

**AN INVESTIGATION INTO THE ADAPTATIONS OF HIGH
ALTITUDE FLORA ON THE KLEIN SWARTBERG, CAPE
PROVINCE.**

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Systematics Project

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ABSTRACT

The morphology of ten of the following thirteen endemics; *Agathosma purpurea*, *Protea pruinosa*, *Restio papyraceus*, *Leucadendron dregei*, *Phylica stokoei*, *Phylica costata*, *Pentameris swartbergensis*, *Thamnochortus papyraceus*, *Cliffortia setifolia*, *Cliffortia crassinerva*, *Euryops glutinosus*, *Erica constatisepala*, *Erica toringbergensis*, were investigated in order to identify possible high altitude adaptations. This was done by comparing the alpine species to their nearest low altitude relatives. The nearest low altitude relatives were determined using a number of different methods, literature search, cladograms and personal communication. The results highlighted a number of trends present in the high altitude flora. Firstly the plants are smaller than the low altitude relatives, but there are exceptions. *Erica torinbergensis* is much taller than its low altitude relative and *Euryops glutinosus* varies a great deal in height. The growth form/certain shrubs tends to be compact with a high number of branches and a low branching angle, the exception being *Cliffortia crassinervis* which has fewer branches and a high branching angle indicating that it has a sprawling habit. These forms are in contrast to the spindly *Erica toringbergensis*. Secondly, the majority high altitude species have small narrow leaves. There are also indications of variation in the arrangement of the tissue layers. Possible adaptations to high irradiance levels, such as hair, shiny leaves and resin ducts on the leaves were also found. The trends highlighted in this study support the theory that there may well be a classifiable alpine community within the fynbos biome.

INTRODUCTION

Regions of the world where alpine conditions occur:

Alpine flora has been recognised in mountainous areas on different continents within different floristic regions. The alpine flora of certain mountains is already fairly well documented. These are the alpine floras of Europe, Australia, Tasmania and New Zealand, Asia and Japan, Java, New Guinea, Tropical East Africa and the Rocky Mountains of North America. Most of the present understanding of alpine habitats and plants arises from studies on these mountains.

Alpine habitats are usually defined as that region between the tree line and the cap of permanent ice and snow. Because they are found in such diverse climatic and floristic zones it is difficult to make general statements about the conditions in alpine habitats. Possibly the only characteristic common of them is the decrease in temperature as the altitude increases. Solar radiation intensity has also been found to increase with altitude, but since many mountains have high density cloud cover total irradiation does not necessarily increase. Rainfall is another factor which increases with altitude but it is possible for the alpine area to lie above the level of the cloud belt and thus experience drought conditions (Walter 1973; Linder et al unpub).

In terms of the seasonality of conditions, these high altitude mountains in temperate areas experience distinct seasons with significant variation of temperatures. Variations in temperature also occur in the high altitude regions of tropical mountains. These, however, are diurnal fluctuations and the harsh environment which is the result of changes from sub

zero to high temperatures over a short period of time has led to many interesting adaptations in the indigenous species (Hedburg 1957).

The mediterranean regions of the world:

The Cape Floristic Region is recognised as one of the five mediterranean ecosystems in the world. The other five occur on different continents around the globe, in Europe along the mediterranean coasts, extending into the mountainous regions as far as Afghanistan, in the Americas in central and southern California and central Chile and in south western and southern regions of Australia (Walter 1973) (Fig 1).

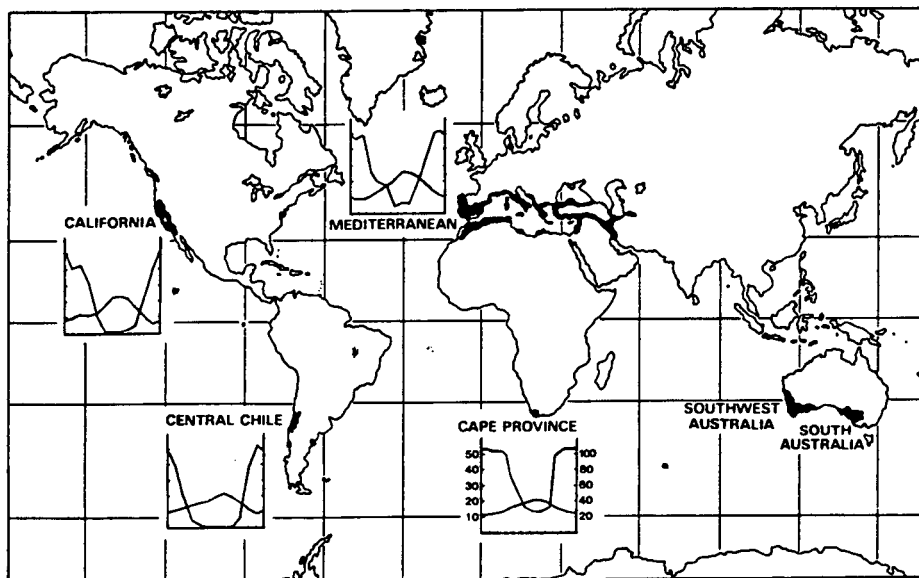


Fig 1: Distribution of mediterranean-climate regions of the world (Black). Climate diagrams of temperature and precipitation represent stations at Fundo Santa Laura, Chile; Boulder Creek, California; Terrubia, Sardinia; and Jonkershoek, South Africa. (After Cody and Mooney 1978)

Generally speaking these environments all have temperate climates with a maritime influence, plants which have sclerophyllous leaves, and fire cycles. There is, however, variation in important environmental factors such as climate and soil, and the community structure. The fynbos of the Cape Floristic Region seems to diverge the most from the other mediterranean ecosystems. Two of the most notable differences are the extremely nutrient poor soils and the high proportion of woody species in the fynbos (Naveh and Whittaker 1979).

Other distinctive characters of the Cape fynbos have been attributed to the nutrient poor nature of the soils in the region, and are possibly also related to limited water availability during the summer months. These secondarily divergent characteristics are particularly prevalent in leaf attributes and growth form. Leaves of fynbos plants tend to be much smaller and less spiny than those of the montane vegetation of southern California and central Chile (Cowling and Campbell 1980), with a greater life span (Campbell and Werger 1988).

In terms of growth form, fynbos plants are generally of lower stature than plants of other mediterranean communities (Campbell and Werger 1988).

General characteristics mediterranean alpine regions:

The high altitude mountains of mediterranean ecosystems, for example Spanish matorral, have clear floristic patterns which follow the altitudinal gradient (pers obs). Mediterranean cork oak forest, *Quercus suber* and *Q. ilex* with typical matorral species below, shifts to chestnut forest, then beech, *Fagus sylvatica*, and holly, *Ilex mitis*, followed by a belt of juniper and fir before opening out into alpine prairie. In this case the occurrence of beech and holly is unusual and on other mountains the oak forest is replaced with a mixture of pines before the alpine prairie's are reached. The common factor, however, is the existence

of a tree line which is in stark contrast to the low lying plants of the alpine prairies. This dramatic change in flora is not evident in the fynbos.

Characteristics of the CFR alpine region:

The alpine flora of the Cape Floristic region can be found on many of the mountain ranges in the region at altitudes above 1800m (Fig 2). Marloth (1902) was the first to notice the changes in growth form which occurred above this altitude. However, as mentioned previously, these changes are not as dramatic as that of the tree-line, vegetable-hedgehog zones, ericoid scrub forests or bamboo forests which are found on other high altitude mountains (Walter 1974). The lack of a sharp distinction between high altitude and other montane fynbos may be ascribed to the preadaptation of the fynbos plants to nutrient and water limitations which are a feature of this biome (Marloth 1902).

