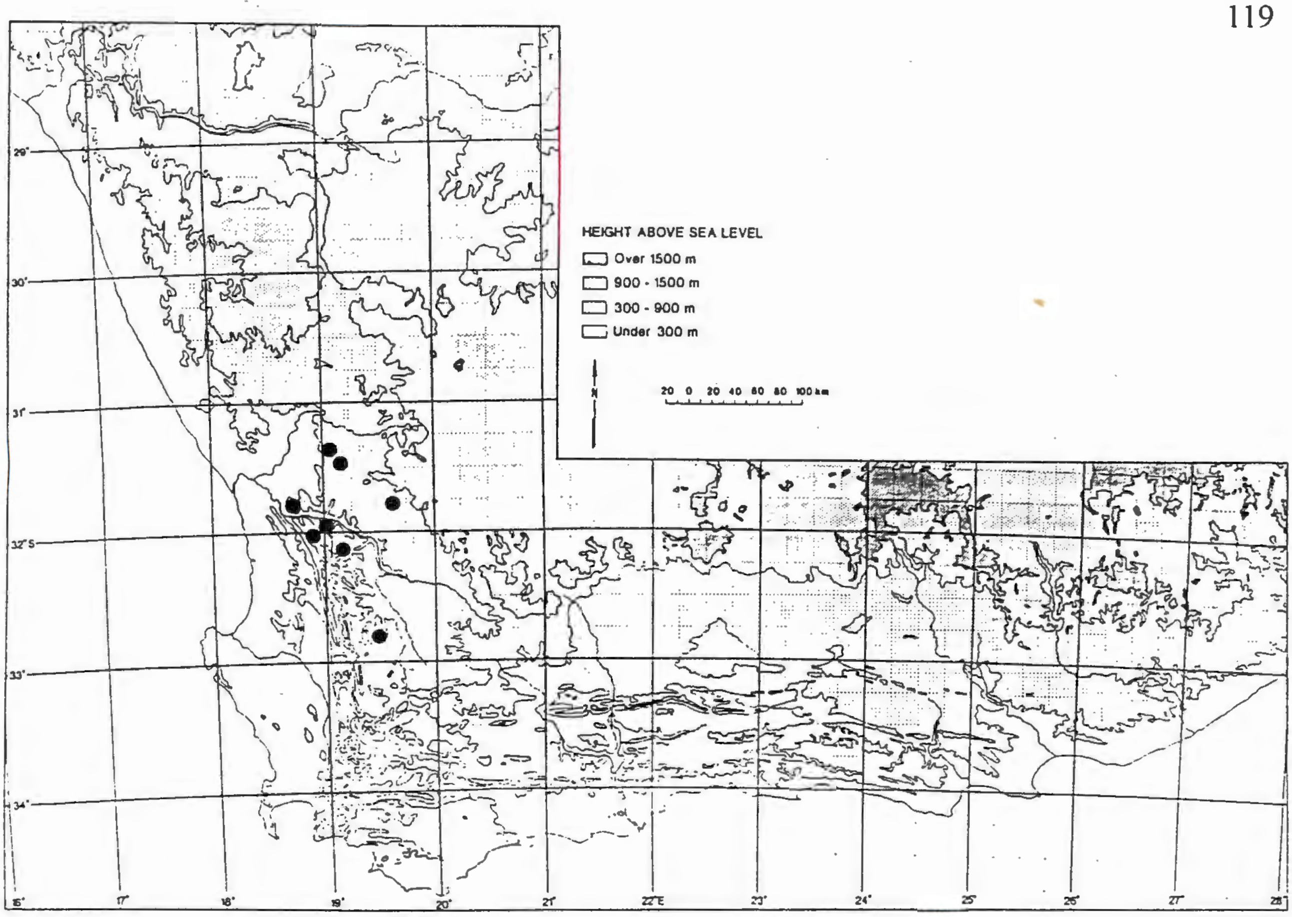

Fig. 8. The distribution of *T.platypteris*.

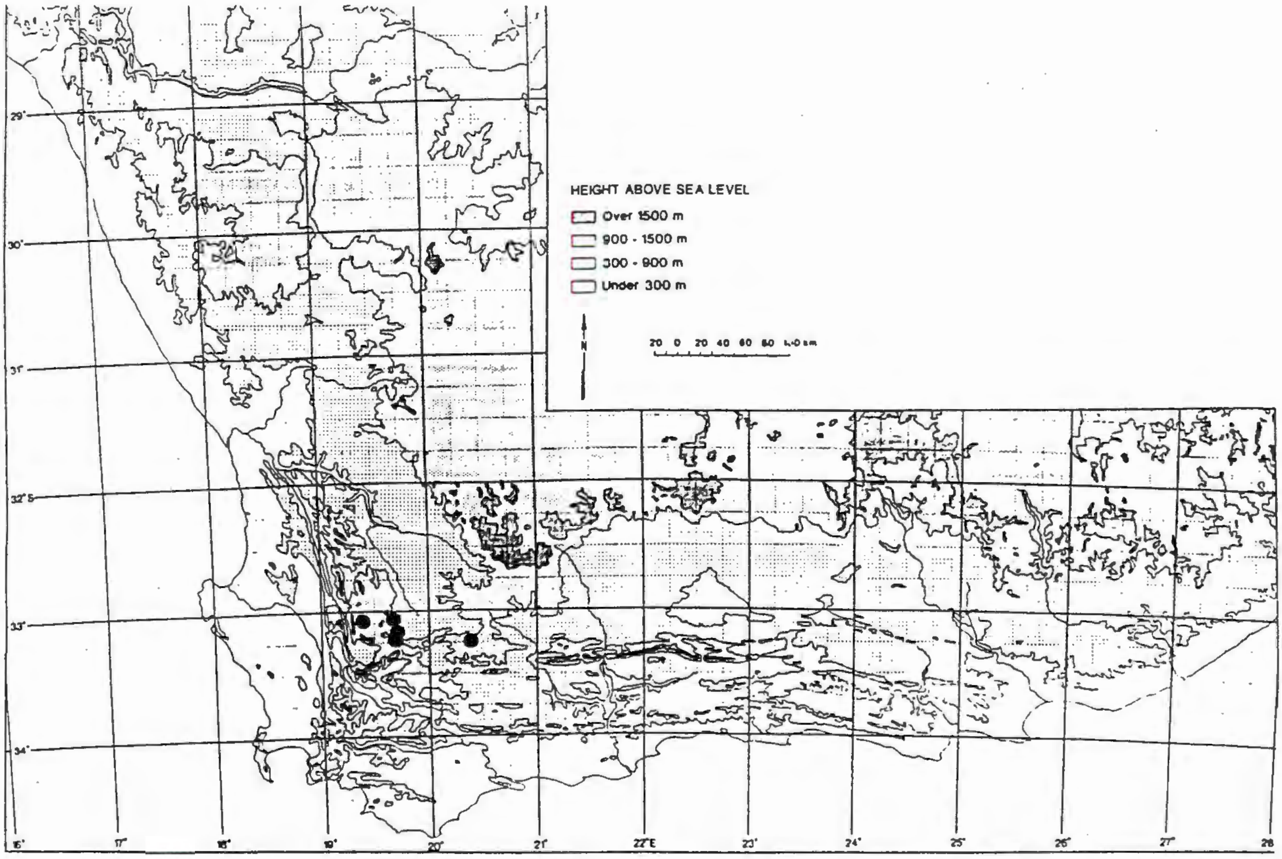

Fig. 9. The distribution of *T.scabridus*.

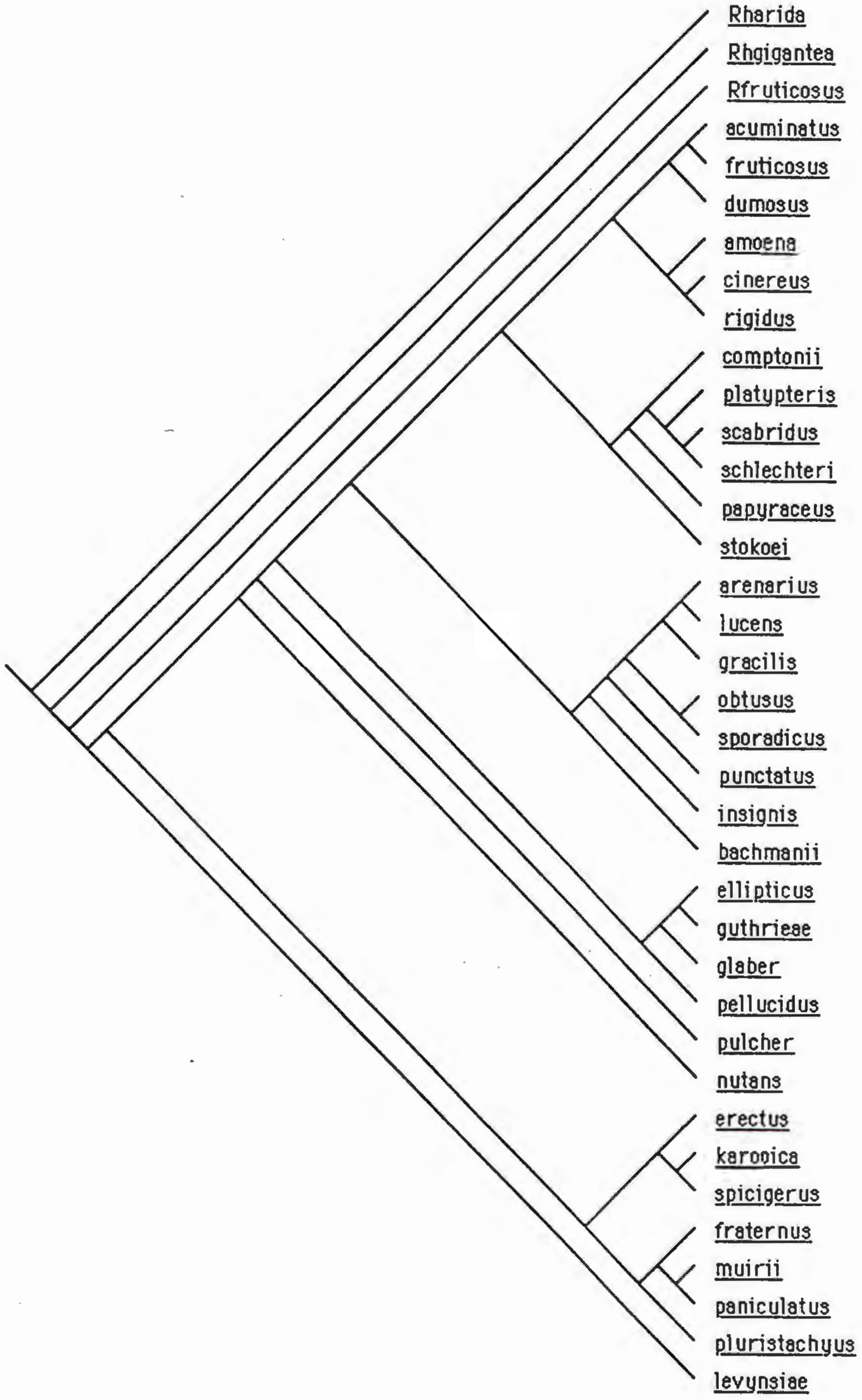

Fig. 10a. The first parsimonius tree produced by the PAUP analysis of the data matrix in Appendix 2.

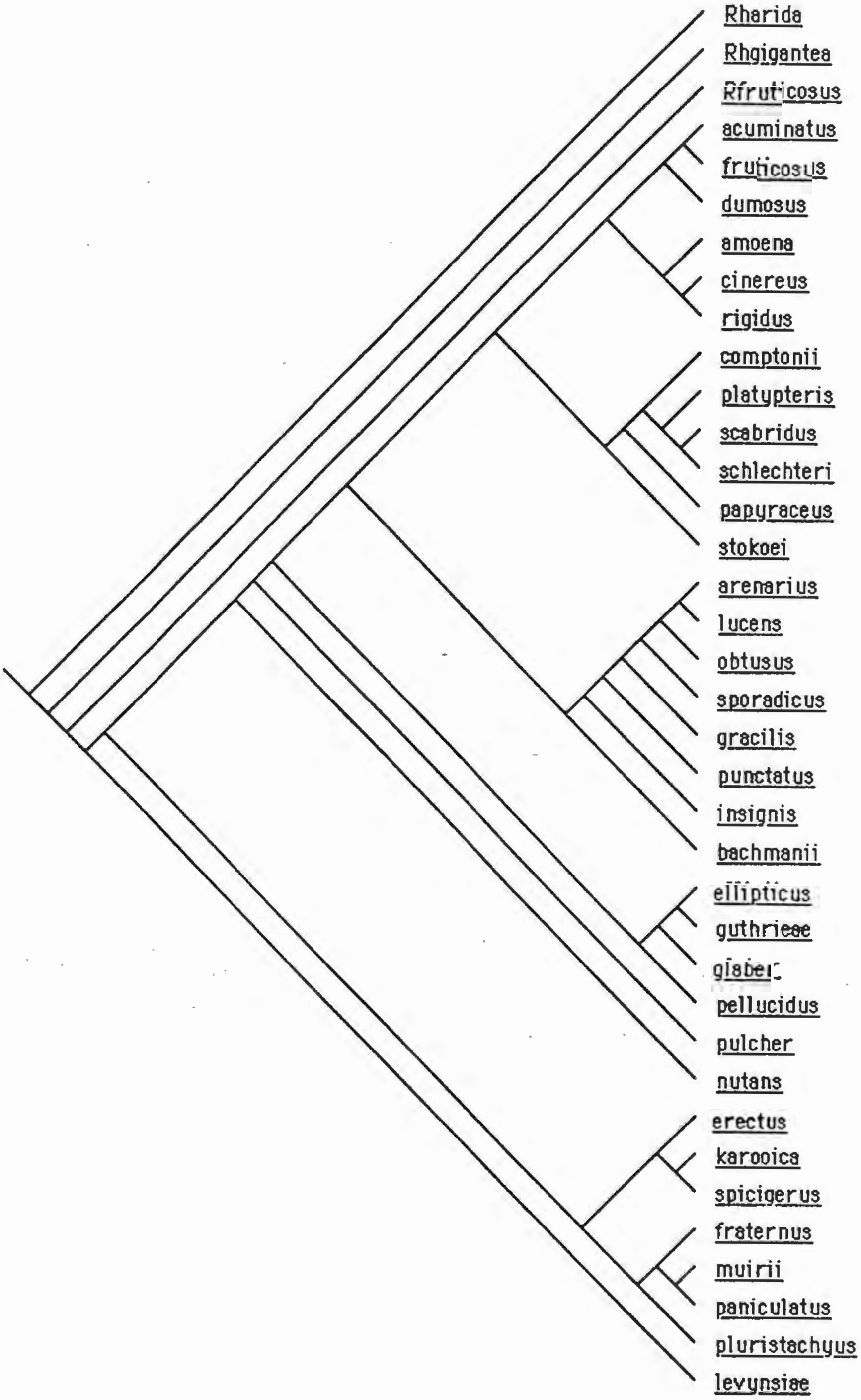

Fig. 10b. The second parsimonius tree produced by the PAUP analysis of the data matrix in Appendix 2.

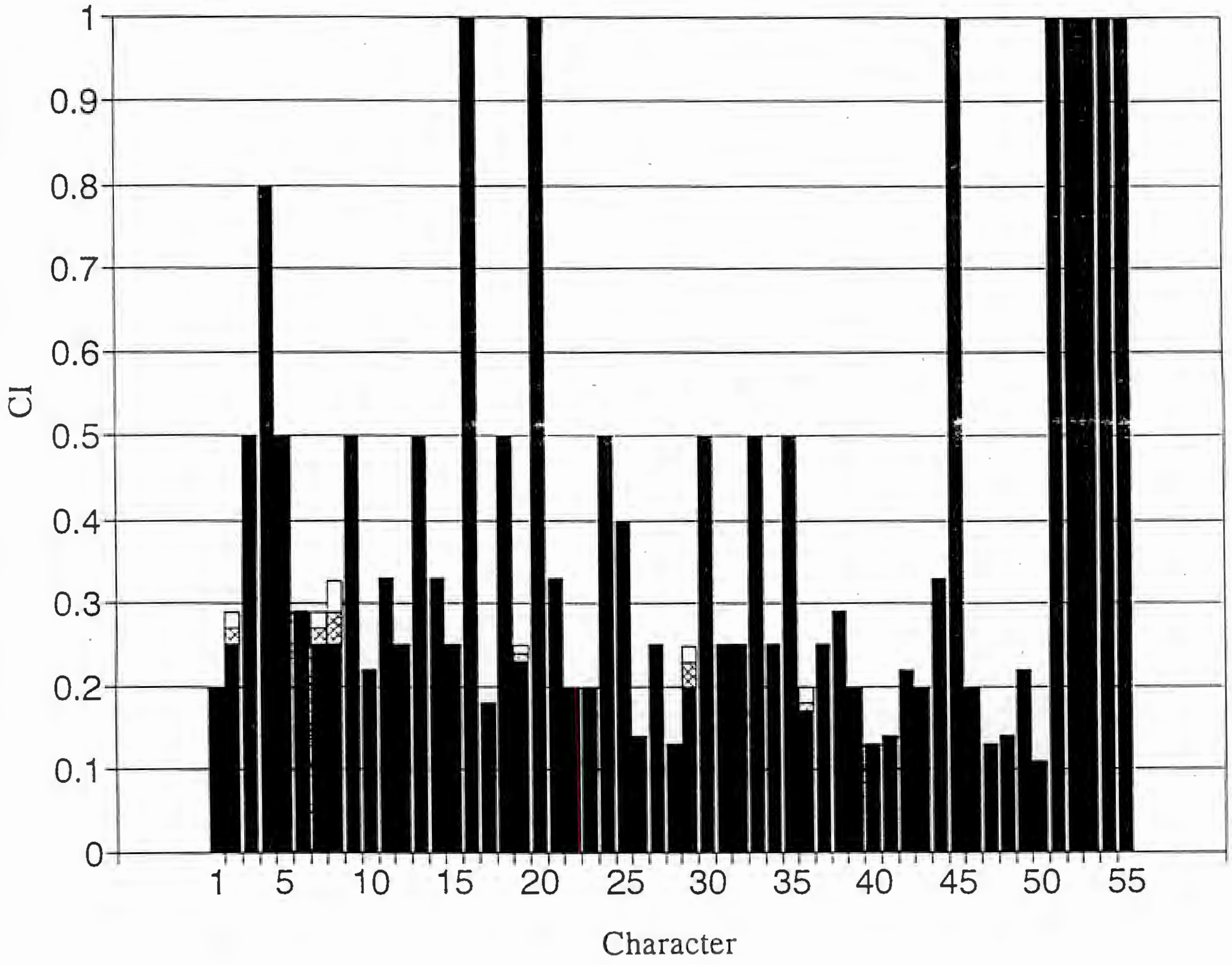

Fig. 11. Graphical representation of the consistency index of each character calculated over the two cladograms. A maximum, minimum and average consistency index has been presented where the consistency index of a character varies across the two cladograms.