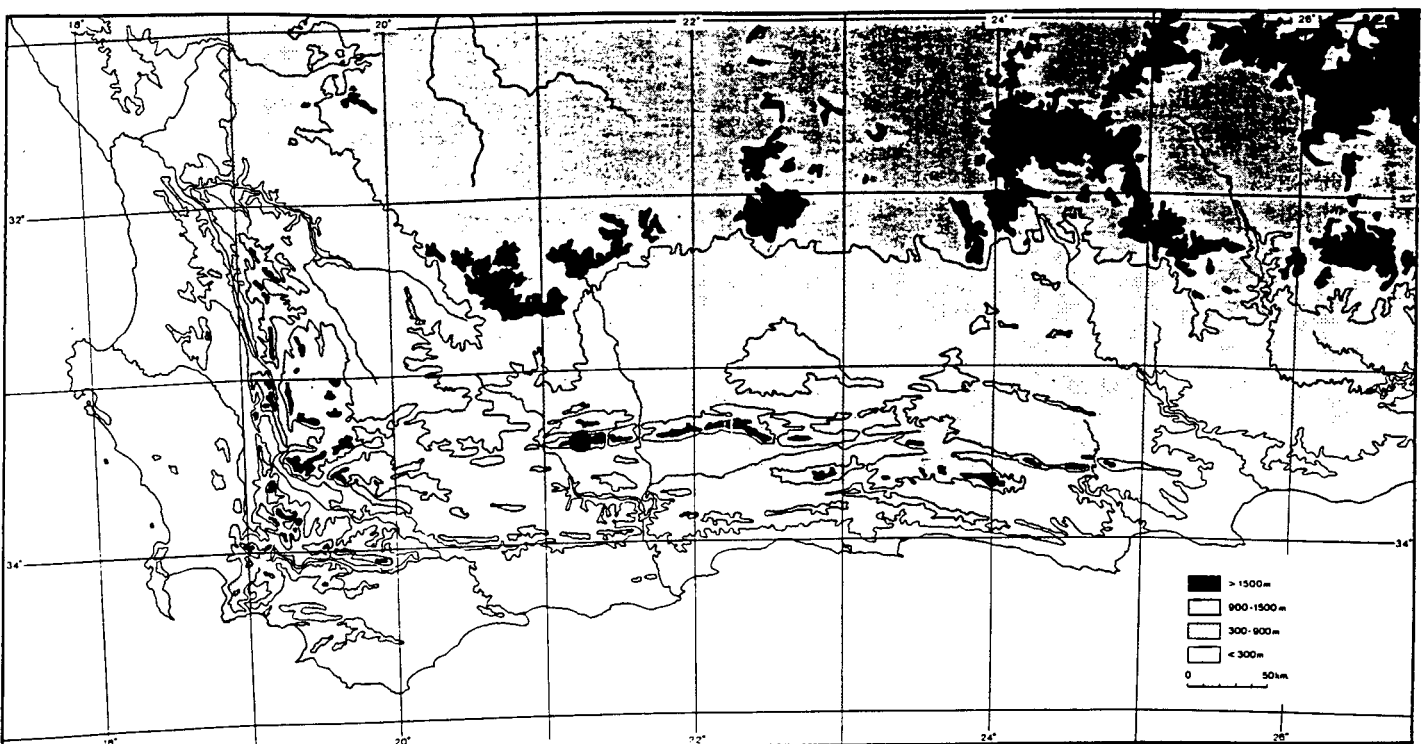


Fig 2: A map of the Cape Floristic region indicating the position of those areas above 1500m. The Klein Swartberg is indicated by the black circle.

Marloth (1902) observed that above about 1200m shrubs tend to become shorter and more compact, while perceptible changes in plant form, similar to those characteristic of other alpine areas, occur above elevations of 1800m. At this altitude plants were generally in the cushion or rosette form with many stems coming off a thick woody root. Those plants which were evergreen had leaves that were densely hairy, or leathery with a thick epidermis. More recently a survey of plant form in the Cape mountains indicated that Ericaceae, Restioids, sedges, evergreen geophytes and evergreen forbs were associated positively with altitude, as were semi-succulent woody plants and pubescent-leaved woody plants (Campbell and Werger 1988).

Potential environmental stresses on the plants of the Klein Swartberg and examples or hypothesis on responses:

Situated in a temperate zone, the Klein Swartberg experiences distinct seasonal variation with regard to temperature and rainfall. (Linder et al unpub).

Unfortunately there is very little data on the seasonal and daily temperature variation on the high altitude peaks. However, temperatures recorded at Besemfontein (1920m) indicate that in the winter month of July the lowest absolute temperature was -3.5°C , the highest was 18.0°C . There was no dramatic difference between the lowest temperature in January, -1.0°C and that of July, but there was a vast difference between the maximums, with the temperature reaching 34.0°C in summer.

While the summer climate of the region is characteristically dry, this is somewhat alleviated at high altitude by cloud cover which is common at this time of year. However, some of the

higher peaks often lie above the level of the rain cloud, and may thus experience considerably drier conditions than the lower slopes. This is just one indication that rainfall patterns in the area, may vary locally with relation to local topography and altitude.

There is no information on irradiance levels, wind velocity or chill factor, or ground temperature. In addition to this the importance of and conditions in microclimates where plants are likely to grow is not documented.

While temperatures in the high altitude regions of the Klein Swartberg may not be as low as those of other alpine regions in the world they do appear to be low enough to cause cold damage. In other high altitude areas plants have different and yet similar adaptations to cope with the conditions. In high tropical Andean plants the classic ground level plants occur in conjunction with intermediate height plants and arborescent forms (Squeo et al 1991). These different growth forms have different methods of coping with the chilling conditions. Cushion forms adopt tolerance mechanisms, by resisting ice formation, while arborescent types exhibited avoidance mechanisms predominantly through supercooling and insulation. Intermediate growth forms demonstrated both mechanisms. Various types of insulation mechanisms, such as dead layers of material and tissue, e.g marcescent leaves, for avoiding low temperatures are present in the two extremes. In arid regions leaf pubescence has been recognised as an insulation mechanism reducing both solar radiation absorption and leaf temperature (Meinzer and Goldstein 1986). In alpine species, such as the giant Andean rosette plants, leaf pubescence has been found to increase the temperature of the leaf by increasing the boundary layer's resistance to heat transfer. A similar effect has been detected in the leaves of other plants and structures, for example inflorescence.

The effect of pubescence on solar radiation absorption has been noted for arid species and similar results have been found in high altitude plants. High levels of irradiation affects both transpiration rate and leaf temperature. More importantly it may damage the light phase of the photosynthetic mechanism, causing a breakdown in the transport of electrons (Ehleringer and Werk 1986).

While pubescence has been shown to reduce the level of absorption of solar radiation, leaf angle and size can affect the incidence of solar radiation on the leaves (Ehleringer 1988). It has been shown that the result of a vertical leaf orientation in the prairie compass plant, in response to light radiation, reduces the incidence of solar radiation on the leaf increasing the carbon gain and water use efficiency of the plant (Jurik et al 1990). Other grassland species have on average a leaf angle of approximately 53.2°.

Leaf angle in alpine plants tends to be lower, falling into the low to middle category of leaf angles at 38.7°. The level of absorptance, however, is virtually the same in the plants of both communities, 80.9% in grassland and 79.5% in alpine meadow (Ehleringer and Werk 1986). However, when traced along an elevation gradient from saltbush communities to alpine communities the leaf angles are found to be high, then low, and then increasing again at high altitudes (Ehleringer 1988).

Leaf position is directly affected by branching pattern of the plant (Fisher 1986). The architecture of the plant, however, is affected by several environmental factors. Two of these which are likely to have a strong influence at high altitudes are wind, which can have a severe pruning affect on plants, and snow (Marloth 1902). Under the influence of these

environmental factors one might expect that plants will have many shorter branches which have smaller branching angles.

If the Cape Floristic Region does indeed have a specific high altitude flora then all these climatic variables are all likely to affect the manner in which the plant functions and performs both physiologically and morphologically. This study hopes to identify some of the possible morphological adaptations to high altitude conditions as well as highlight areas where further research could identify interesting physiological responses to the alpine conditions of the Cape.

Theory of project design:

The subtlety of the species turn over from montane fynbos to alpine fynbos means that it is difficult to identify, with clarity, the particular characteristics of the high altitude species. Ideally transplant experiments should be performed, growing the alpine and the ordinary montane species at both high and low altitudes and recording the changes in morphology and physiology in the different conditions. However, due to time constraints this was not possible. Instead the closest, low altitudinal relatives of the high altitude endemics were identified and various aspects of the biology of the species were compared. The basis of the comparison was a cladogram similar to the example, Fig 3. Characters in the alpine species, which differed in state to those at the node where the alpine and sister species diverged (A), were noted as potential adaptations in the alpine species. Character states in the alpine species which were different to the sister species but the same as the state in the rest of the genus were noted as potential preaptations to the alpine environment.

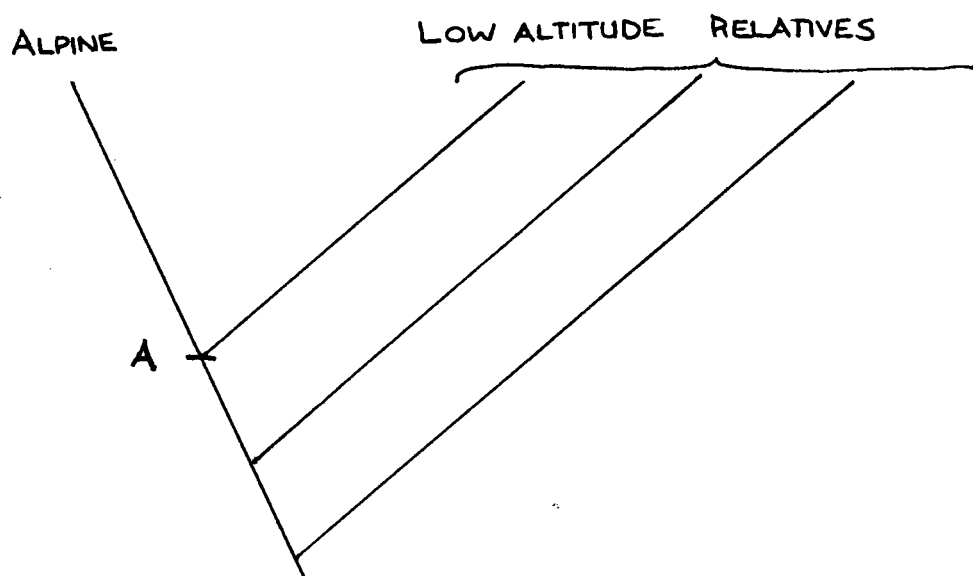


Fig 3: A cladogram illustrating the method used to determine which characters may be high altitude adaptations.

The list of species endemic to the high altitudinal regions of the Klein Swartberg originated with an expedition to the Klein Swartberg (Fig 2) in 1992 which produced a checklist of 100 species from the Toverkop region. The biogeographic distribution of these species was determined using information from the herbarium sheets in the Bolus Herbarium, University of Cape Town. This study identified a list of thirteen species that are endemic to the Klein Swartberg.

The thirteen species belonged to the following genera, *Erica*, *Agathosma*, *Pentameris*, *Leucadendron*, *Protea*, *Phylica*, *Restio*, *Thamnochortus*, *Cliffortia* and *Euryops* representing eight families Ericaceae, Rutaceae, Poaceae, Proteaceae, Rhamnaceae, Restionaceae, Rosaceae, Asteraceae. The extent of character variation within each genus differs, some genera being more conservative than others. Thus it is expected that the response of certain species will be less marked than that of others. For example *Erica* is relatively conservative

when compared to genera such as *Cliffortia* and *Euryops*. This cross section of genera should provide an indication of the adaptations which are commonly found in the high altitude flora, and possibly some interesting anomalies.

METHODS

Several different methods were employed to identify the closest relatives of the following the high altitude endemics.

Agathosma purpurea

Protea pruinosa

Restio papyraceus

Leucadendron dregei

Phyllica stokoei

Phyllica costata

Pentameris swartbergensis

Thamnochortus papyraceus

Cliffortia setifolia

Cliffortia crassinerva

Euryops glutinosus

Erica constatisepala

Erica toringbergensis

Literature search:

The authors of the descriptions of *Pentameris swartbergensis*, *Thamnochortus papyraceus*,

Phylica costata and *Phylica stokoei* and *Cliffortia setifolia* identified the nearest low altitude relatives of these alpine species.

Cladistic analysis:

The associate for *Leucadendron dregei* was identified by creating cladogram using the four species from the same section as this species. This was done by isolating characters from the descriptions and observations of herbarium material. The character states were polarised and used in a cladistic analysis using Hennig86.

Assumption from the literature

A low altitude relative for *Euryops glutinosus* was not identified in the literature, nor was it possible to perform a cladistic analysis due to a lack of information on suitable characters and so the three species which were placed either side of it in the descriptions were used in the comparisons.

Personal communication:

For *Cliffortia crassinerva*, *Erica toringbergensis* and *E. costatisepala*, *Agathosma pupurea*, *Protea pruinosa* and *Restio papyraceus* there was no indication in the literature of which were the closely associated low altitude species, and the descriptions were not ordered in such a way that it was possible to use the species associated with them in the literature. In these cases it was necessary to consult with the people presently working on the genera in order to identify the closest low altitude relative.

This method suggested relatives for *Cliffortia crassinervis* (Fehling pers com) and the two

Erica species (Oliver pers com). Unfortunately, it was not possible to go into to much detail for *Erica toringbergensis* because the description of the low altitude relative, *E. incarnata*, was unavailable.

Agathosma purpurea proved to be unsuitable for further study because the identity of a low altitude species was not certain (Bean pers com). *Protea pruinosa* belongs to a well defined group of high altitude species which includes *P. cryophylla* and *P. scolopendriifolia*. The latter seems to represent the basal stock of this group. *P. scolopendriifolia* has both a wide geographical and altitudinal range. However, within *P. scolopendriifolia* there is a great deal of morphological variation which is very erratic with no pattern being detectable (Rourke pers com). This meant that *P. pruinosa* was an unsuitable species for this study.

Examination of the herbarium specimens also pinpointed aspects of the plant's morphology which were thought to be important adaptations to high altitude conditions. It was possible to investigate some of these characters in more detail using the following methods.

Measurements:

The following measurements provided an indication of how densely branched the *Phyllica* and *Cliffortia* species were.

Number of nodes per 20cm

Ten herbarium specimens were measured for each species and three counts were taken per specimens. These were then averaged. The 20cm was measured from the top of each plant so that it was consistent and the counts were comparable.

Branch angle

The angle of the branch from the main axis was determined using a protractor. Branches which looked like they were the least affected by the pressing process were selected. At least three angles were measured per specimen, but preferably as many as possible (the maximum number measured on a specimen was 10). A mean for each specimen (to obtain an idea of variation) as well as each species was then determined.

Measurements given in the literature were also utilised in order to detect differences between the Klein Swartberg endemics and their low altitude associates.

These measurements included leaf length, leaf width, plant height, flower width, flower length and number of flowers. For *Euryops glutinosus* it was possible to include data on the chromosome number and for *Thamnochortus papyraceus* and it was possible to include anatomical data from the literature. The information given in the literature varied, in some cases ranges were given, in other cases a single measurement had been recorded.

Descriptive data on hair density of the branches, leaves and flowers, flower shape, leaf shape, leaf surface texture, leaf colour and leaf thickness was also included.

This data was compared for each of the low and high altitude relatives in an attempt to identify characters which could be high altitude adaptations.

RESULTS

Leucadendron dregei

The cladogram (Fig 4), which was constructed using the species in the sub section *Leucadendron*, showed that *L. rubrum* was the closest low altitude relative to *L. dregei*. *L. rubrum* is a widespread species occurring at altitudes from 800 to 4000ft. Related species in the section are *L. album*, another high altitude species, and *L. argenteum*, a low altitude species restricted to the Cape Peninsula.

L. dregei and *L. rubrum* differ in several respects. *L. dregei* is a smaller plant (Fig 5) with shorter, narrower leaves (Fig 6 and 7) which are fleshy. The leaves of *L. album* and *L. argenteum* are narrower, which implies that narrowness in *L. dregei* may be a preadaptation. In *L. dregei* the female leaf is occasionally concave on the inside of the leaf.

Flower size in both species differs between in male and female plants. The male flowers of *L. dregei* are larger (Fig 8 and 9) than those in *L. rubrum* this may be linked to the pollination syndrome. The flower bud of the male flowers has a greater number of matted hairs, and is surrounded at the base by a denser tuft of hair.