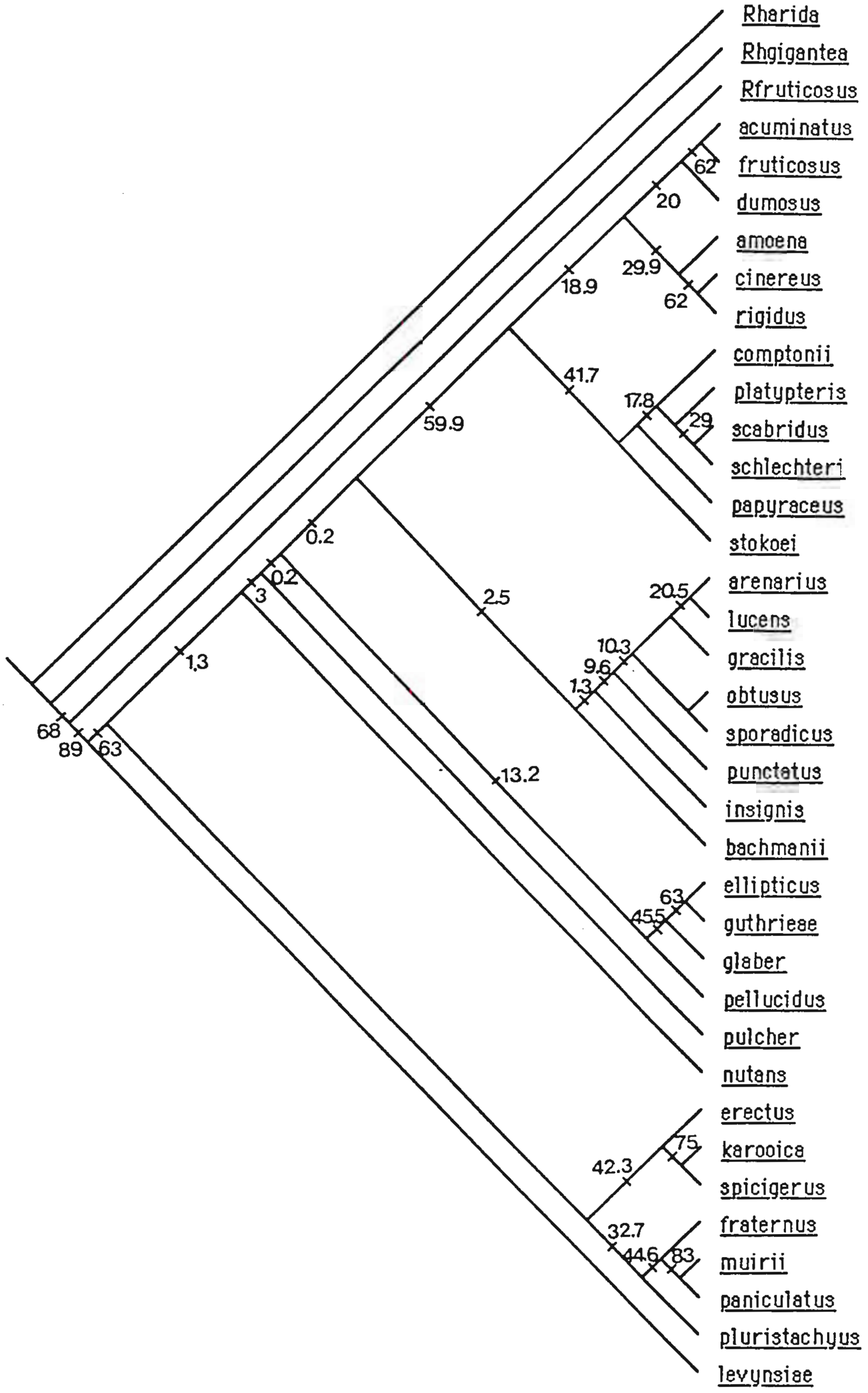

Fig. 12. Bootstrap values for the clades in the first tree.

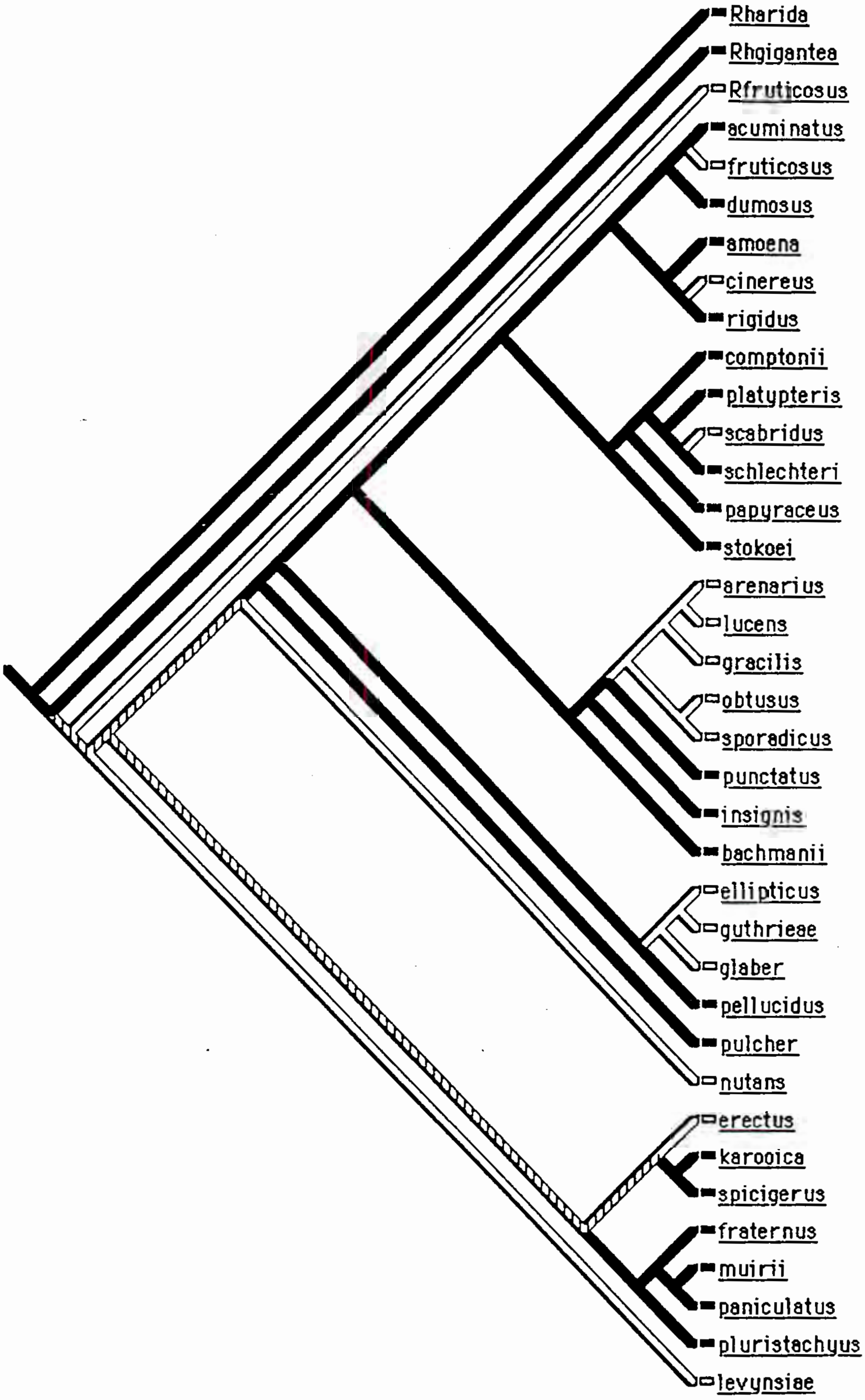

Fig. 13. The cladogram displaying the hypothesised pattern of evolution of seeding and resprouting fire survival strategy in *Thamnochortus*. Clear branches represent the resprouting habit and black branches the seeding habit, hatched branches are equivocal.

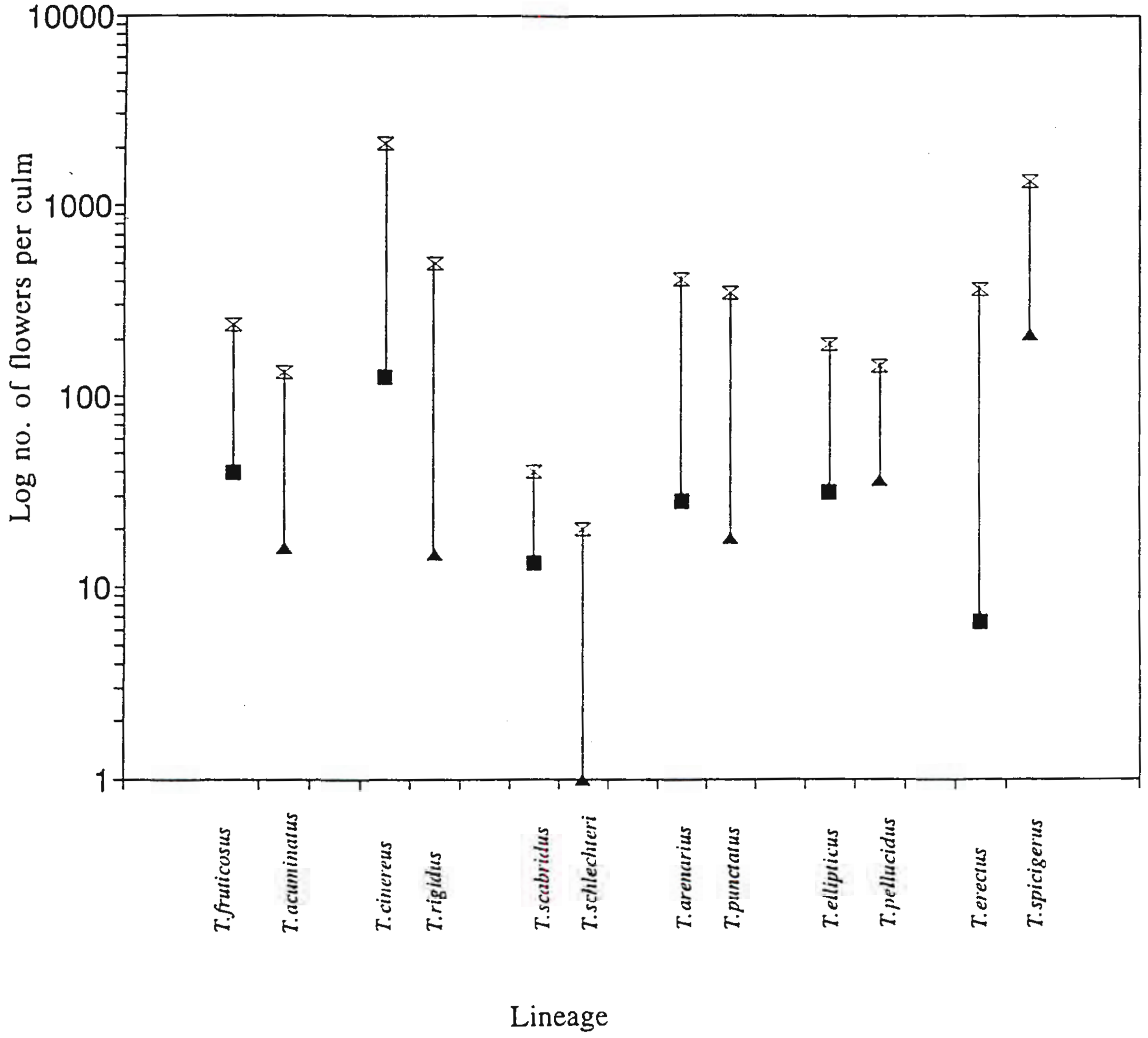

Fig. 14. The range in the number of flowers for each seeding and resprouting sister lineage. Seeding lineages are have a triangle indicating the minimum limits. Resprouters have a square indicating the minimum limits.

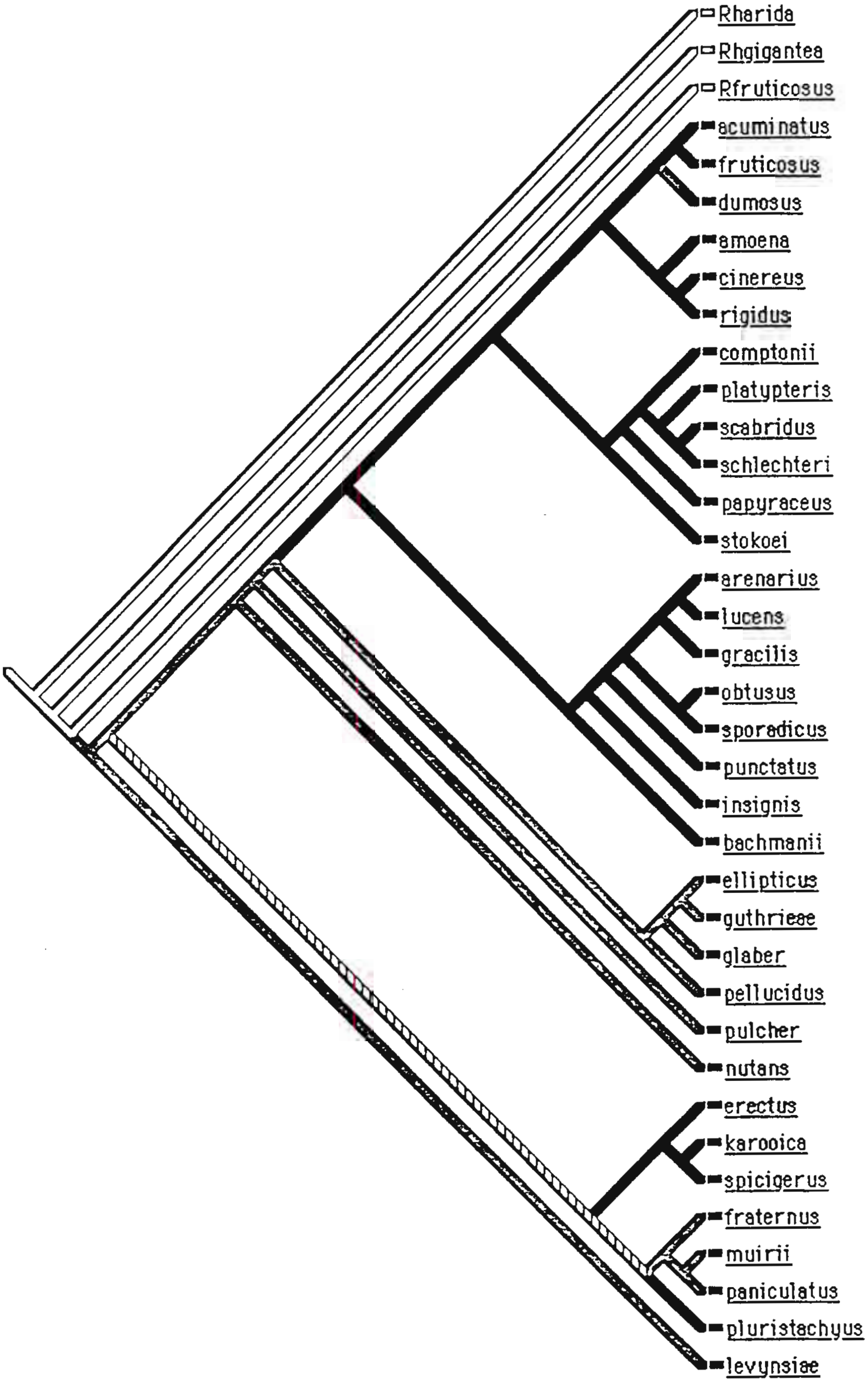

Fig. 15. The cladogram displaying the hypothesised pattern of evolution of wings and keels in *Thamnochortus*. Black branches represent the presence of wings and the tan branches the presence of keels, hatched branches are equivocal. A lack of tepal specialisation is indicated by clear branches.

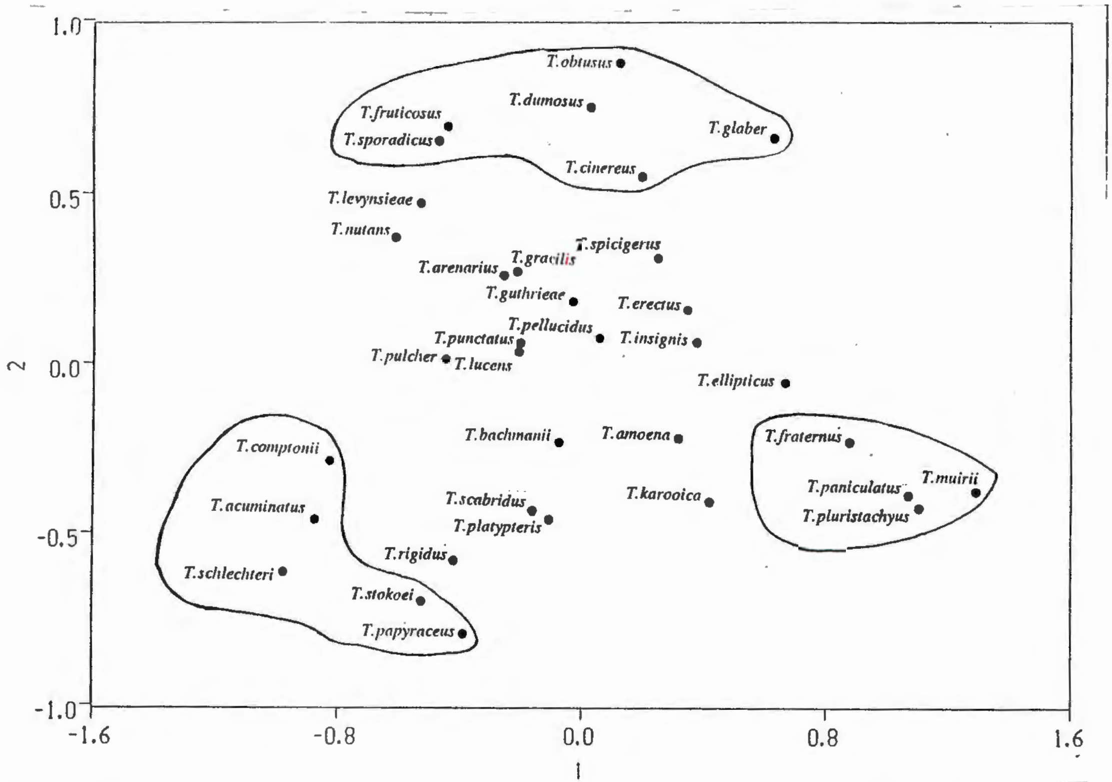

Fig 16. Ecological associations of *Thamnochortus* species resulting from a PCA analysis.

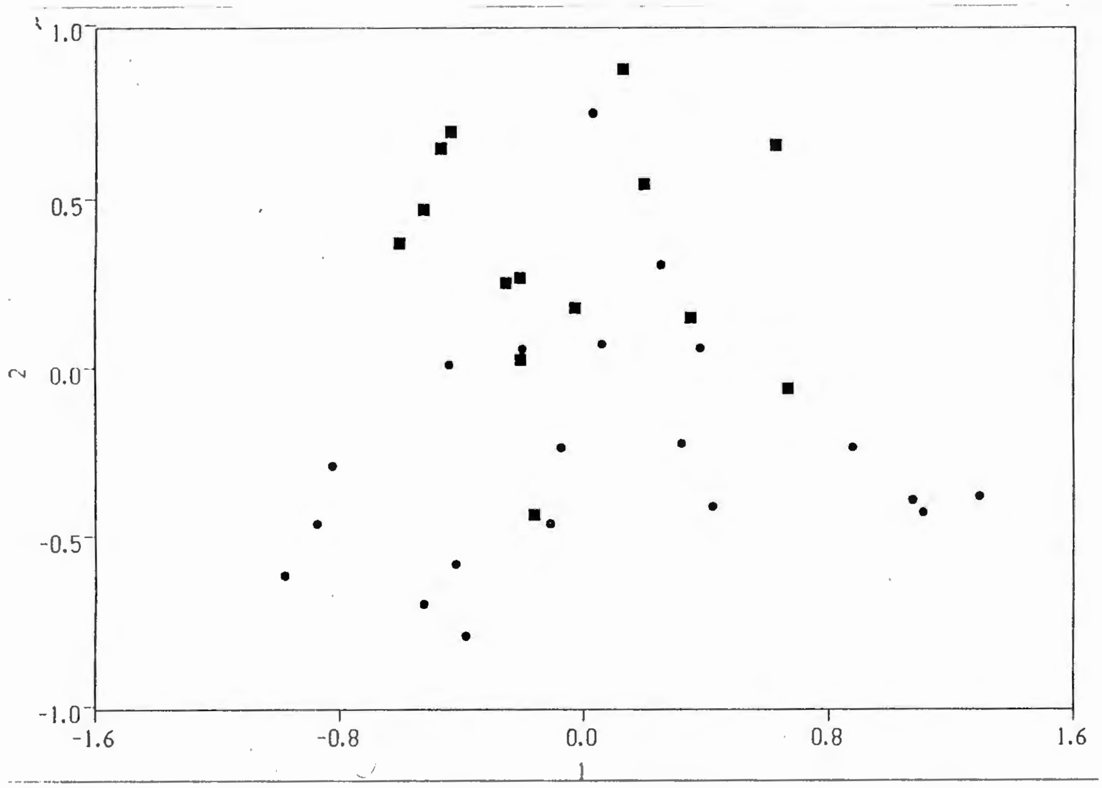

Fig 17. The distribution of seeding and resprouting fire survival stratefies in the context of the ecological pattern of species. Squares indicate those species with the resprouting habit, circles indicate the seeding species.