The female inflorescence of *L. dregei* is only half as long as that of *L. rubrum* (Fig 8). Certain flower parts of *L. dregei*, namely the hook and the claw have a denser covering of hair than those in *L. rubrum*. The flower bud, however, is as densely villous as that of *L. rubrum*. Similarly, the ovary, in both species is equally villous. In both species the perianth

is persistent and acts as a parachute dispersal mechanism.

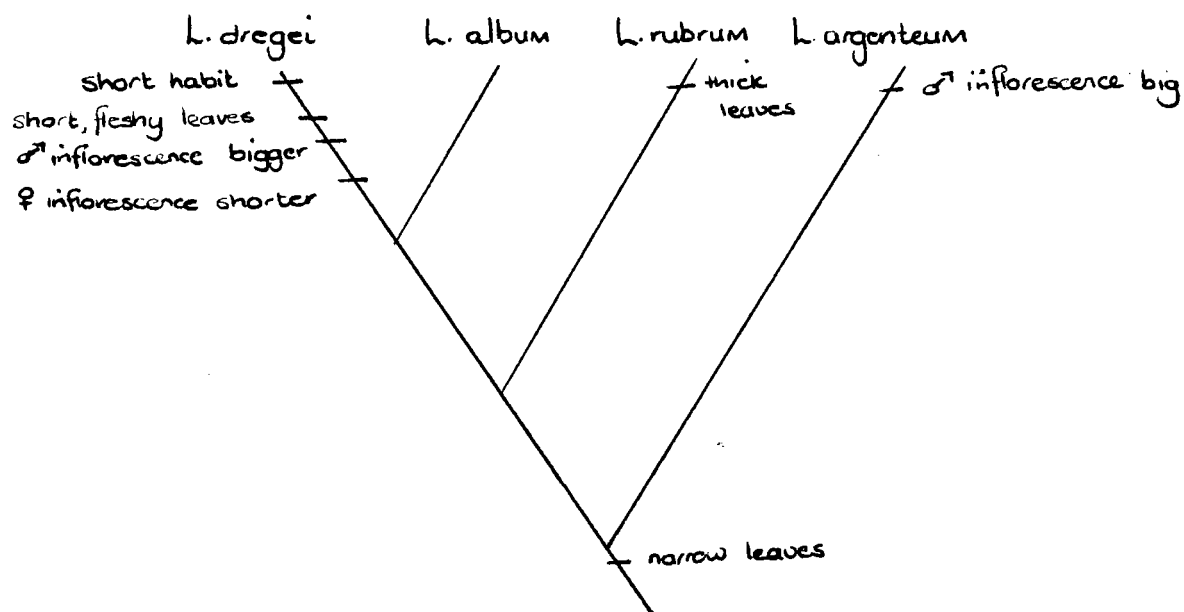


Fig 4: A cladogram indicating the relationships among species in the sub-section *Leucadendron* and the change of character states.

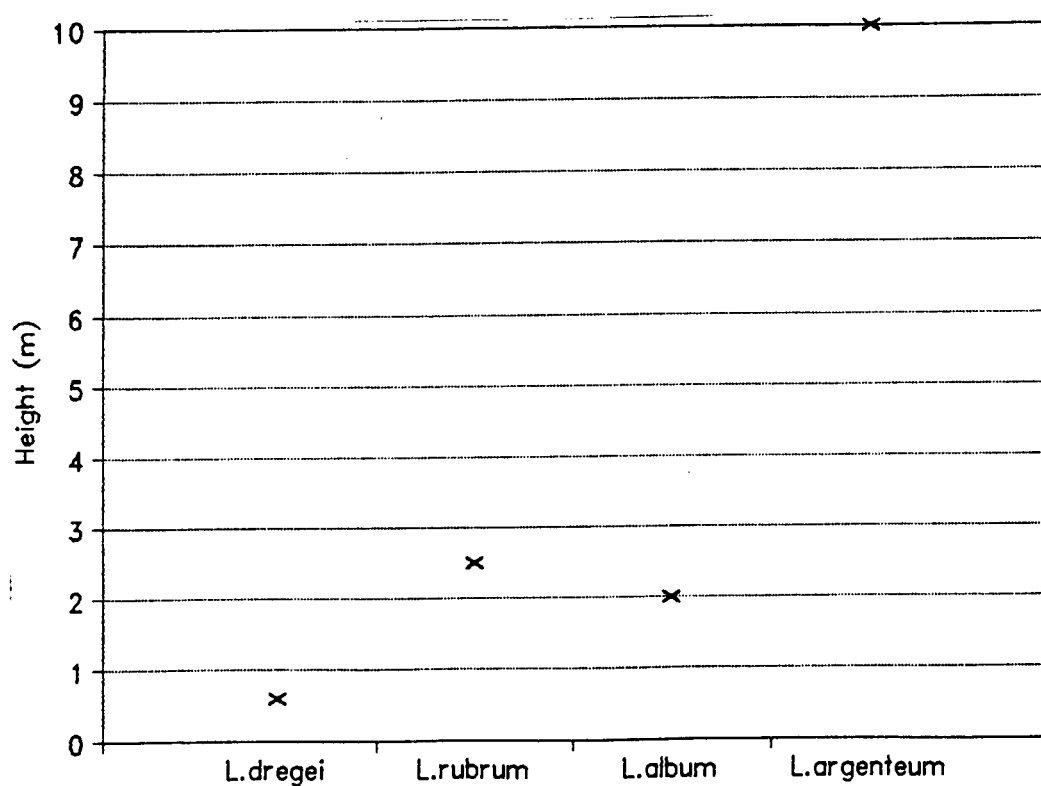


Fig 5: Height variation in *L. dregei* and associates.

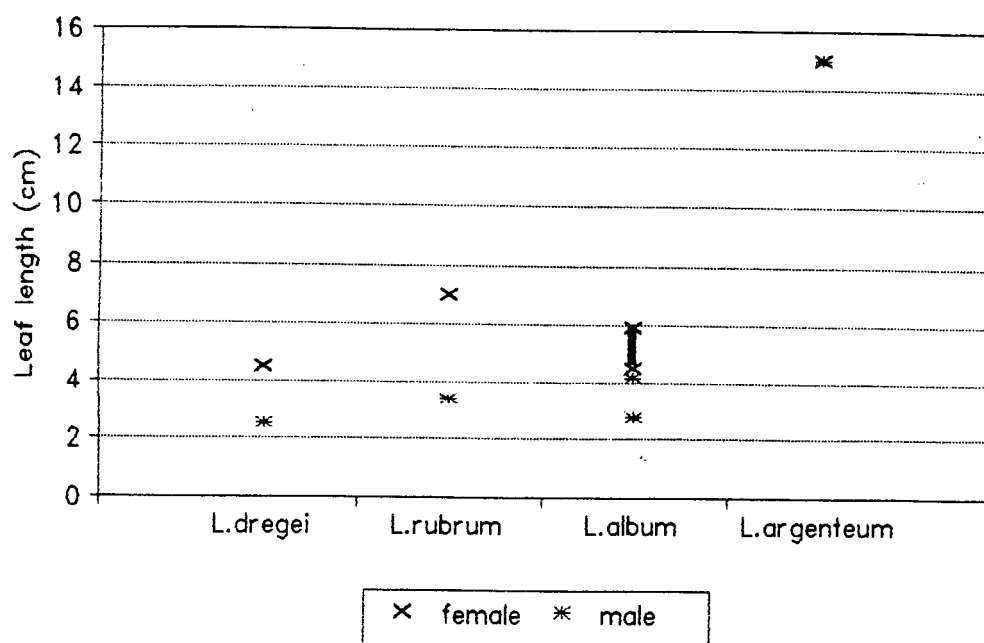


Fig 6: Leaf length variation in female and male plants of *L. dregei* and associates.

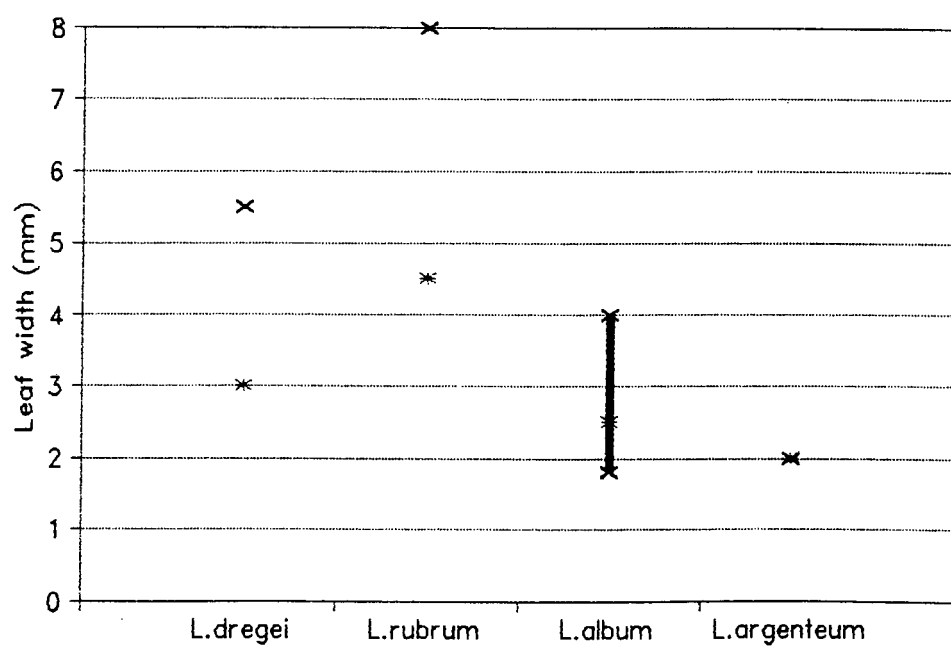


Fig 7: Leaf width variation in *L. dregei* and associates.

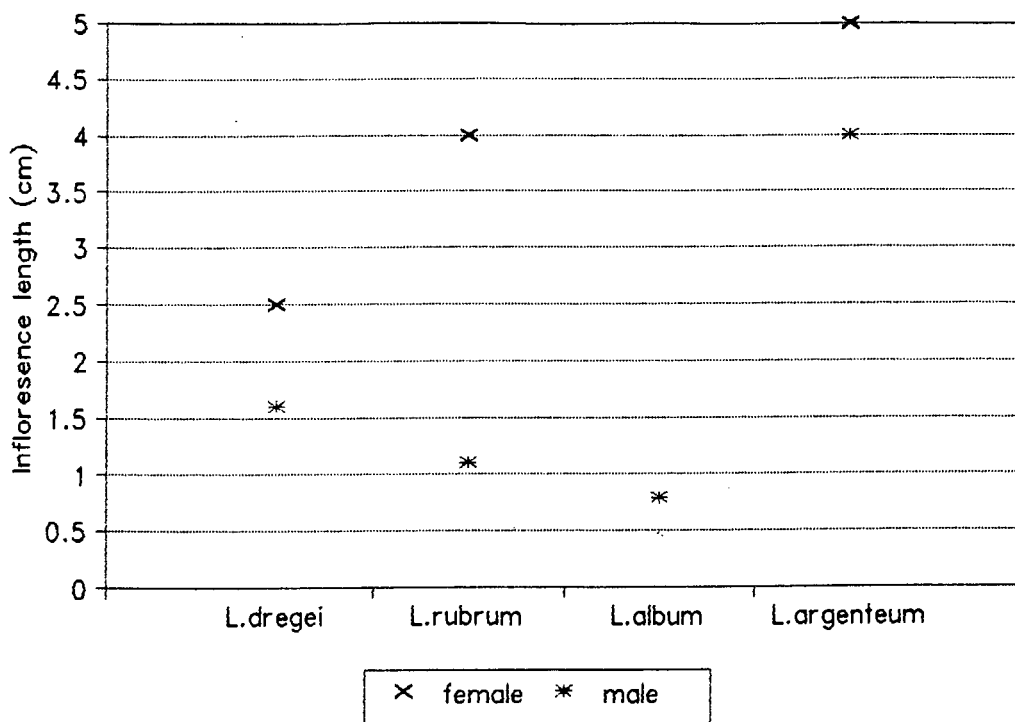


Fig 8: Variation in length of inflorescence of plants of *L. dregei* and associates.

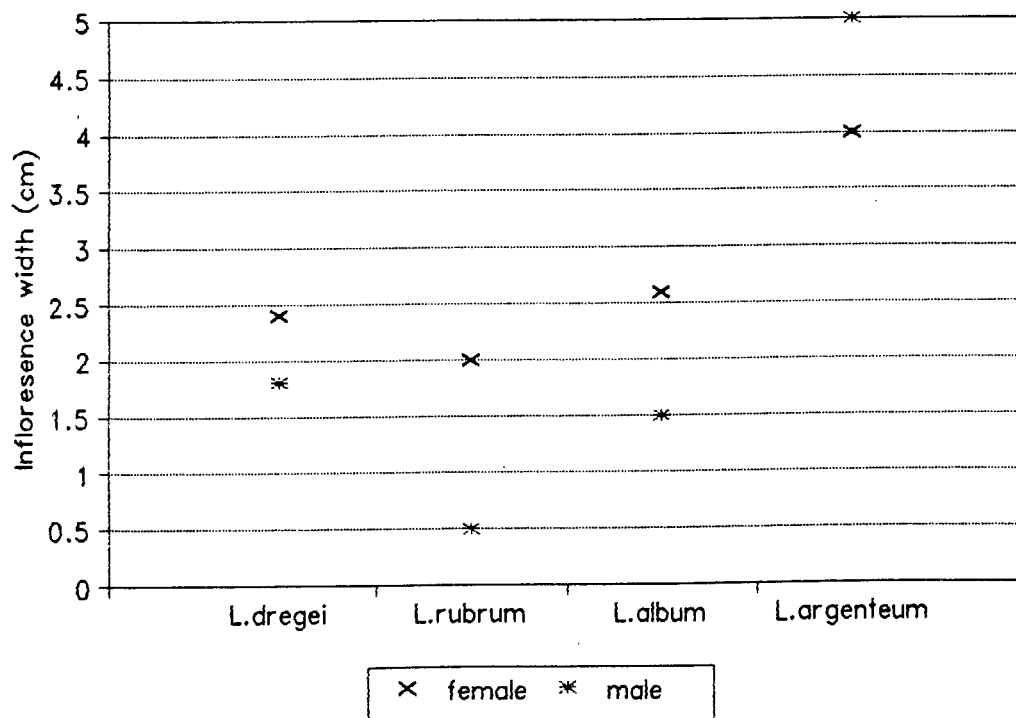


Fig 9: Variation in the width of inflorescence of plants of *L. dregei* and associates.

Phylica stokoei

According to Pillans (1942) the species most closely allied to *P. stokoei* is *P. excelsa*. *P. excelsa*, has a distribution in the mountains of the Cape, Caledon and Worcester divisions.

The change in character states is illustrated in Fig 10. *P. stokoei* has a lower growth habit than *P. excelsa* (Fig 11). *P. stokoei* lacks bracteoles. The variation in leaf length of *P. stokoei* is far less than in *P. excelsa* and falls into the lower part of *P. excelsa*'s range (Fig 12). The description and examination of herbarium specimens indicates that the leaves are narrower and possibly thicker than those of *P. excelsa*.

Inspection of the herbarium specimens also indicated that the density of the hairs on the leaves and at the apex and base of the branches is higher on *P. stokoei*.

The architecture of *P. stokoei* seems to be more compact than that of *P. excelsa*. While it is not significantly different from *P. excelsa*, *P. stokoei* has a greater number of nodes and a slightly smaller branching angle (Fig 13 and 14).

Within the flowers the hairs on the calyx tube and the ovary point in opposite directions.

Both species have leaves which are revolute and tubercled.