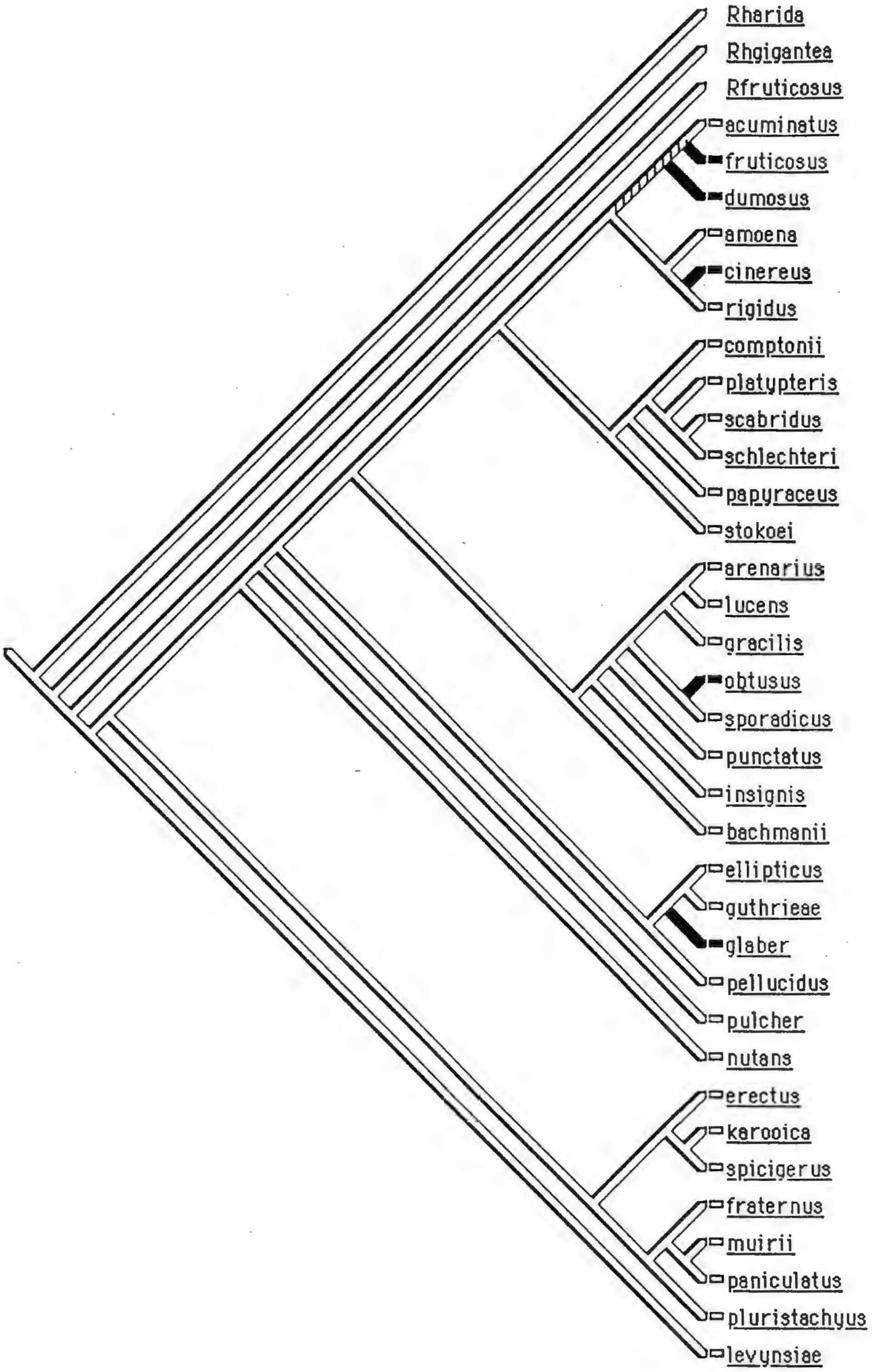

Fig. 18. The cladogram indicating those species that are found in seasonally inundated or marshy habitats. Black branches indicate the preference for damper habitats.

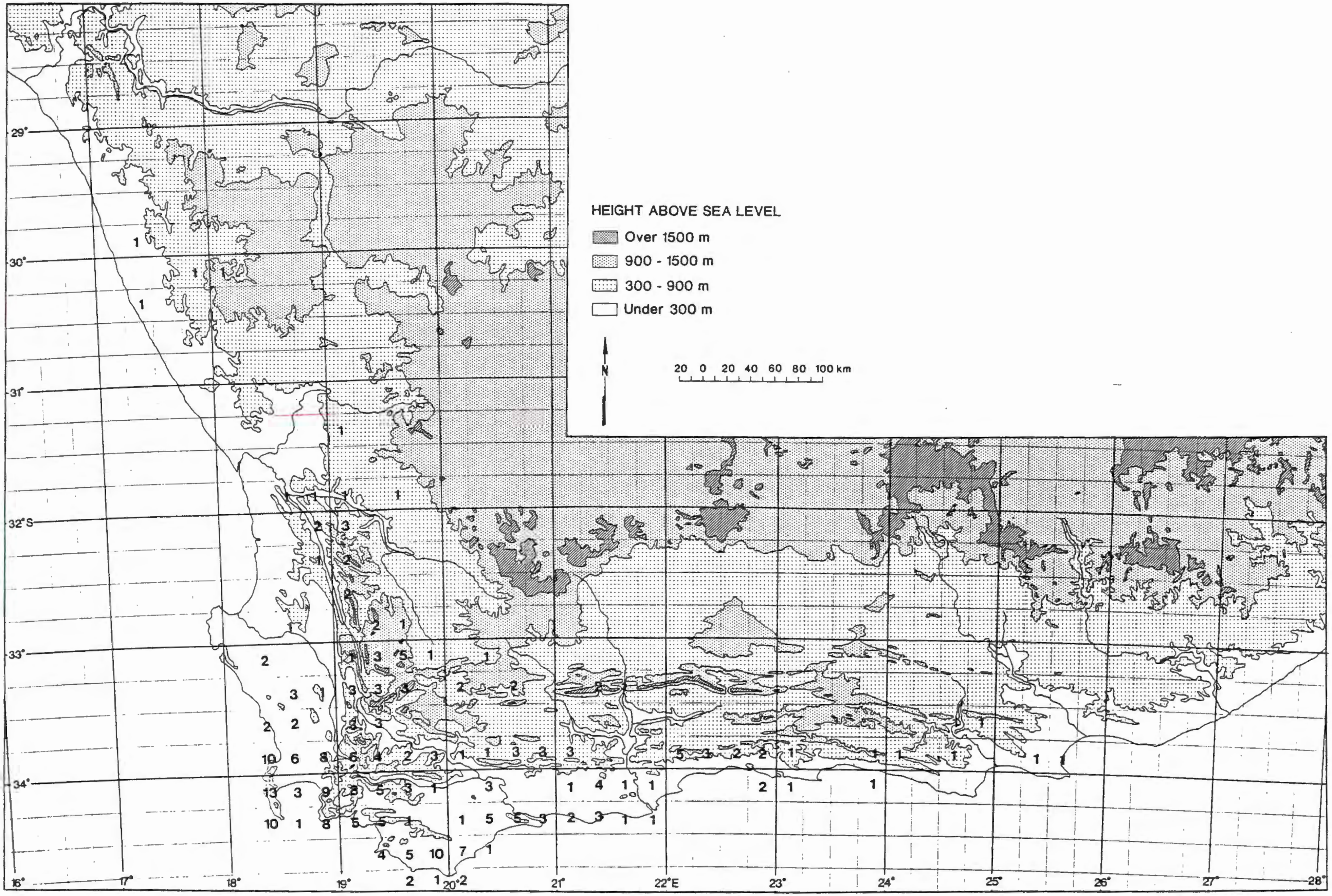

Fig 19. Species diversity in *Thamnochortus* within the Cape Floristic Region. The number of species found in each grid square are presented.

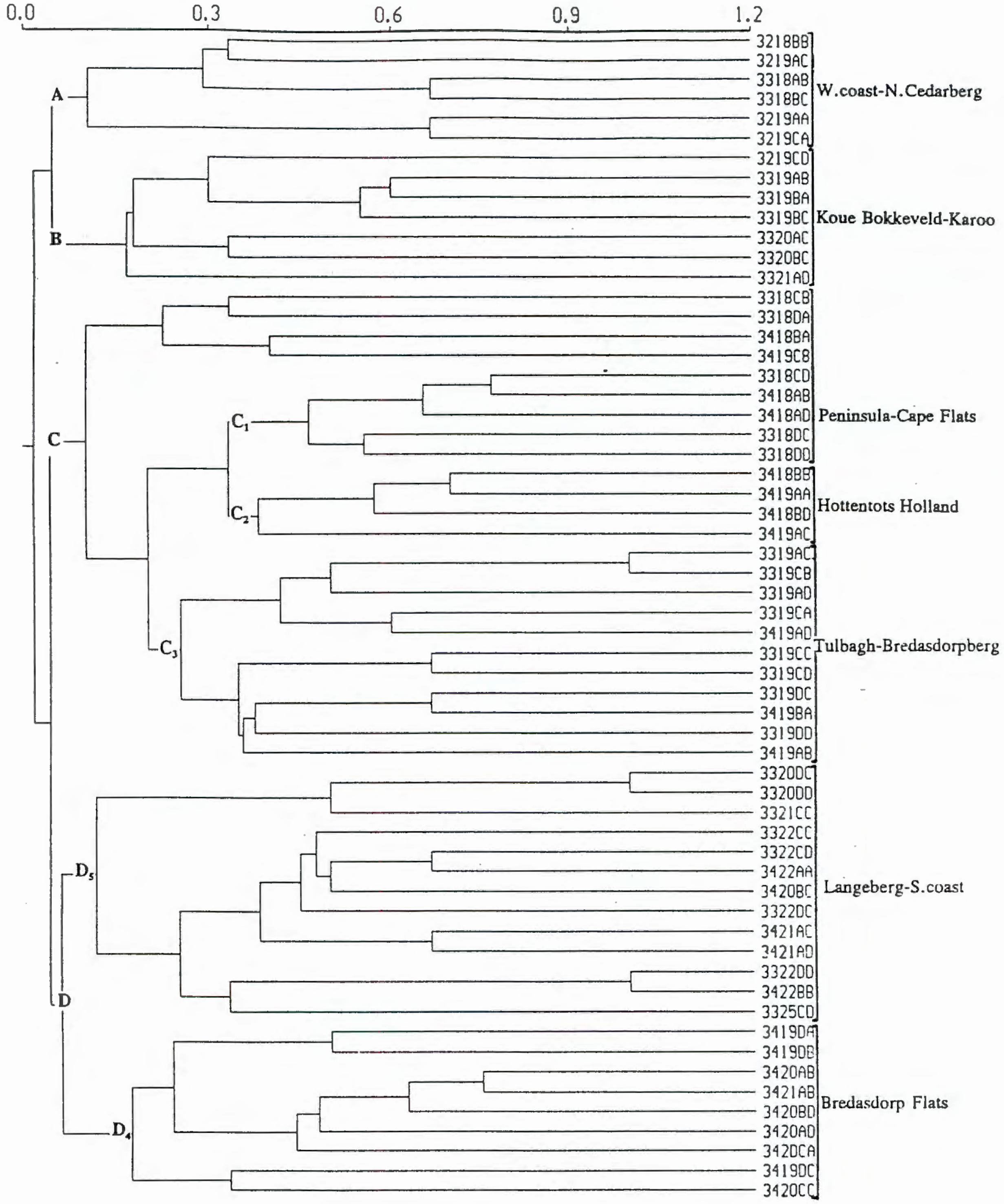

Fig. 20. The phenogram of 1/4° grid squares defining phytogeographic areas for the genus *Thamnochortus*.

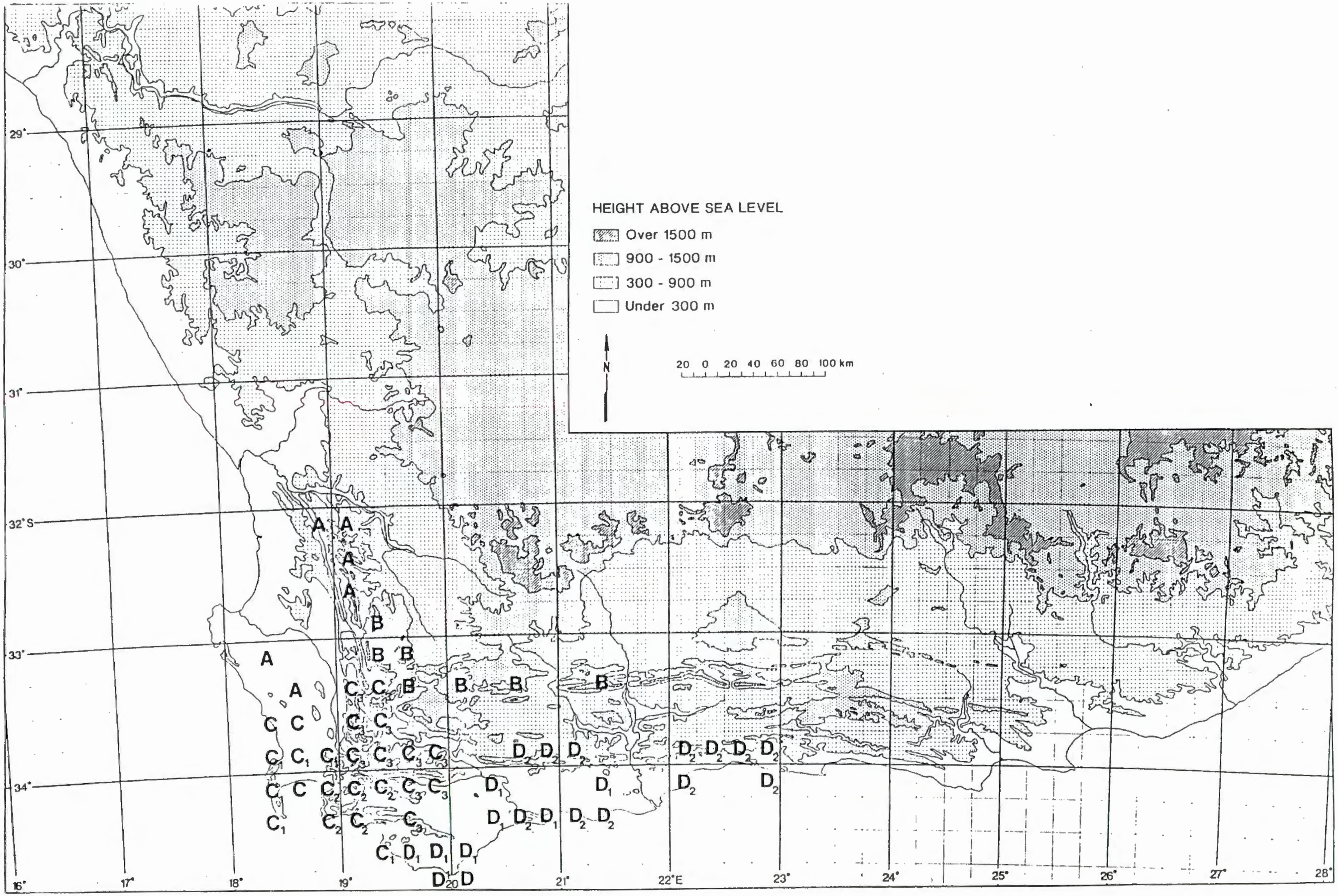

Fig. 21. The phytogeographic areas of the genus *Thamnochortus*. Sub-areas of area C and D, defined in the phytogeographic phenogram, are indicated by C_1, C_2, C_3, D_1 and D_2.

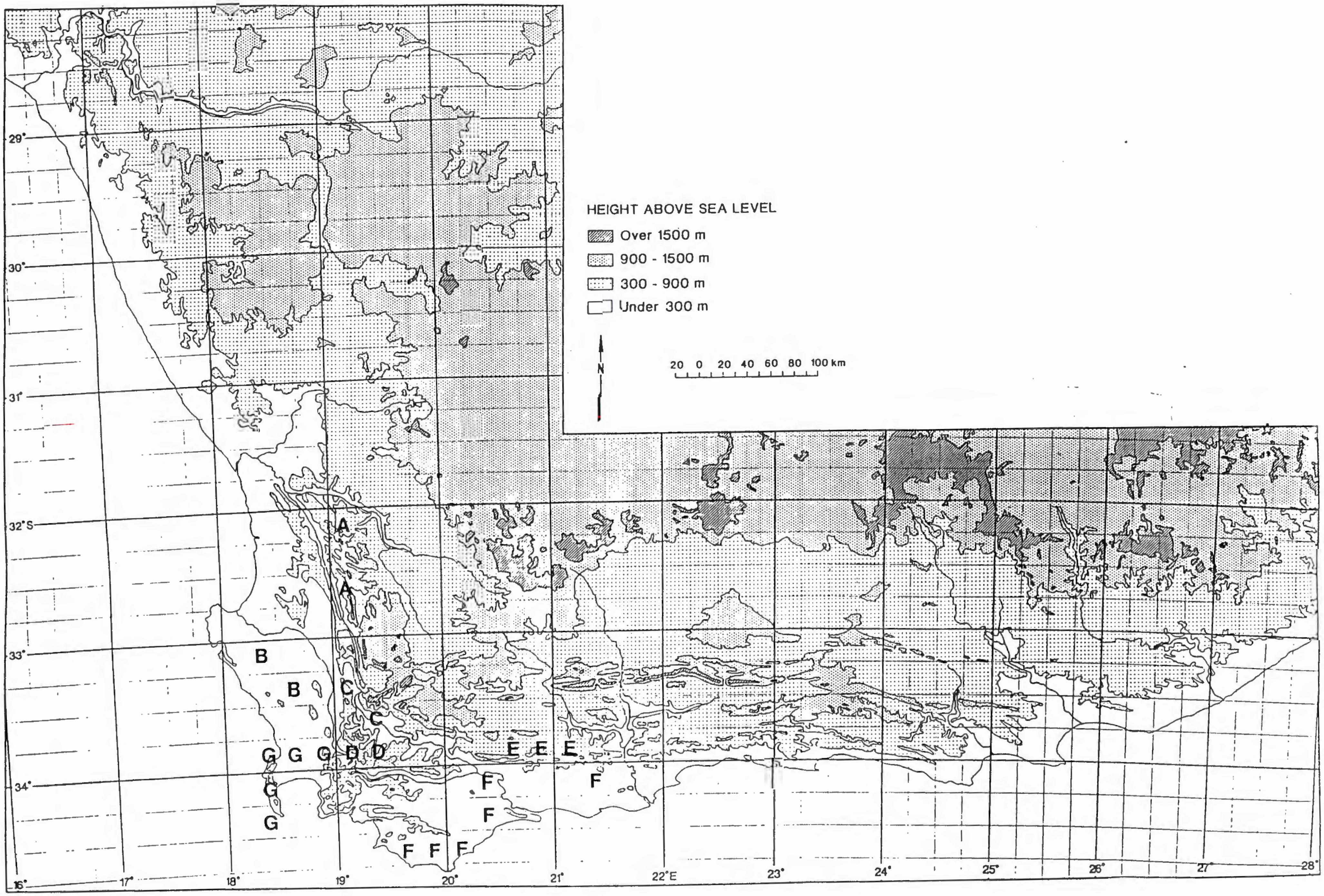

Fig. 22. Areas of endemism located using the parsimony method.