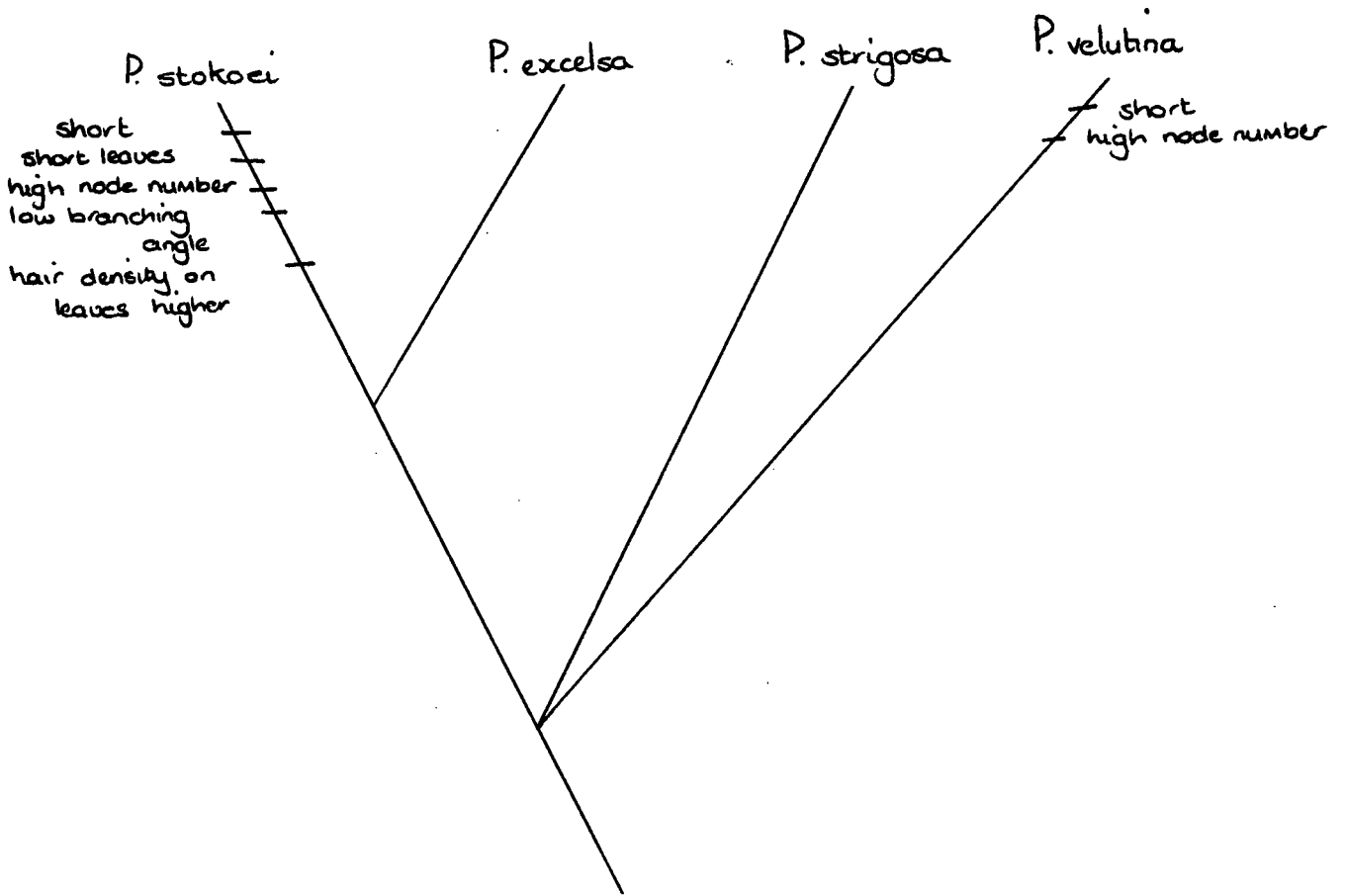


Fig 10: A cladogram illustrating the character state changes among *Phylica stokoei* and associates

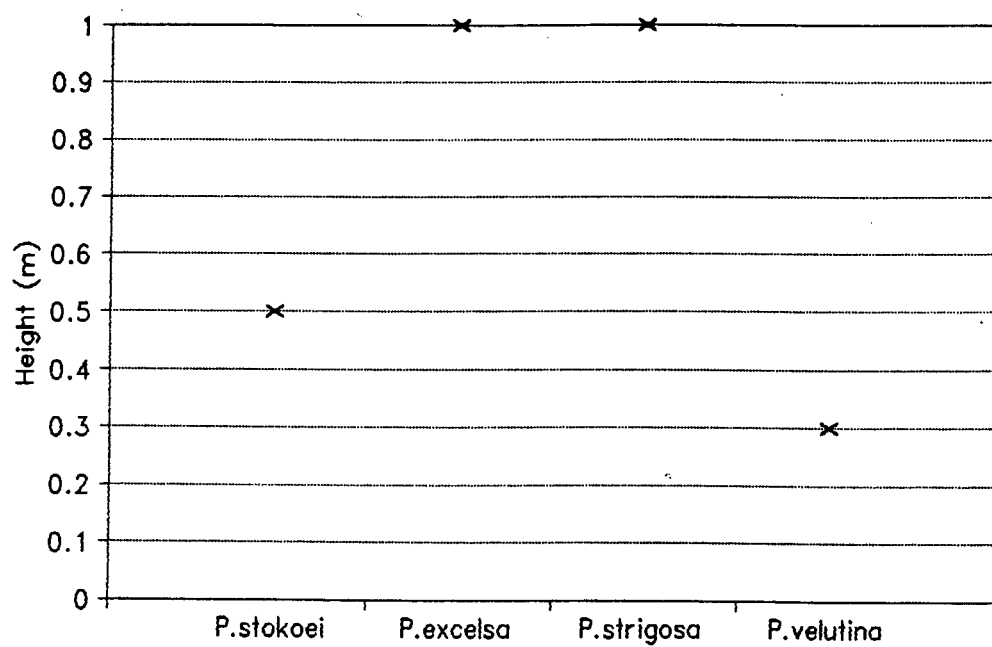


Fig 11: Height variation in *Phylica stokoei* and associates

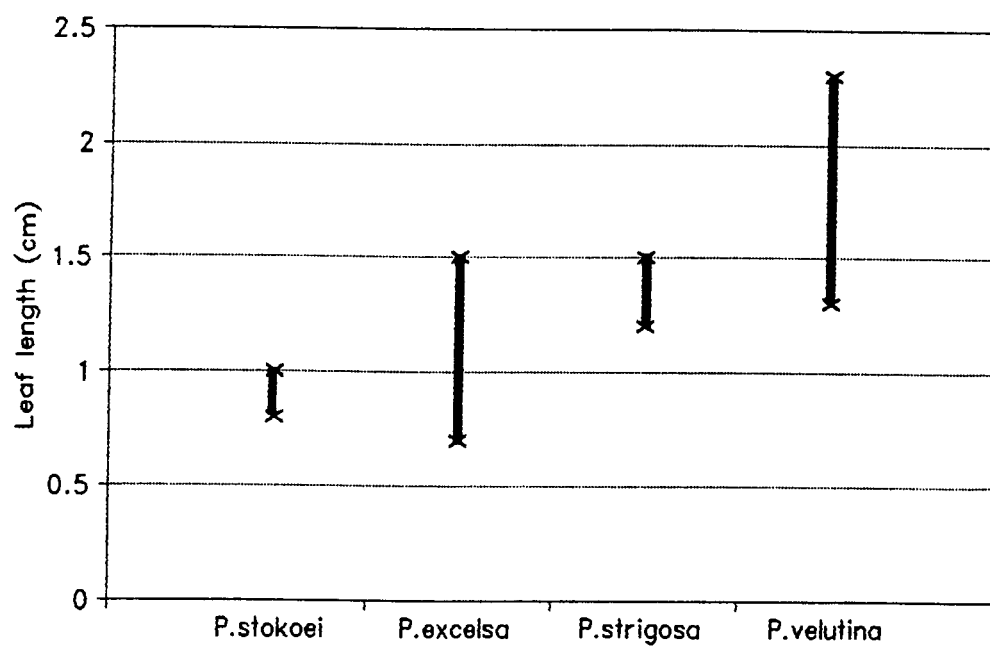


Fig 12: Leaf length variation in *Phylica stokoei* and associates

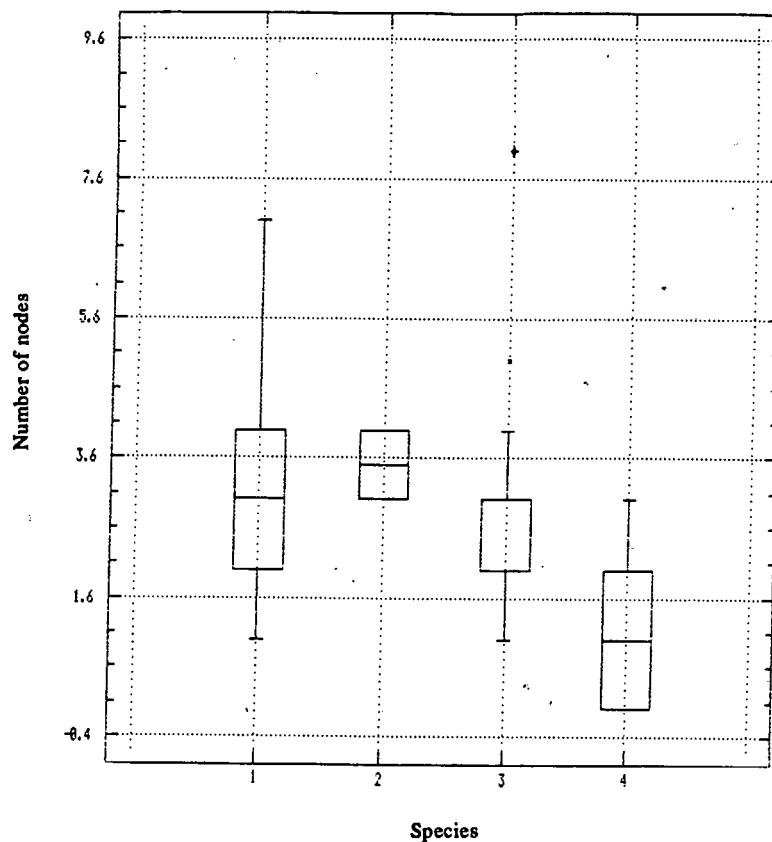


Fig 13: The variation in the node number of *Phylica stokoei* and associates. 1. *Phylica strigulosa*, 2. *P. stokoei*, 3. *P. excelsa*, and 4. *P. velutina*

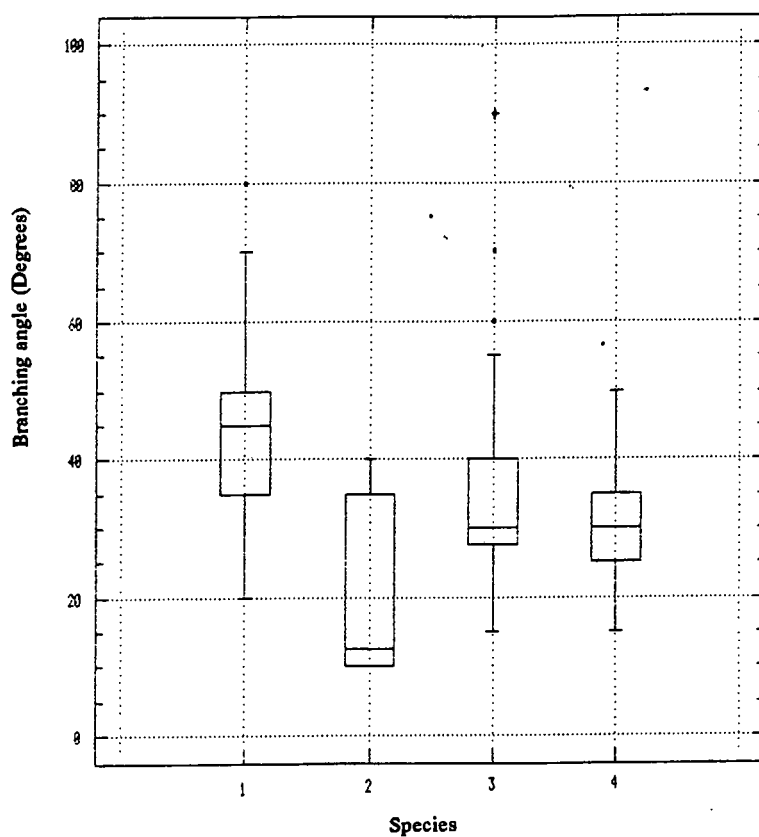


Fig 14: The variation in branching angle values for *Phylica stokoei* and associates. 1. *Phylica strigulosa*, 2. *P. stokoei*, 3. *P. excelsa*, and 4. *P. velutina*

Phylica costata

Pillans (1942) identified *P. wildenowiana* as the closest relative to *P. costata*. The collection sites for *P. wildenowiana* indicate that it is found in the Eastern Cape in the George, Uitenhage, Port Elizabeth divisions.

The important changes in character state are illustrated in Fig 15. *P. costata* is a smaller plant than *P. wildenowiana* (Fig 16). While the leaves appear distinctly smaller in the herbarium specimens, the length range of *P. costata* is less variable and overlaps with that of *P. wildenowiana* (Fig 17) and is similar to the other relative *P. lucens*. The description indicates that the leaves are possibly thicker than those of *P. wildenowiana*. Examination of the herbarium specimens indicated that the hair density on the leaves of *P. costata* is possibly greater than on the leaves of *P. wildenowiana*.

While there is no statistically significant difference in the number of nodes or in branching angle between *P. costata* and *P. wildenowiana*, the overall habit of the *P. costata* is more compact than *P. wildenowiana*. Fig 18 indicates that *P. costata* has a greater number of nodes than *P. wildenowiana* or *P. lucens* and *P. diocia*, the species either side of the relatives in the descriptions. Similarly, with branching angle (Fig 19) *P. costata* has a much lower branching angle than the other three species.

The position of the flowers differs in that they are a terminal in *Phylica costata* with the flowers being stipitate.

Both species have tomentose branchlets. The leaves of both species are revolute, tubercled,

initially being silky villous but becoming glabrous. Bracteoles are absent in both species.