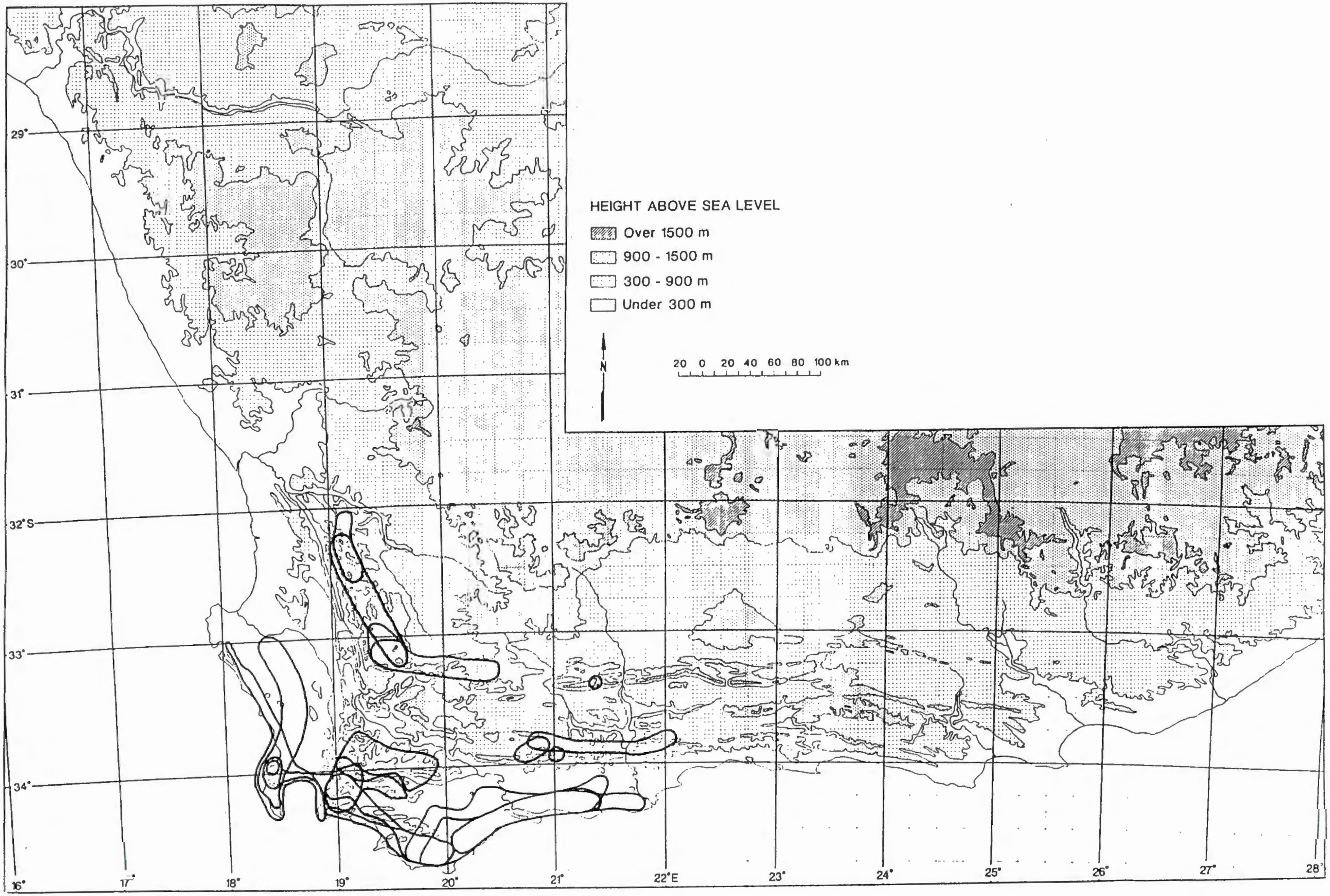

Fig. 23. Areas of endemism defined by the distributions of more restricted species. The extensive overlap between areas is highlighted.

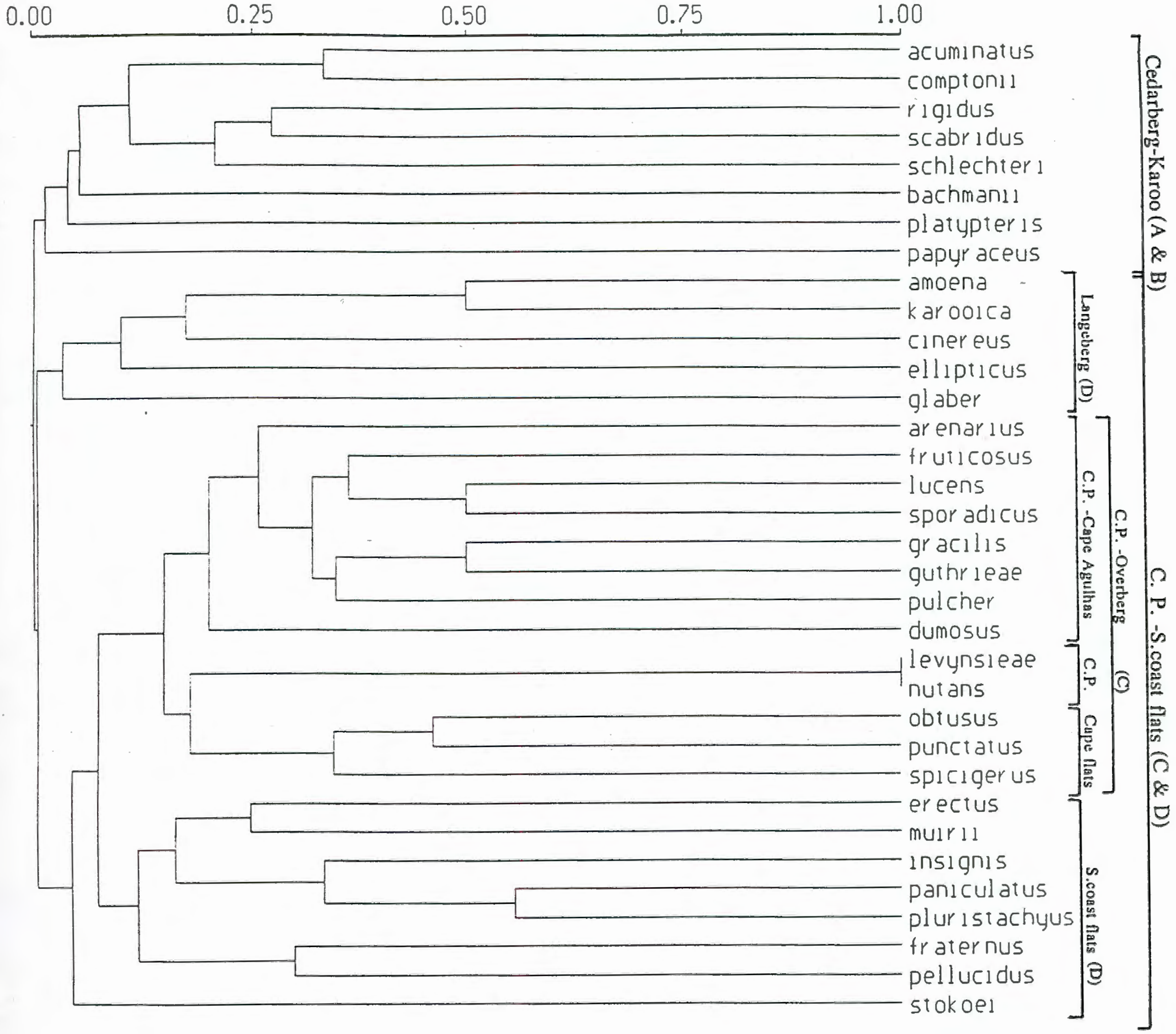

Fig. 24. The phenogram of species associated according to 1/4° grid squares.

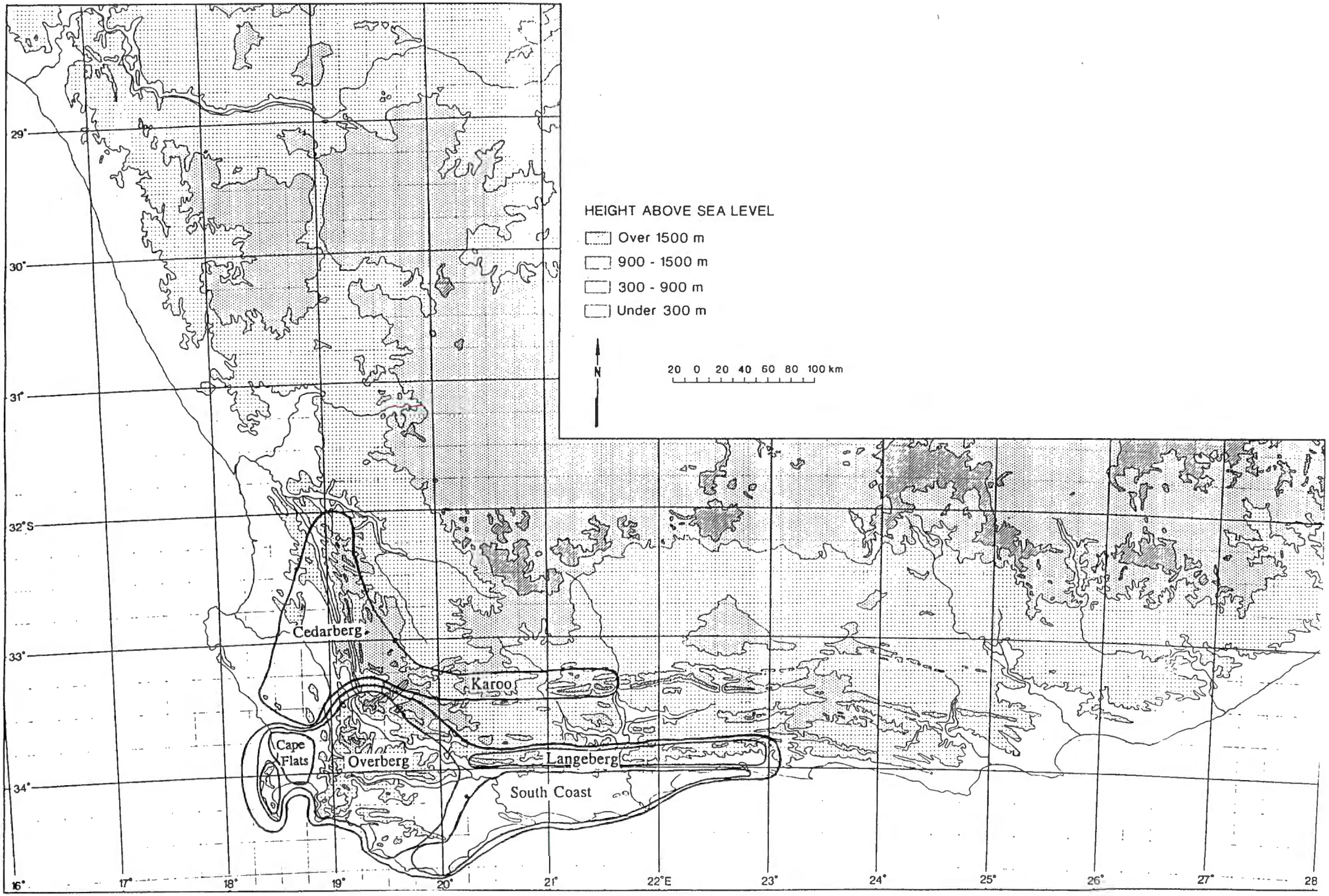

Fig. 25. Map indicating the pattern of distribution of phytogeographical groups of species.

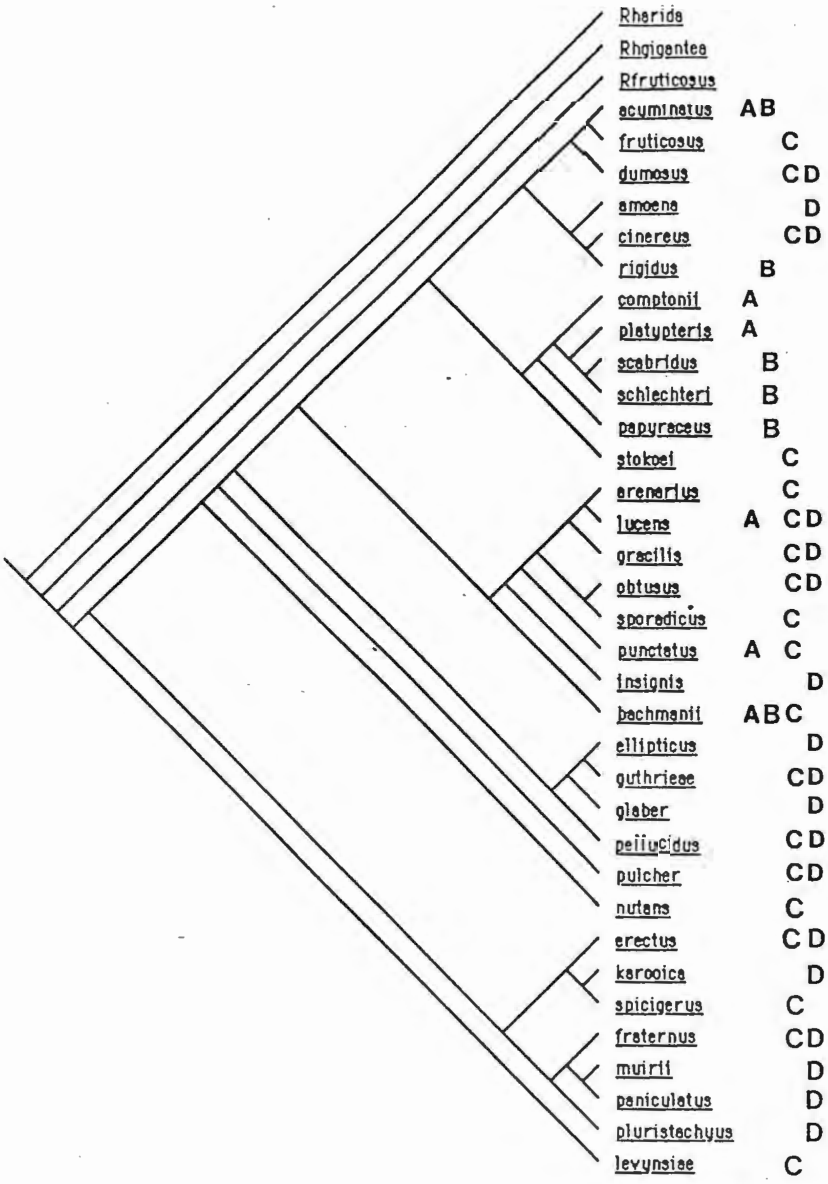

Fig. 26a. Taxon-area cladogram of areas of similarity for the entire genus *Thamnochortus*.

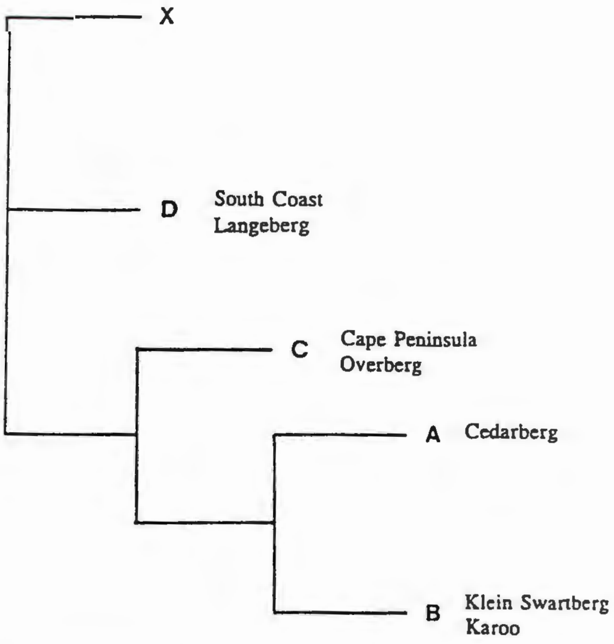

Fig. 26b. Area cladogram of phytogeographic areas.

Key of symbols used in ecological diagrams:

Table Mountain Group Sandstone

▨ gravel-rock

▤ sandy-gravel

⬡ sand

Limestone

☰ restricted to shallow soil over limestone pavements

▒ deeper soils on and adjacent to limestone pavements

Flowering times

Early Spring ○

Late Spring ▲

Early Autumn △

Late Autumn □

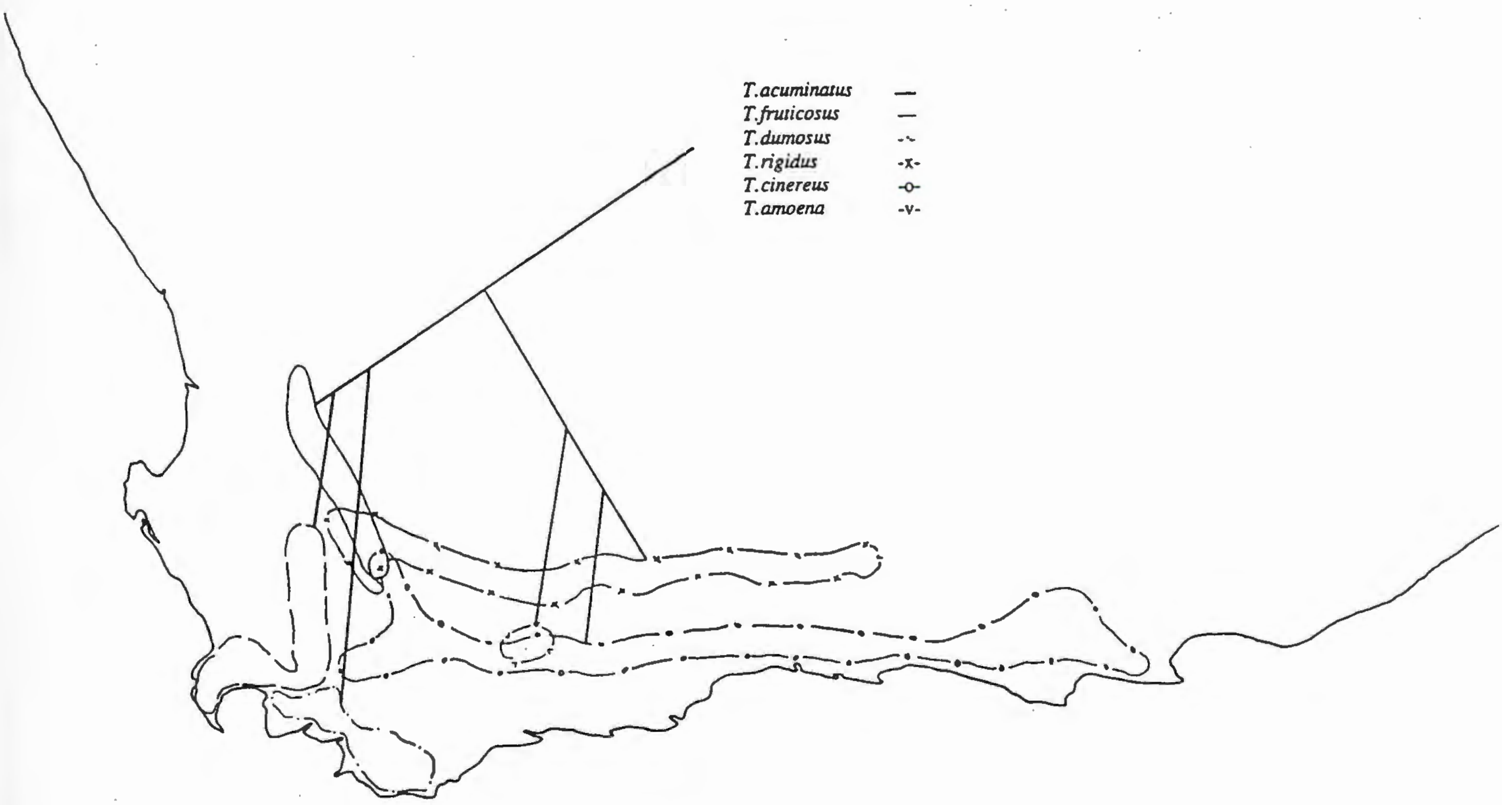

Fig. 28. The distribution of species in the *T.acuminatus*-*T.rigidus* clade.

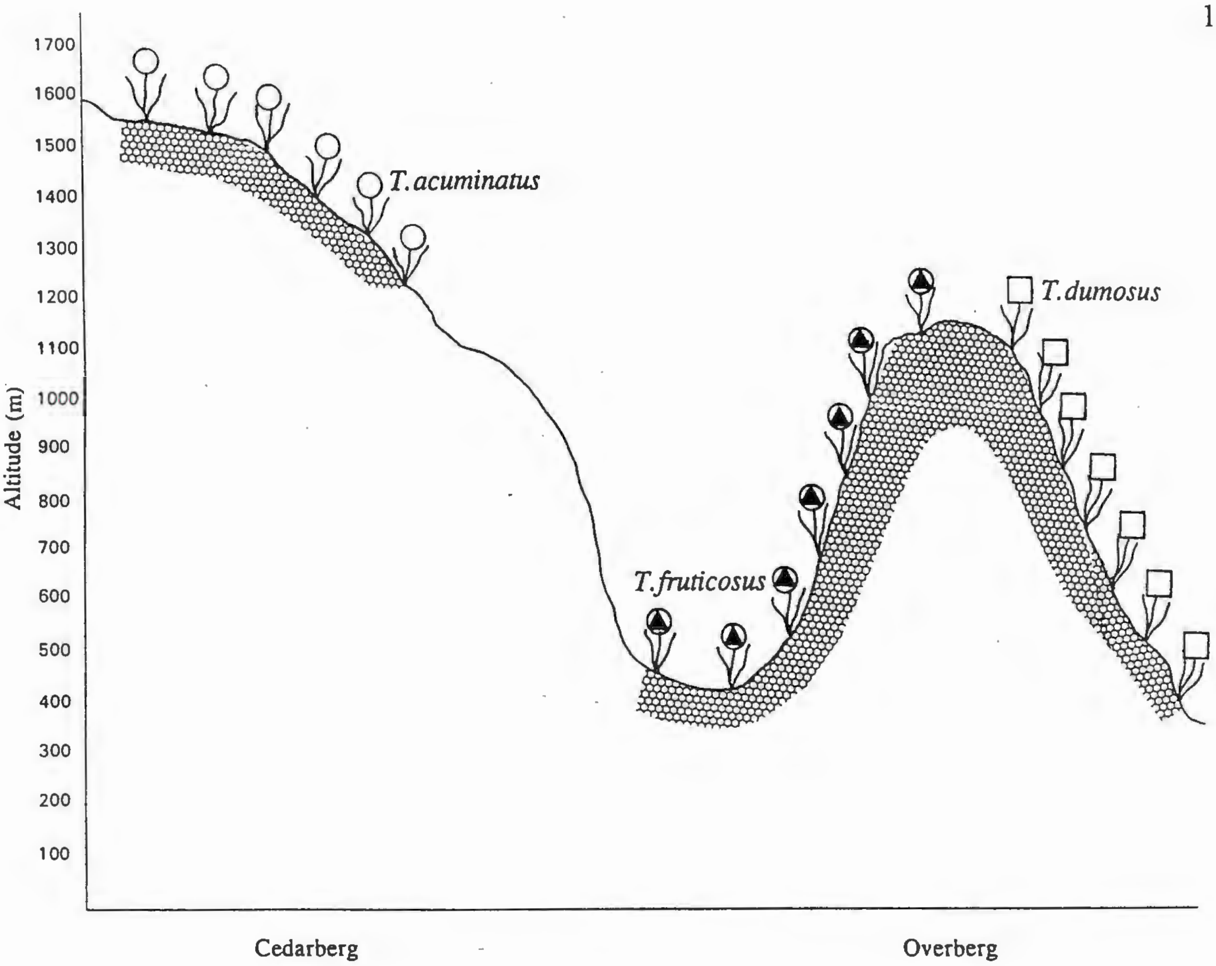

Fig. 29a. Diagramatical representation of ecological specialisation for species in the *T.acuminatus-T.dumosus* clade.

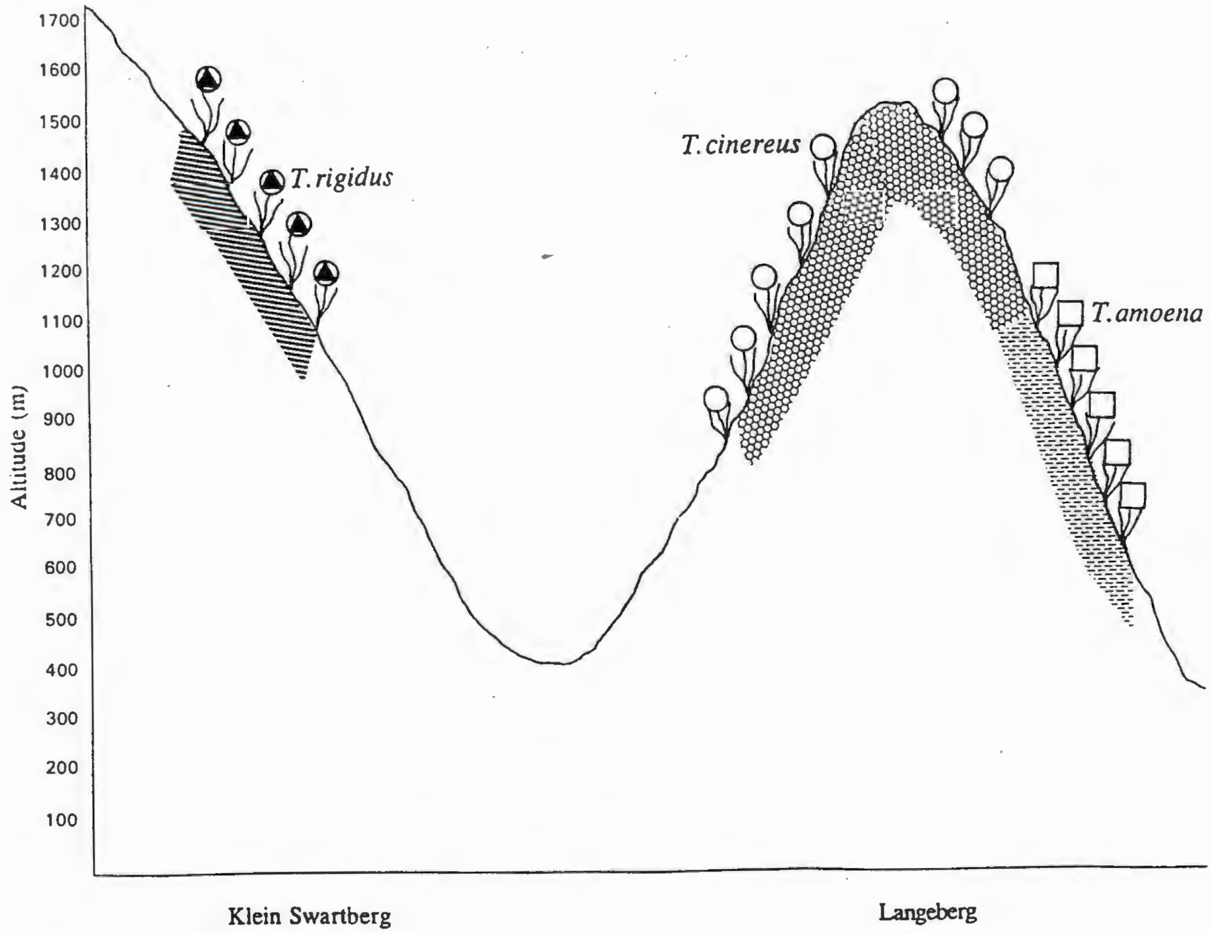

Fig. 29b. Diagramatical representation of ecological specialisation for species in the *T.rigidus-T.amoena* clade.

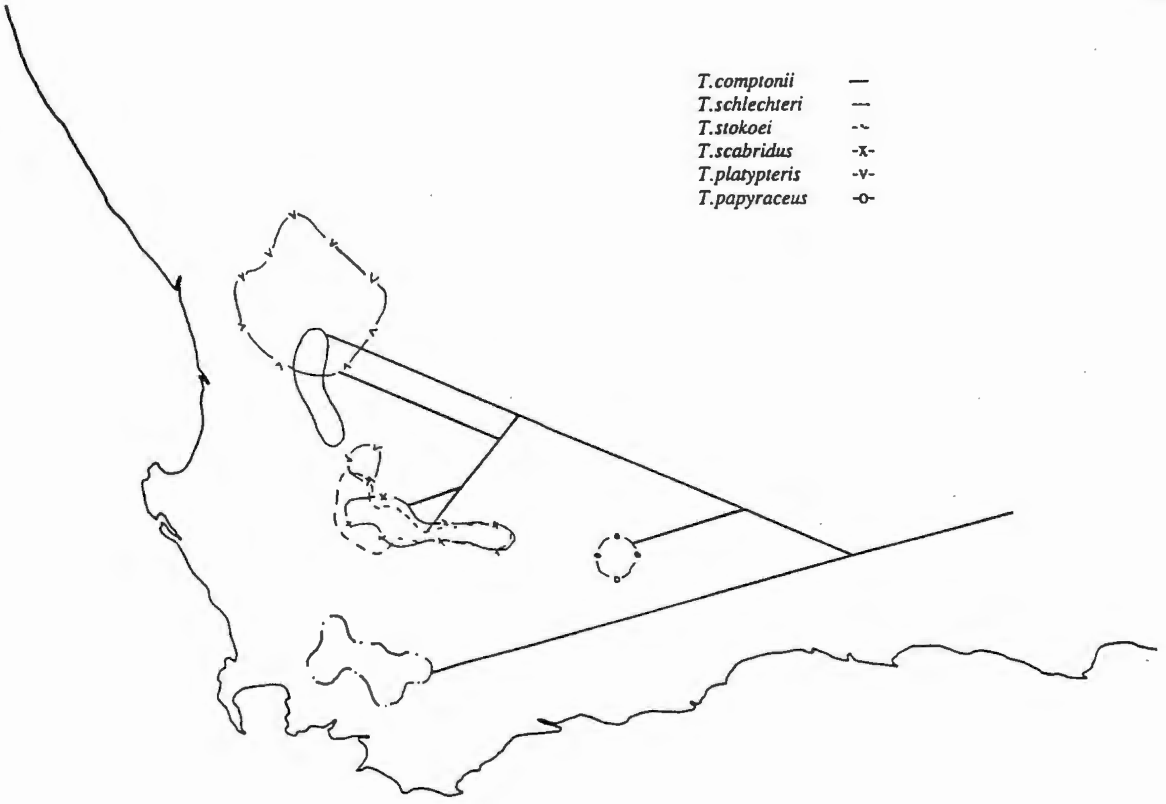

Fig. 30. The distribution of species in the *T.comptonii* clade.

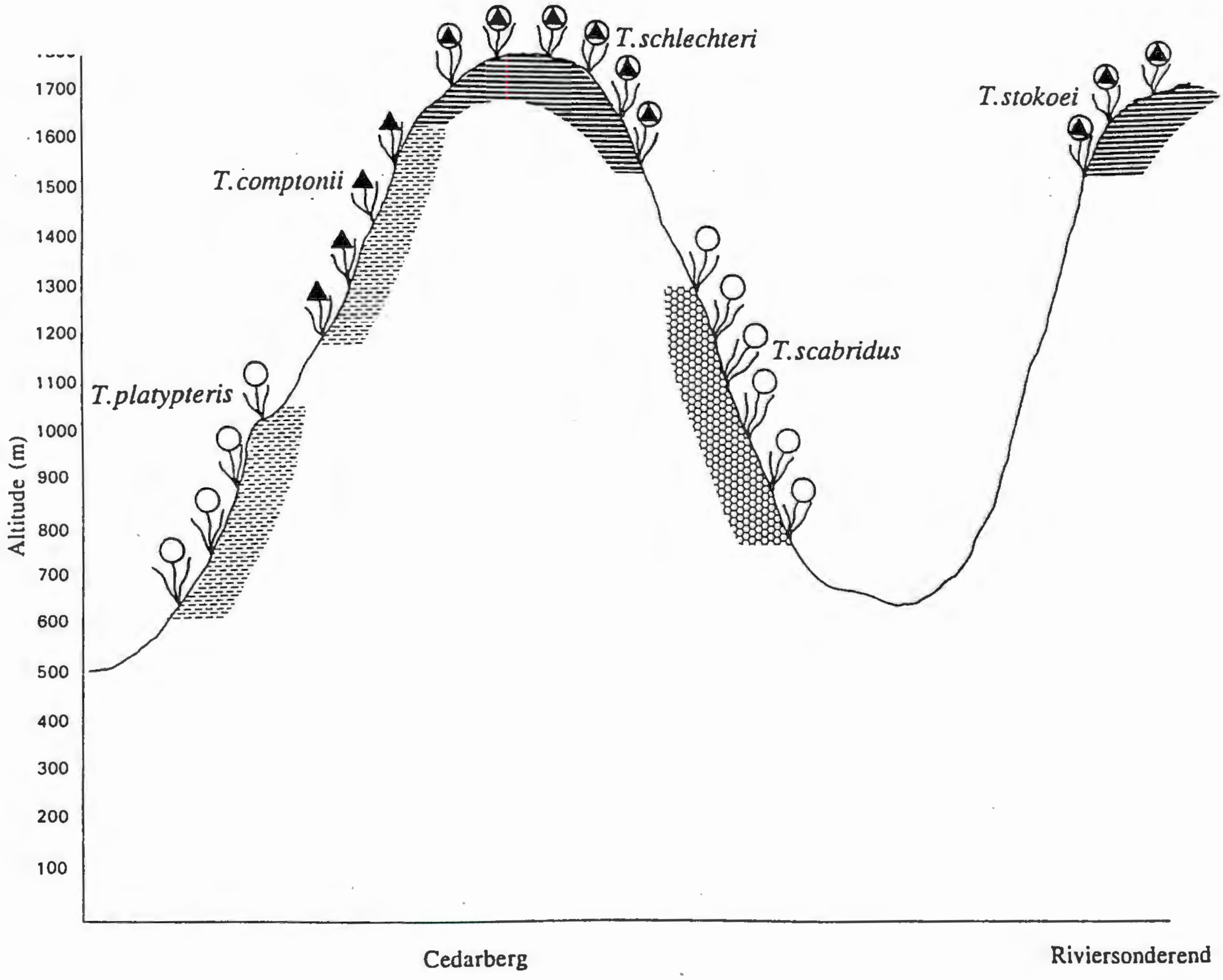

Fig. 31. Diagramatical representation of ecological specialisation for species in the *T.comptonii* clade.

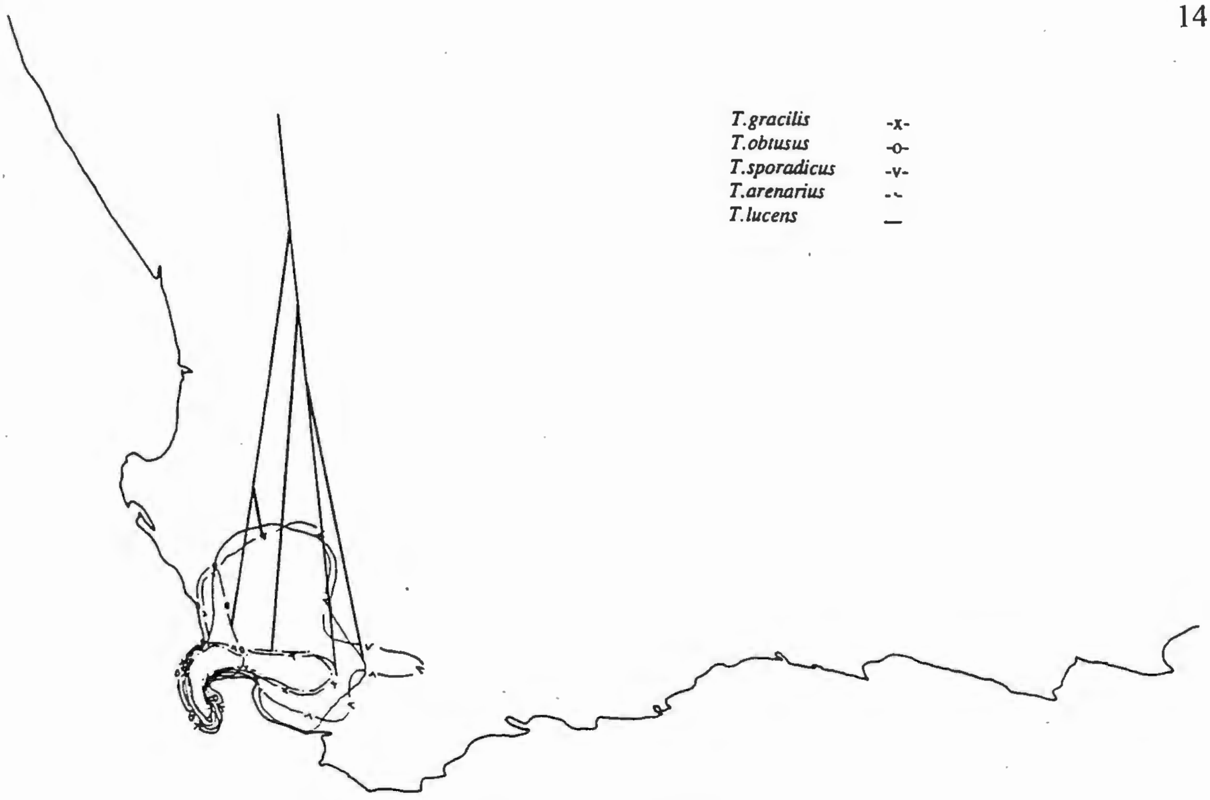

Fig. 32. The distribution of species in the *T.arenarius-T.sporadicus* clade.

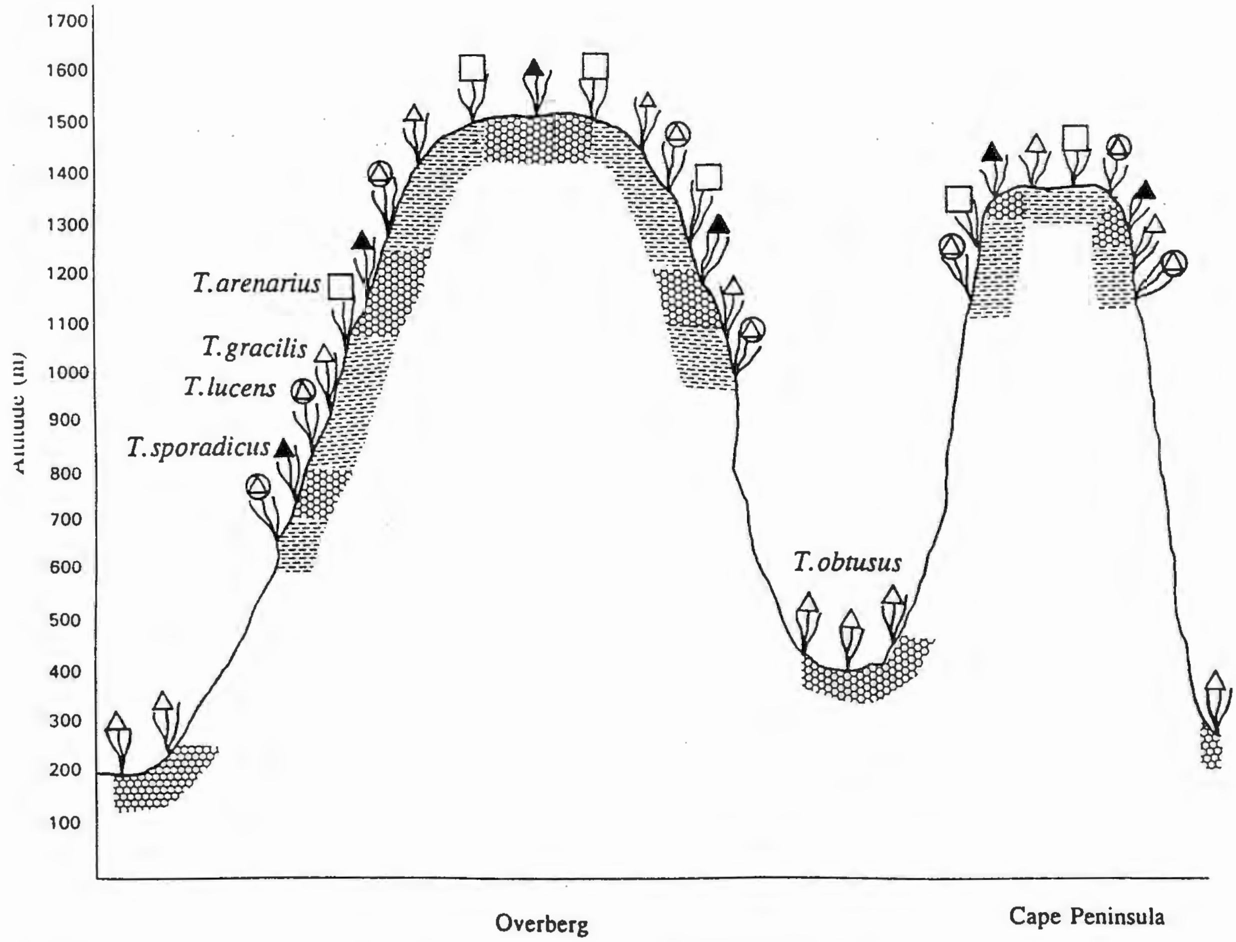

Fig. 33. Diagramatical representation of ecological specialisation for species in the *T.arenarius-T.sporadicus* clade.

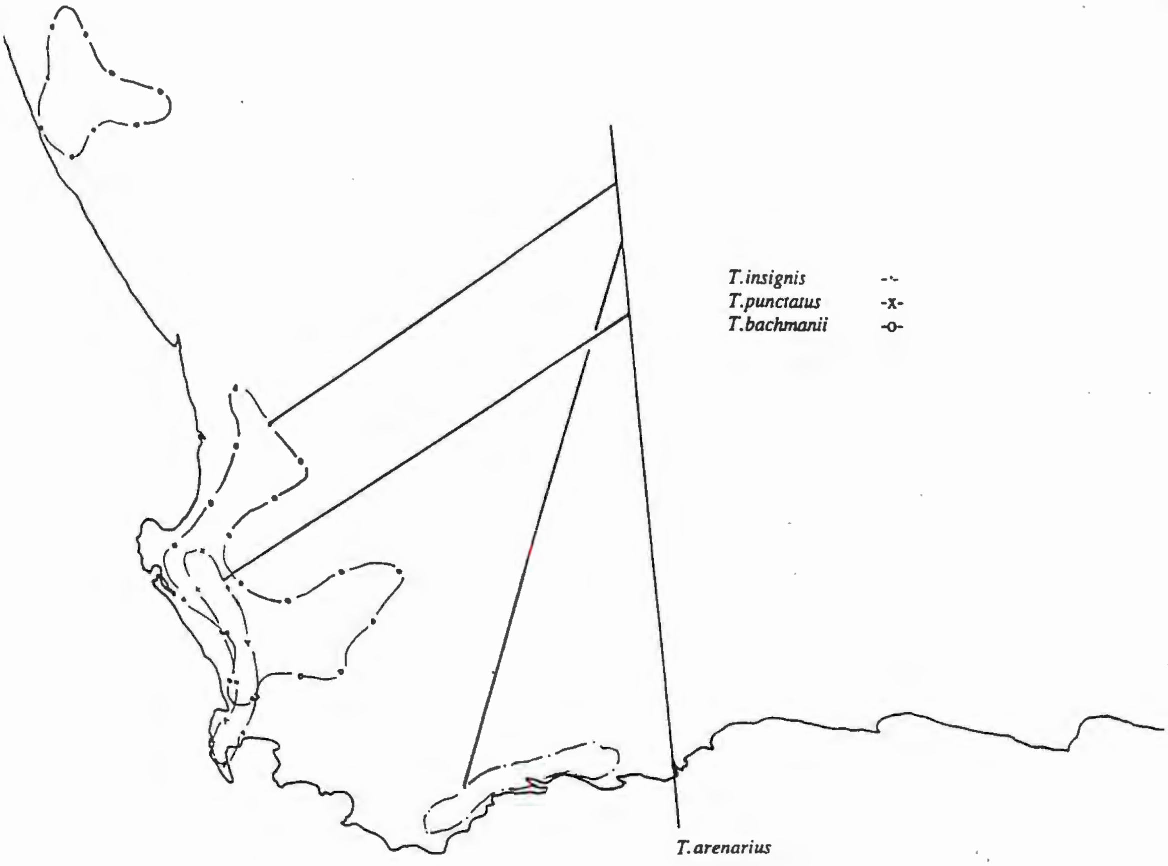

Fig. 34. The distribution of species in the *T.bachmanii-T.punctatus* clade.

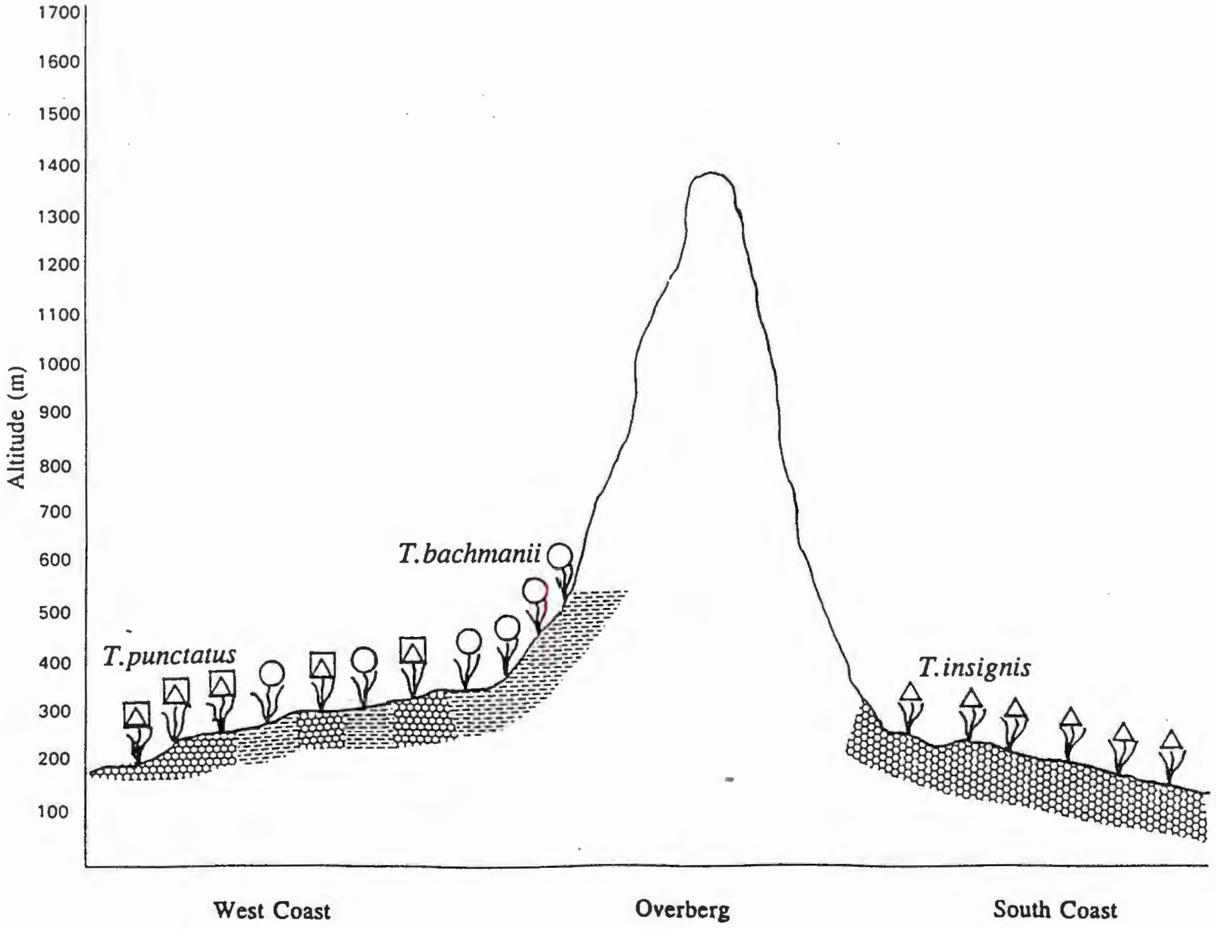

Fig. 35. Diagramatical representation of ecological specialisation for species in the *T.bachmanii-T.punctatus* clade.

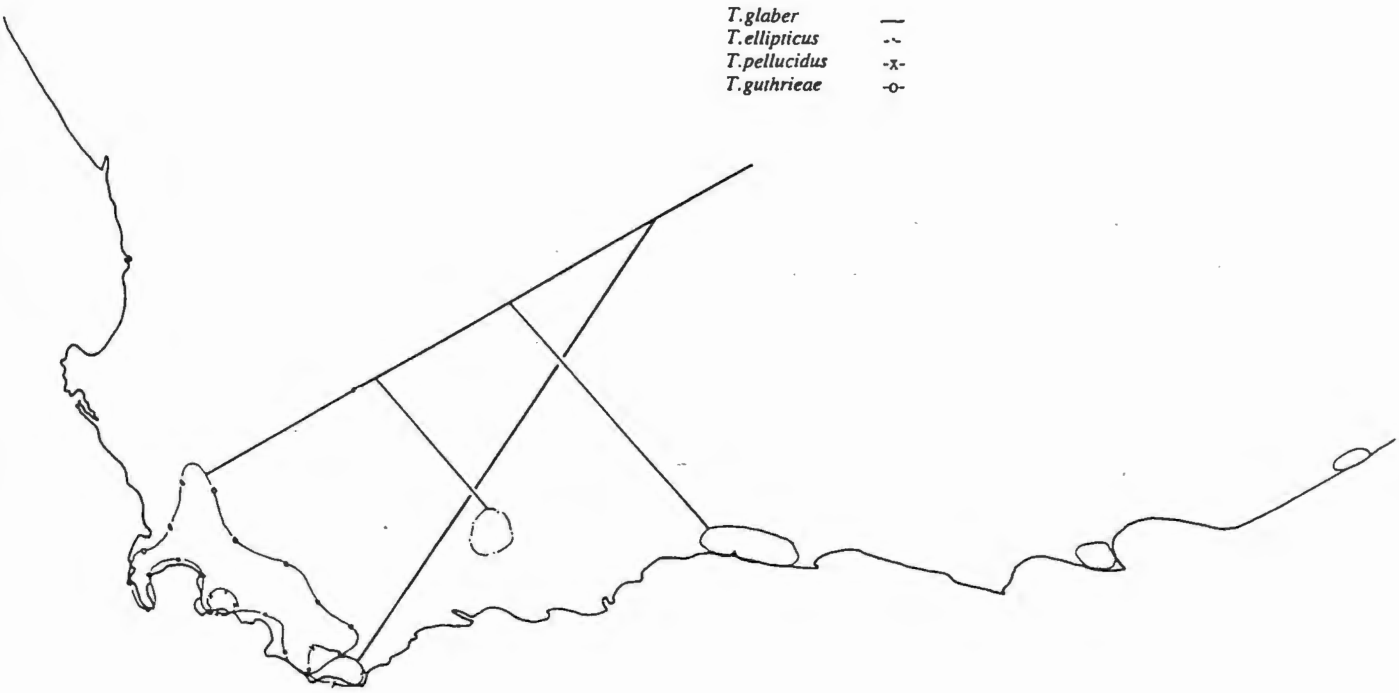

Fig. 36. The distribution of species in the *T.ellipticus* clade.

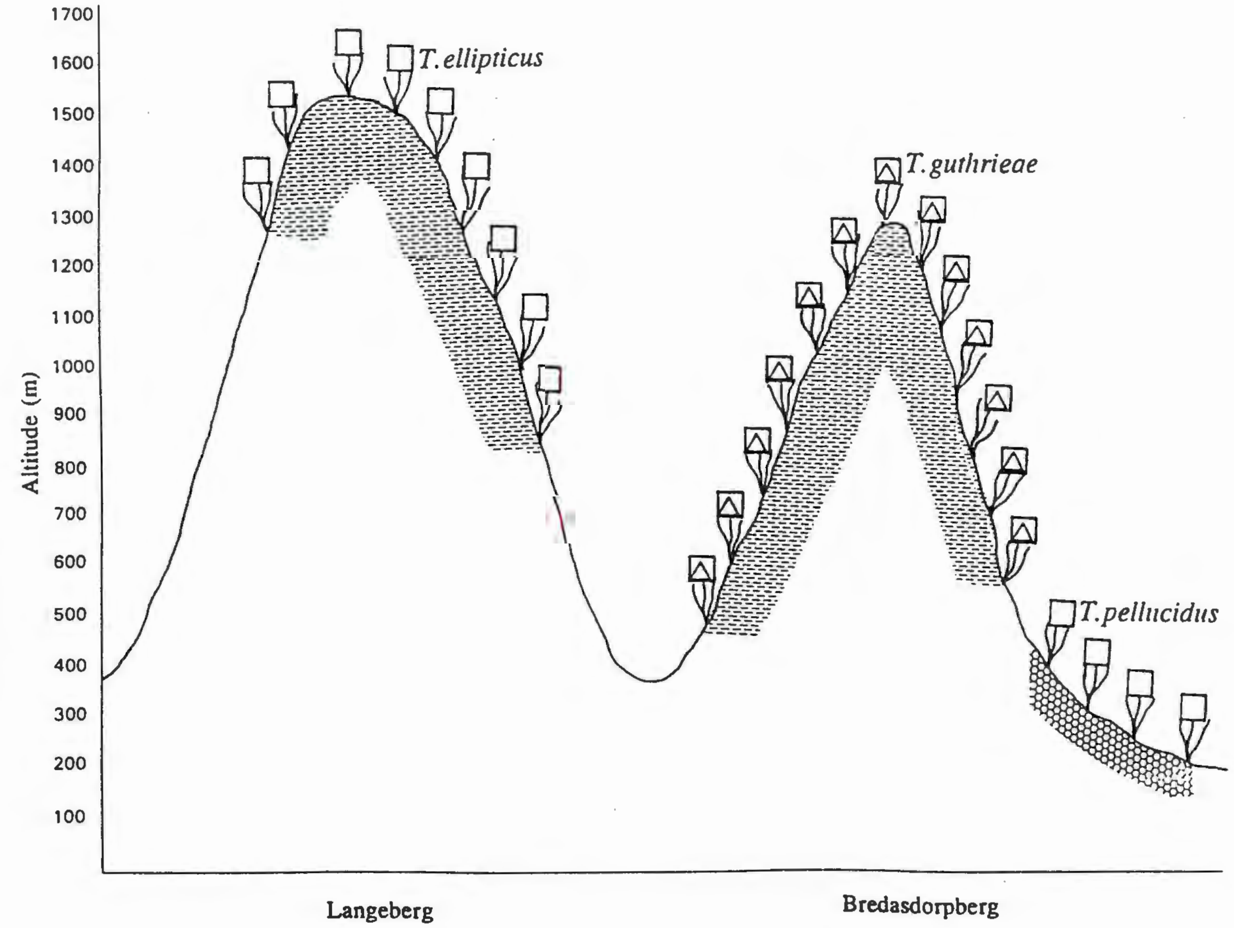

Fig. 37. Diagramatical representation of ecological specialisation for species in the *T.ellipticus* clade.

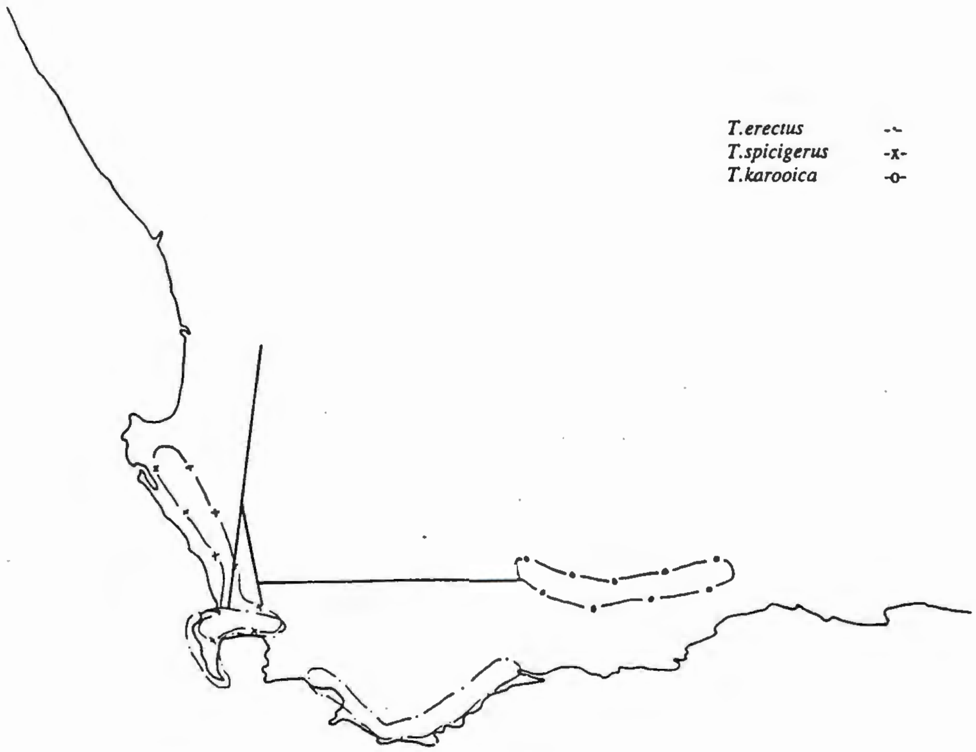

Fig. 38. The distribution of species in the *T.spicigerus* clade.

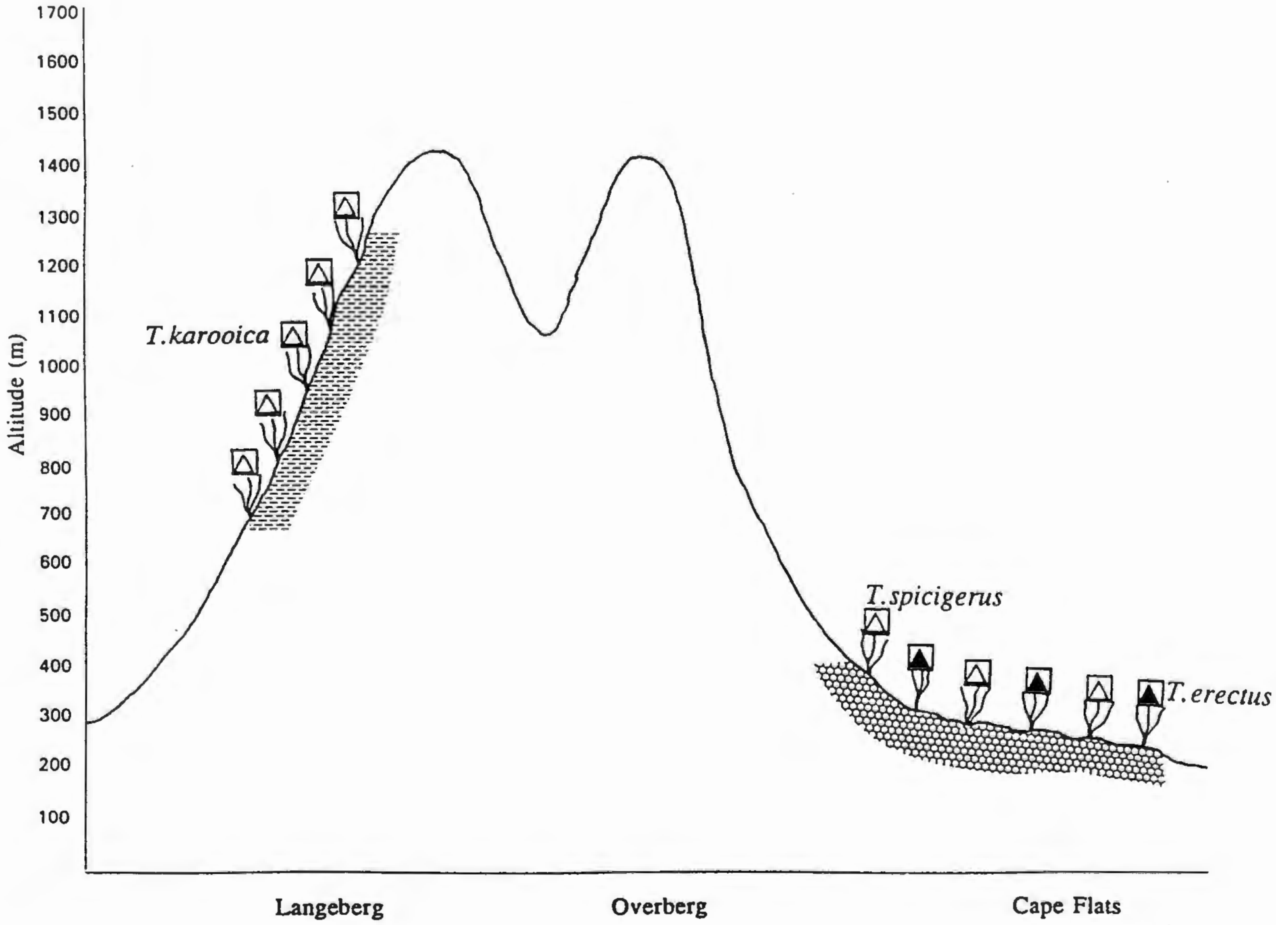

Fig. 39. Diagramatical representation of ecological specialisation for species in the *T.spicigerus* clade.

Fig. 40. The distribution of species in the *T.pluristachyus* clade.

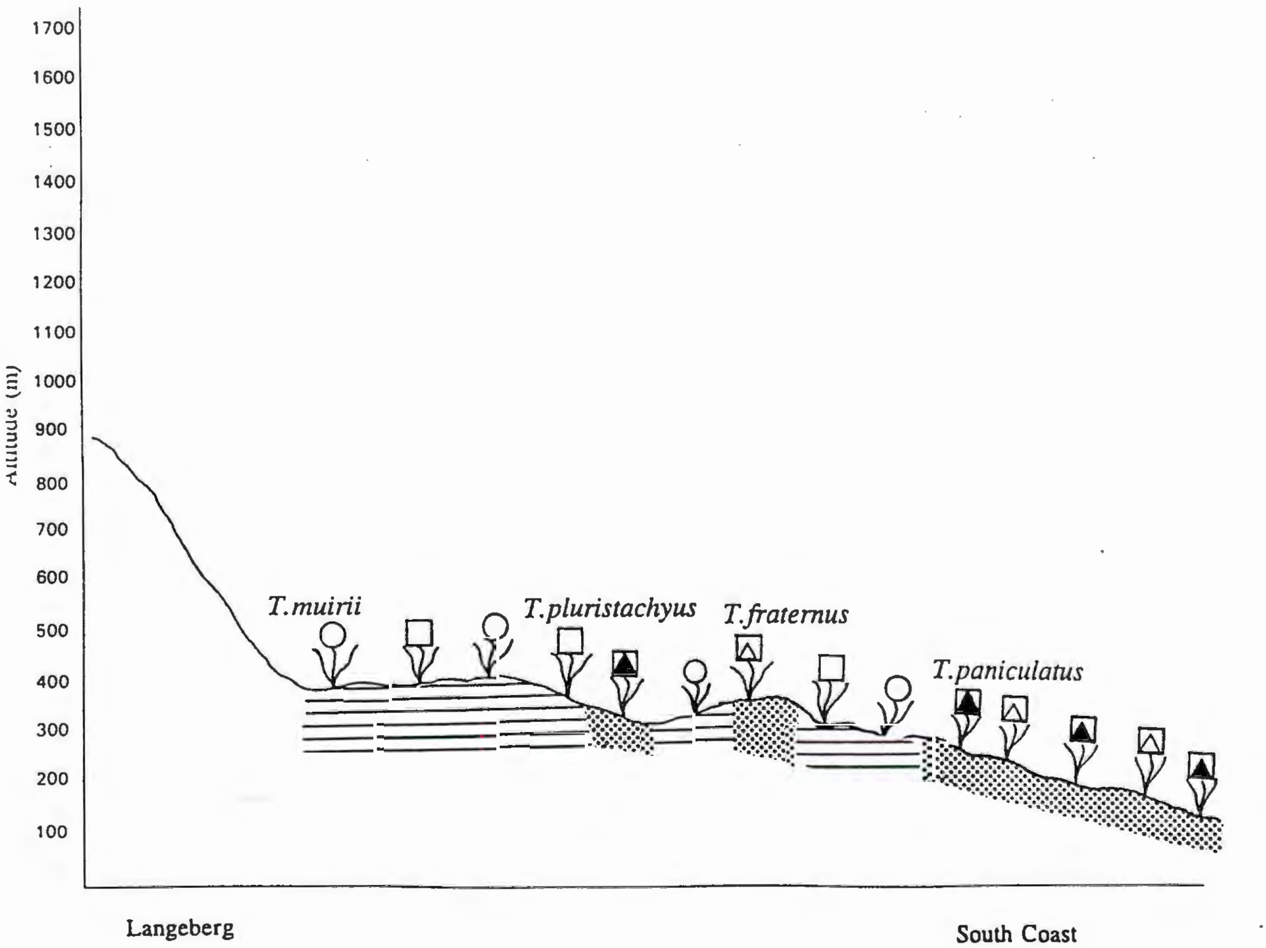

Fig. 41. Diagramatical representation of ecological specialisation for species in the *T.pluristachyus* clade.

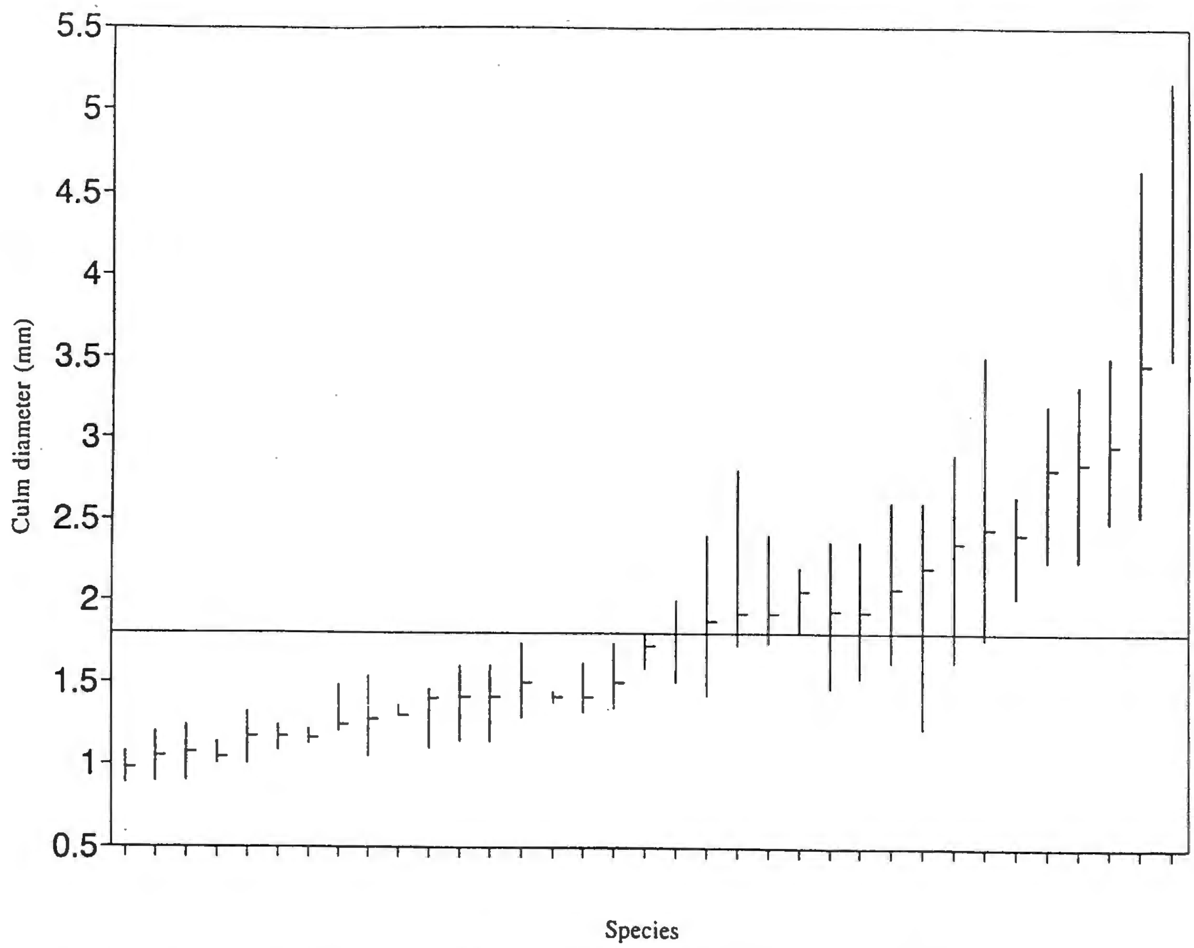

Fig. 42. Ranges in culm diameter for *Thamnochortus* species. The average of three measurements is indicated with a dash. The solid line at 1.8mm indicates the point of distinction between states 0 and 1.

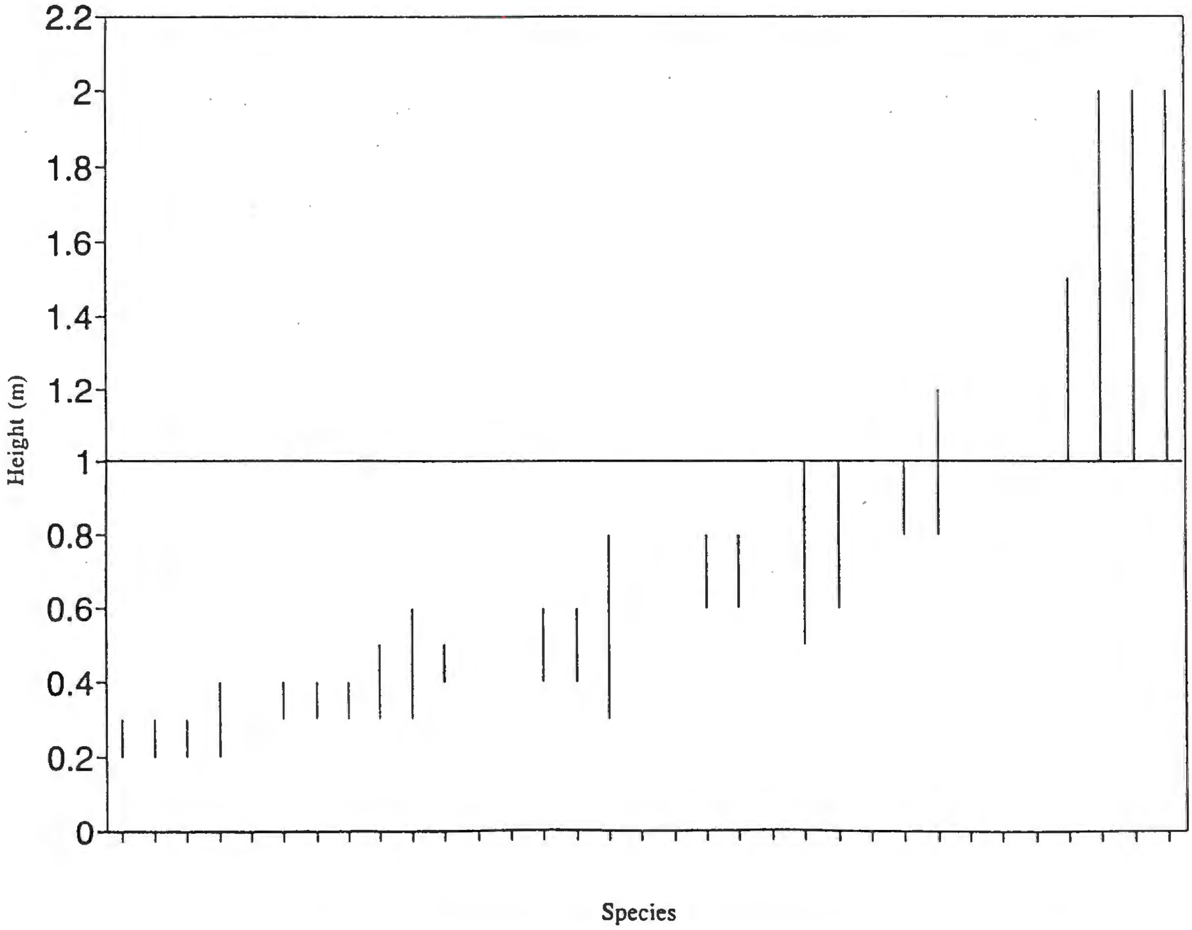

Fig. 43. Ranges in height for *Thamnochortus* species. The solid line at 1m indicates the point of distinction between states 0 and 1.

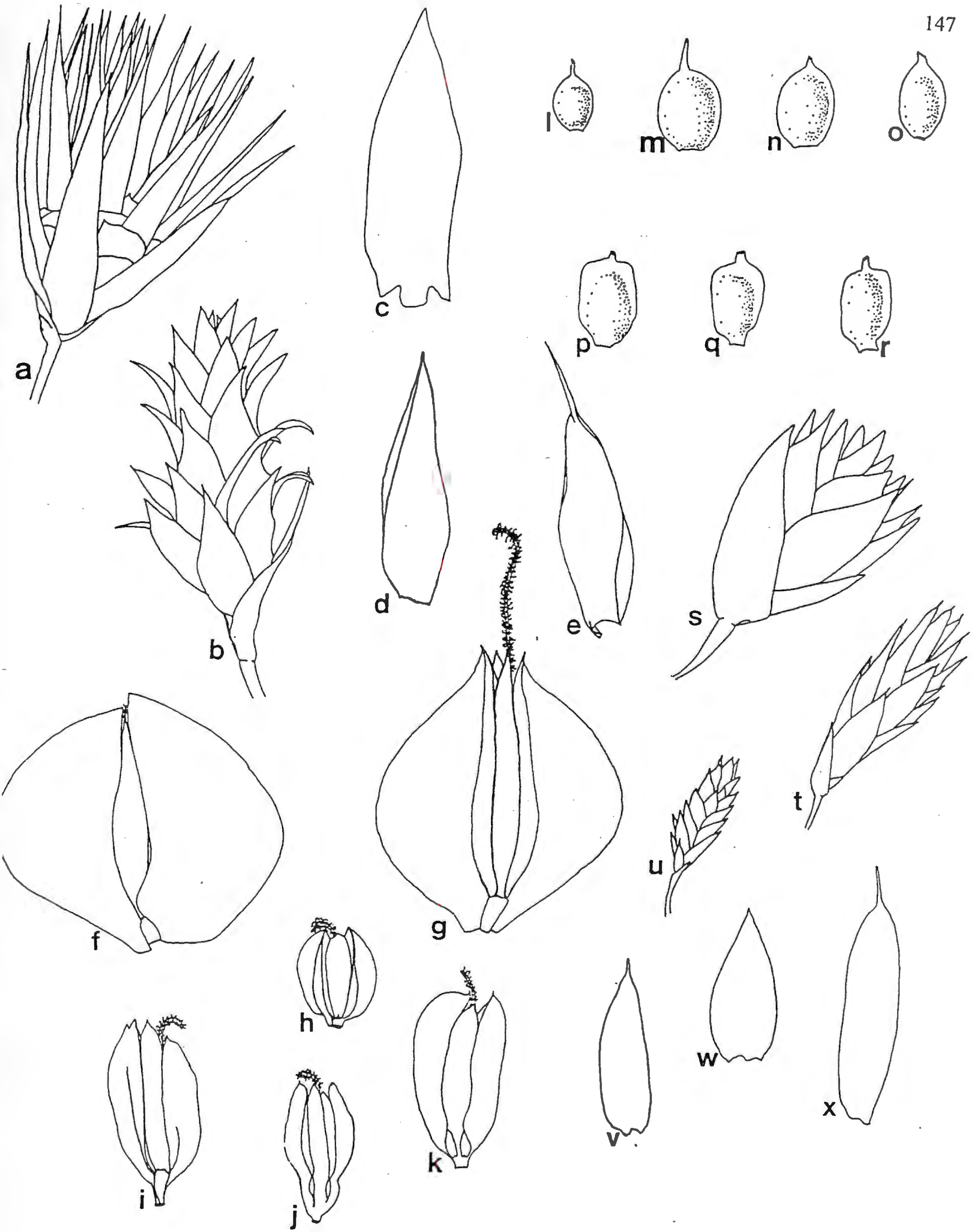

Fig. 44. Morphology of female and male reproductive parts. Female parts - Spikelet (a & b) a: *T.acuminatus*, b: *T.paniculatus*, Bracts (c-e) c: *T.muirii*, d: *T.arenarius*, e: *T.dumosus*, Flowers (f-k) f: *T.fruticosus*, g: *T.acuminatus*, h: *T.arenarius*, i: *T.glaber*, j: *T.fraternus*, k: *T.paniculatus*, Fruits (l-r) l: *T.arenarius*, m: *T.acuminatus*, n: *T.schlechteri*, o: *T.nutans*, p: *T.paniculatus*, q: *T.ellipticus*, r: *T.fruticosus*, Male parts - Spikelets (s-u), s: *T.schlechteri*, t: *T.ellipticus*, u: *T.glaber*, Bracts (v-x) v: *T.arenarius*, w: *T.paniculatus*, x: *T.dumosus*. Drawings are not to scale.

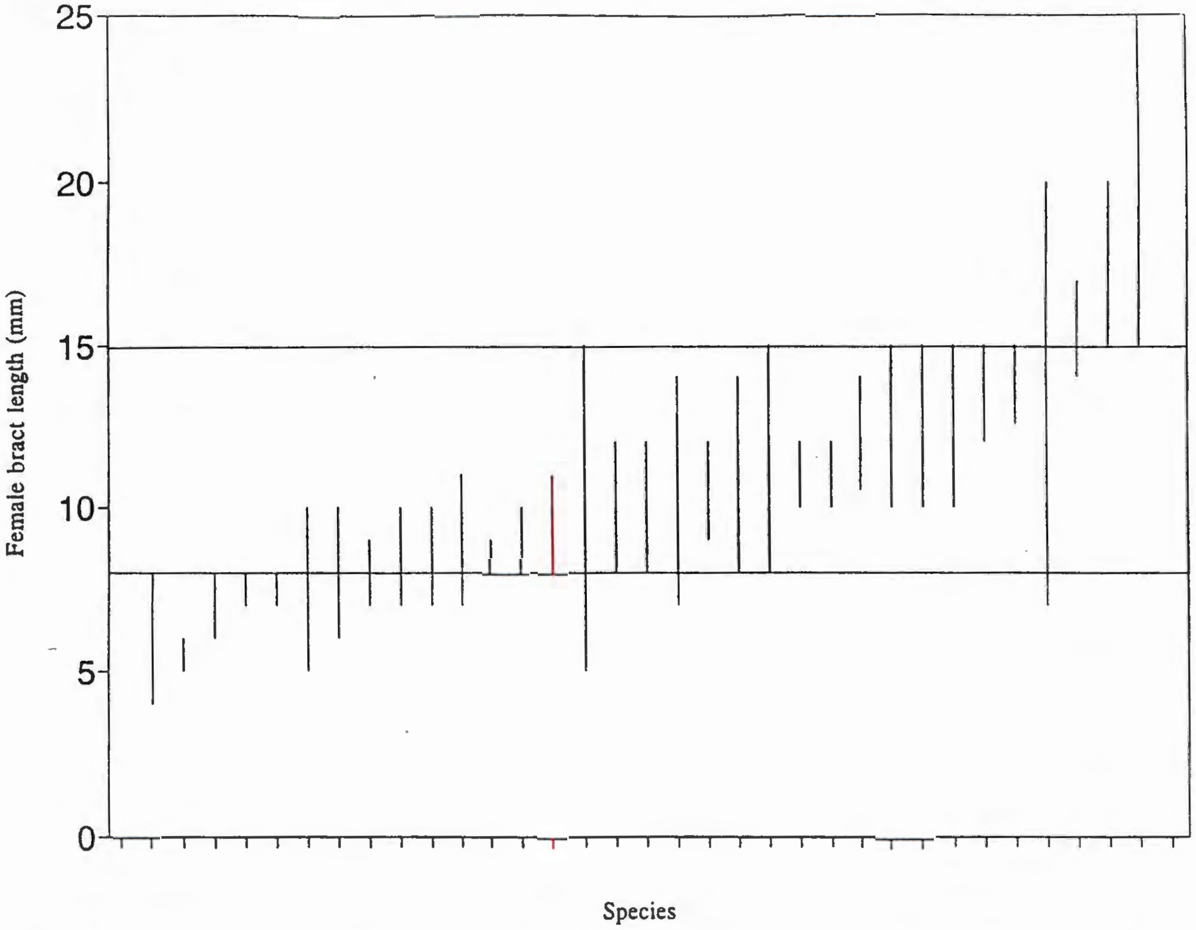

Fig. 45. Ranges in female bract length for species of *Thamnochortus*. Two points of distinction were found at 8mm and 15mm respectively.

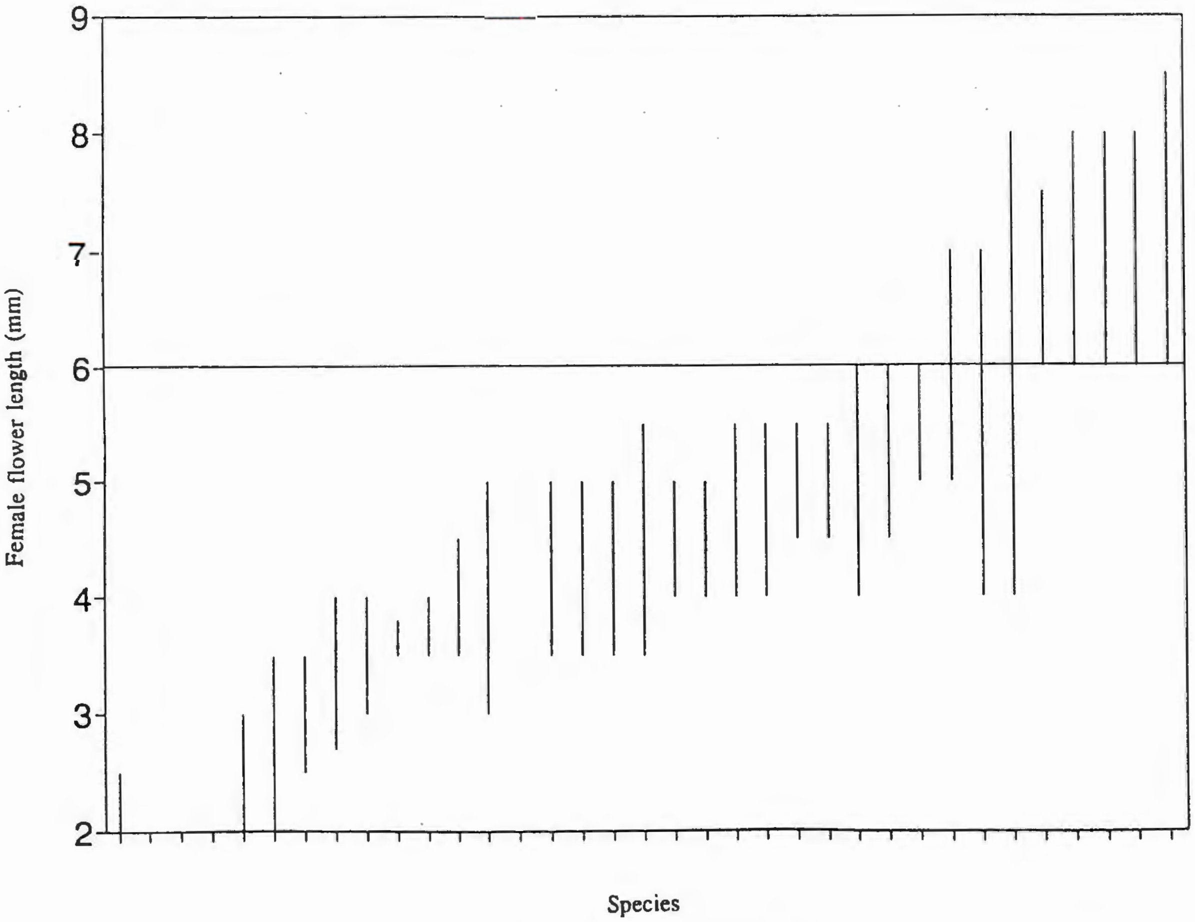

Fig. 46. Ranges in length of female flowers. The solid line at 6mm indicates the point of distinction between states 0 and 1.

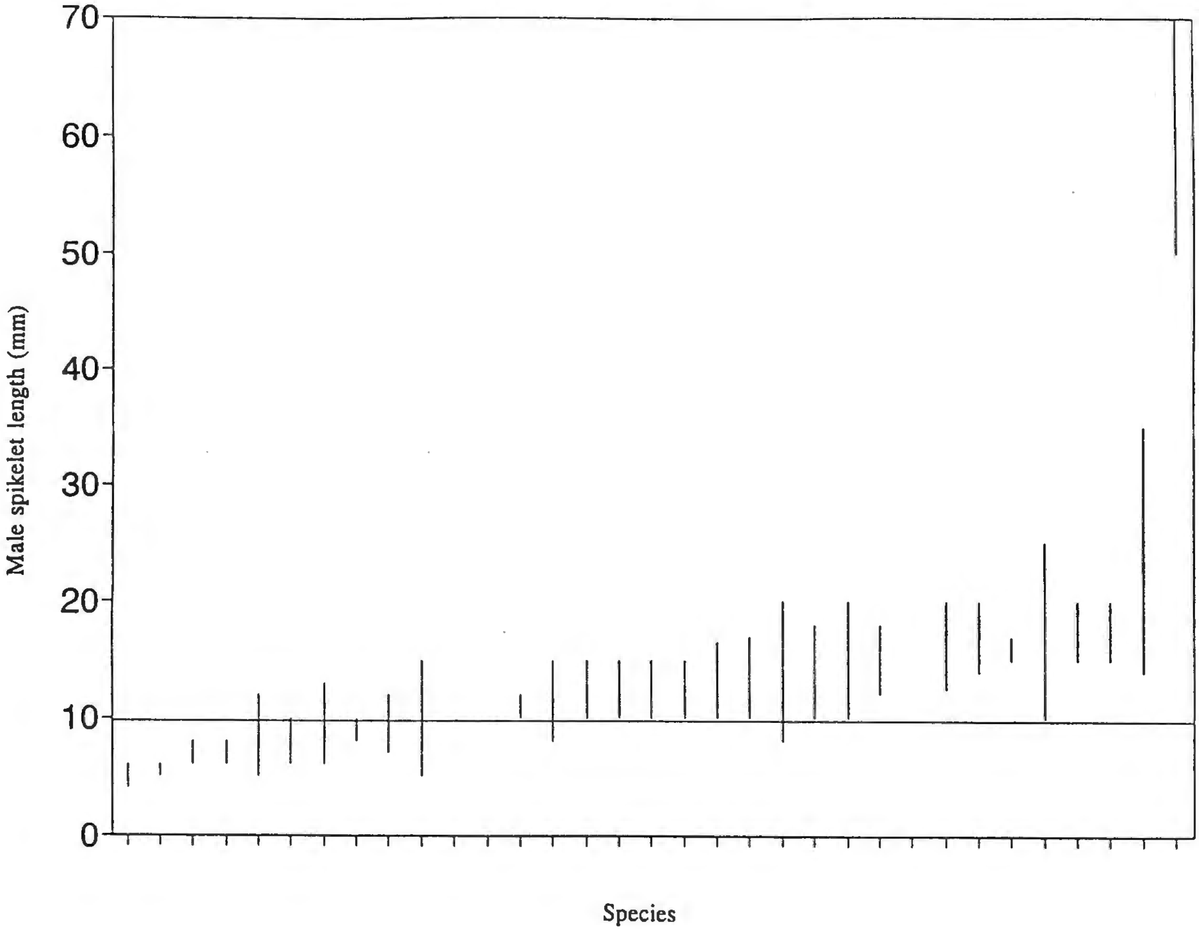

Fig. 47. Range in male spikelet length. The point of distinction is at 10mm.

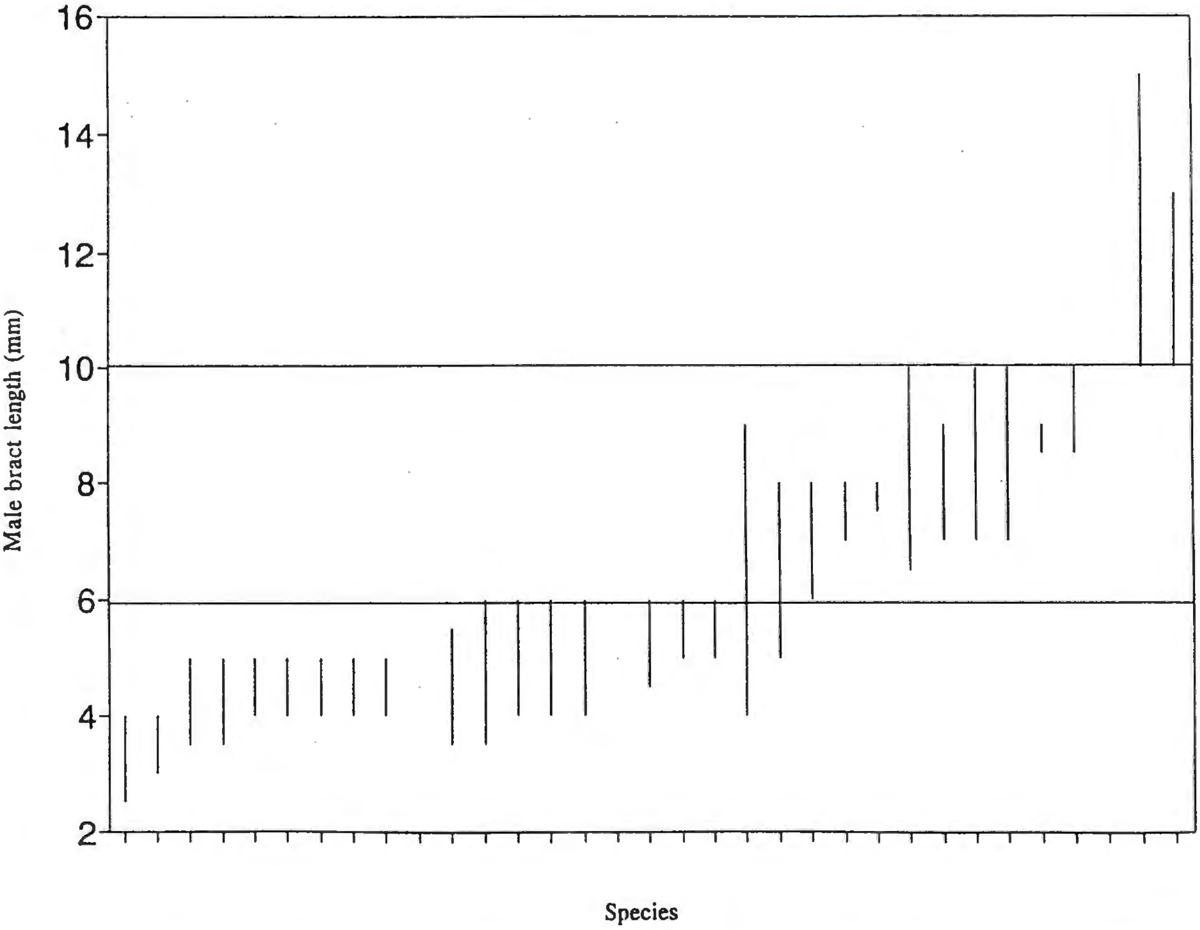

Fig. 48. Ranges in the length of the male bracts. Two points of distinction are recognised, 6mm and 10mm respectively.

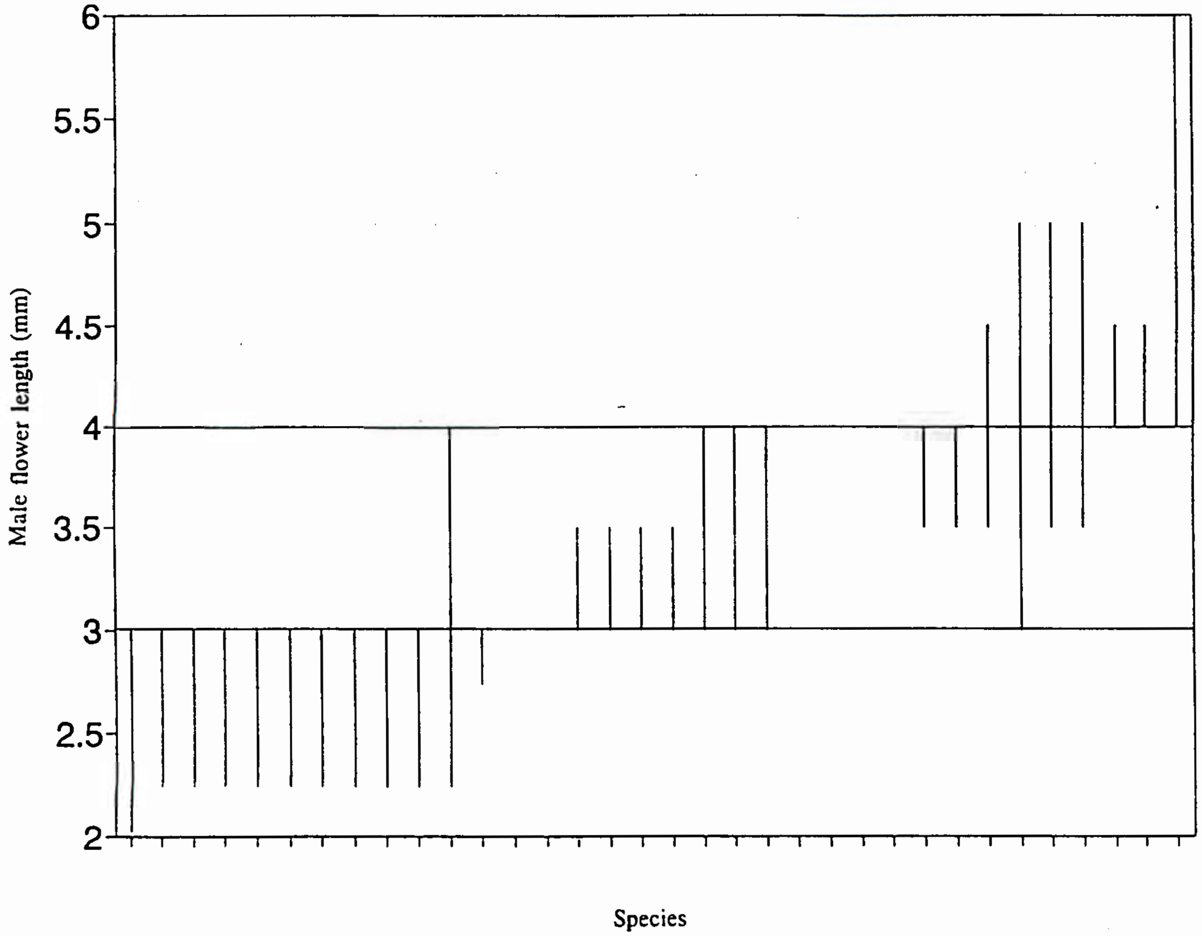

Fig. 49. Ranges in male flower length. Two points of distinction are recognised at 3mm and 4mm respectively.

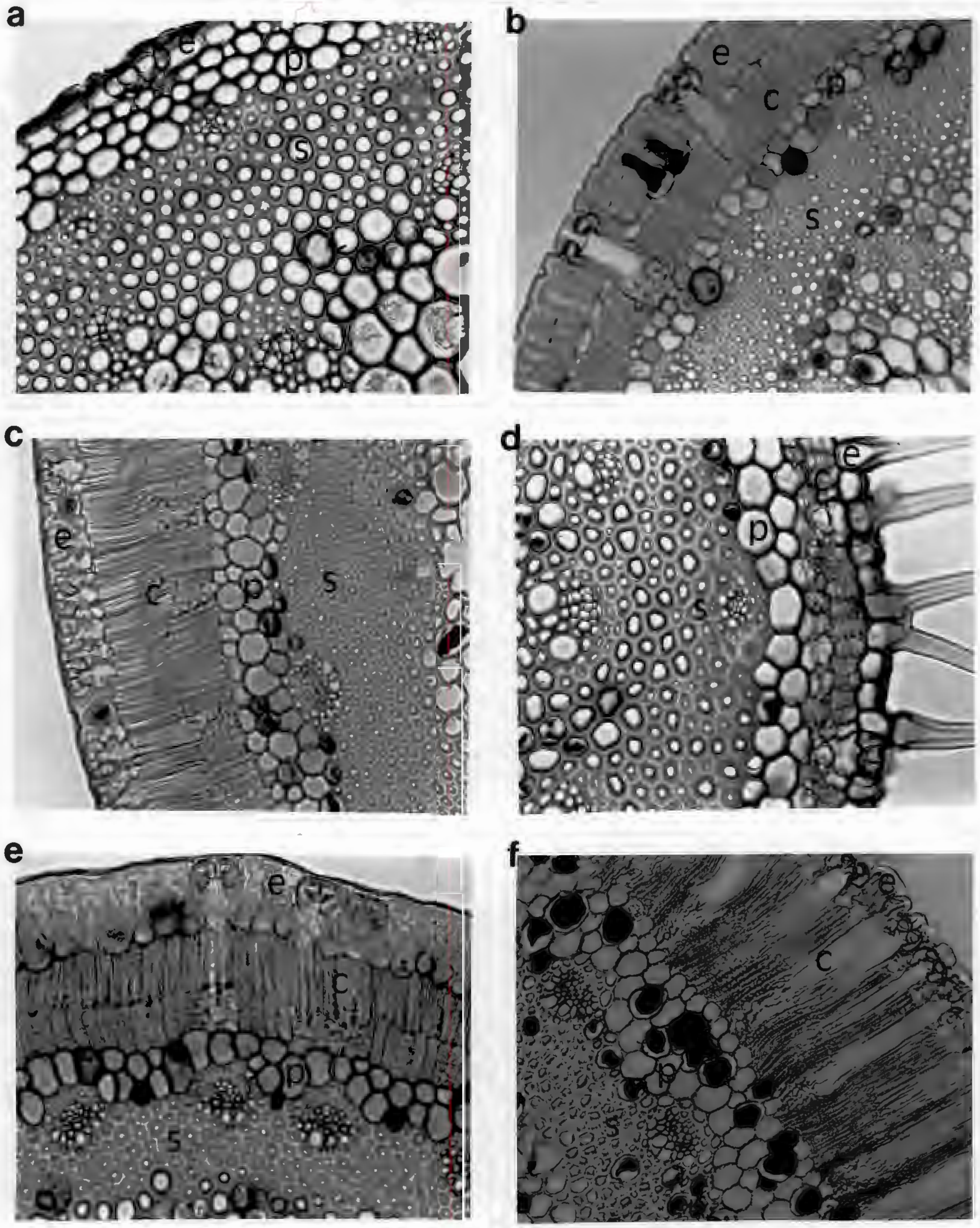

Fig. 50. Anatomical sections of six species of *Thamnochortus*, a:*T.acuminatus*, b:*T.arenarius*, c: *T.erectus*, d: *T.fruticosus*, e: *T.schlechteri*, f: *T.spicigerus*. Tissues are indicated with letters; e-epidermis, c-chlorenchyma, p-parenchyma and s-schlerenchyma.