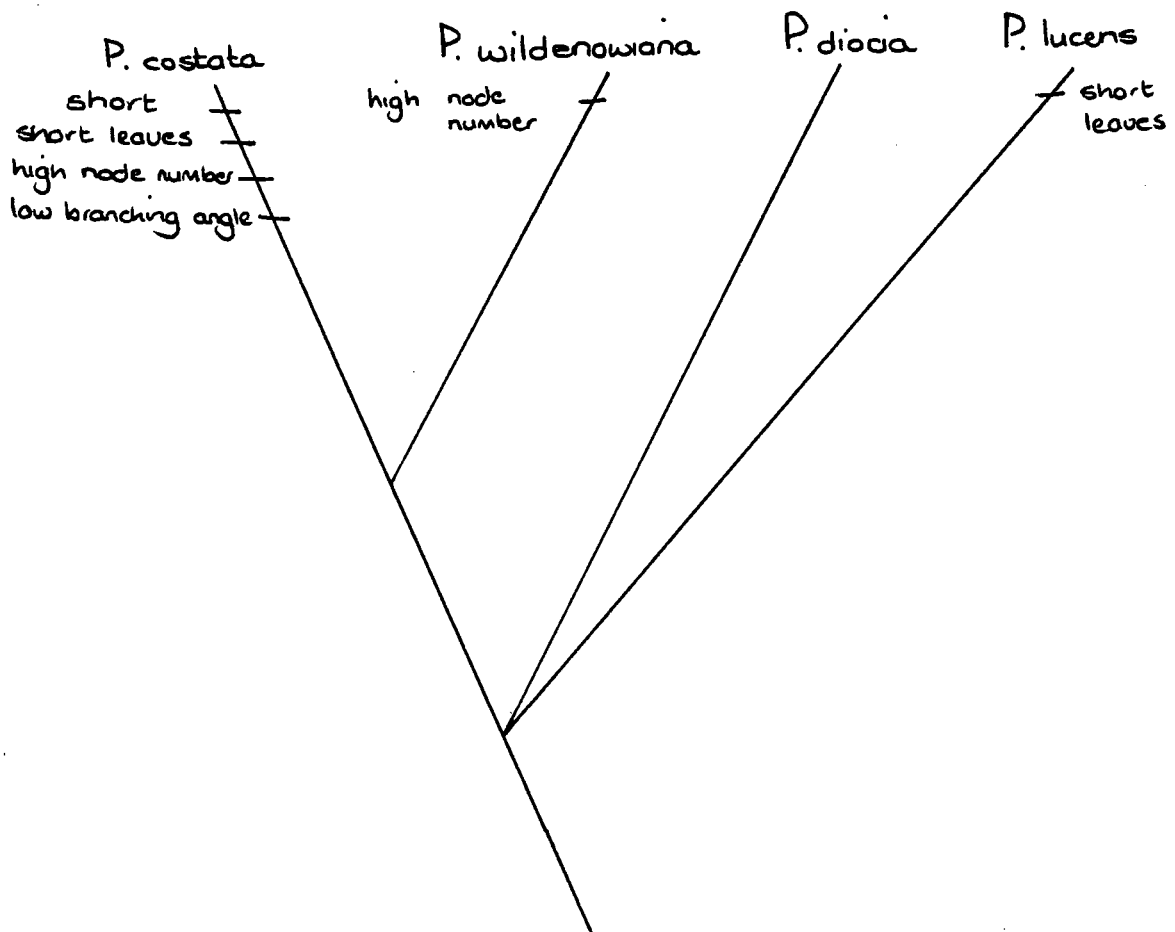


Fig 15: A cladogram illustrating the character state changes for *Phylica costata* and associates.

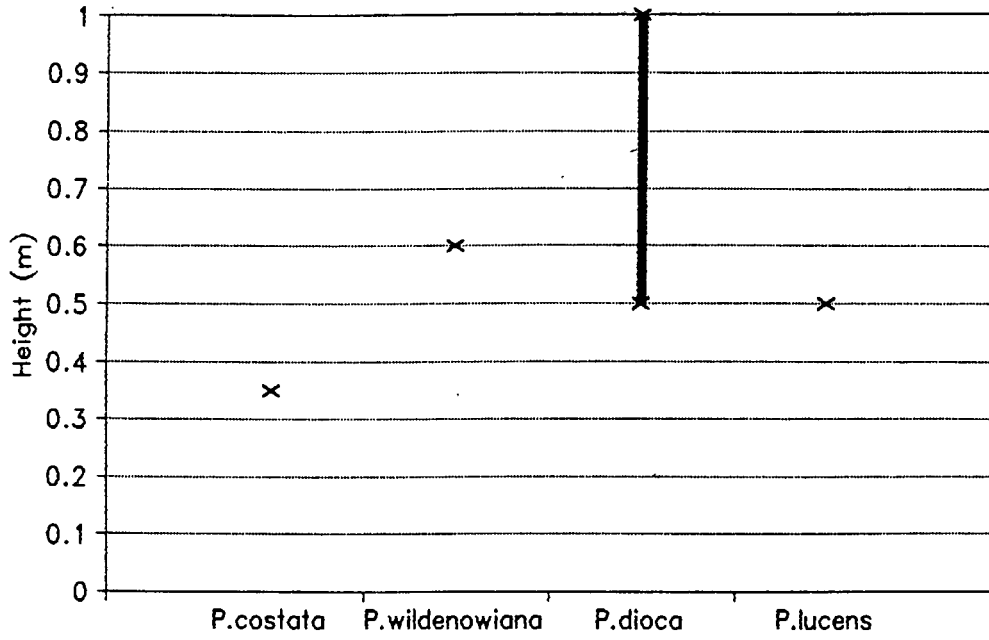


Fig 16: Height variation in *Phylica costata* and associates

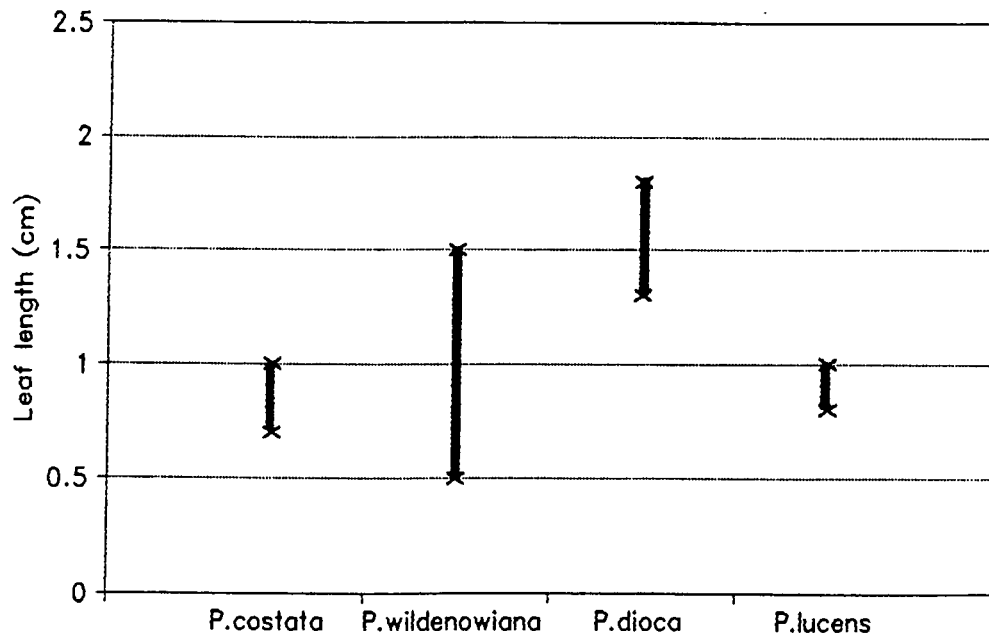


Fig 17: Leaf length variation in *Phylica costata* and associates

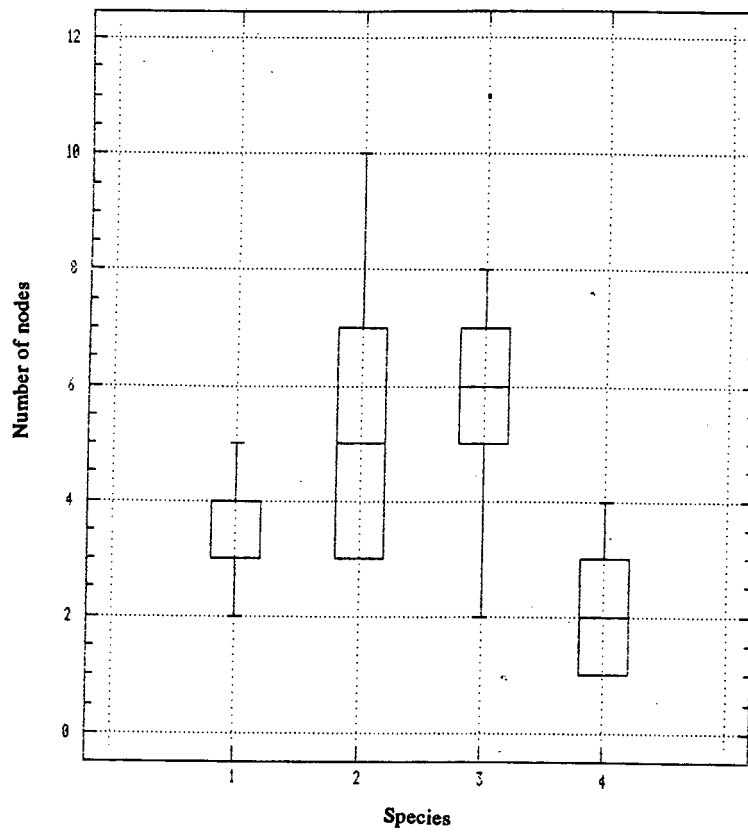


Fig 18: The variation of node number in *Phylica costata* associates. 1. *Phylica lucens*, 2. *P. wildenowiana*, 3. *P. costata*, and 4. *P. diocia*

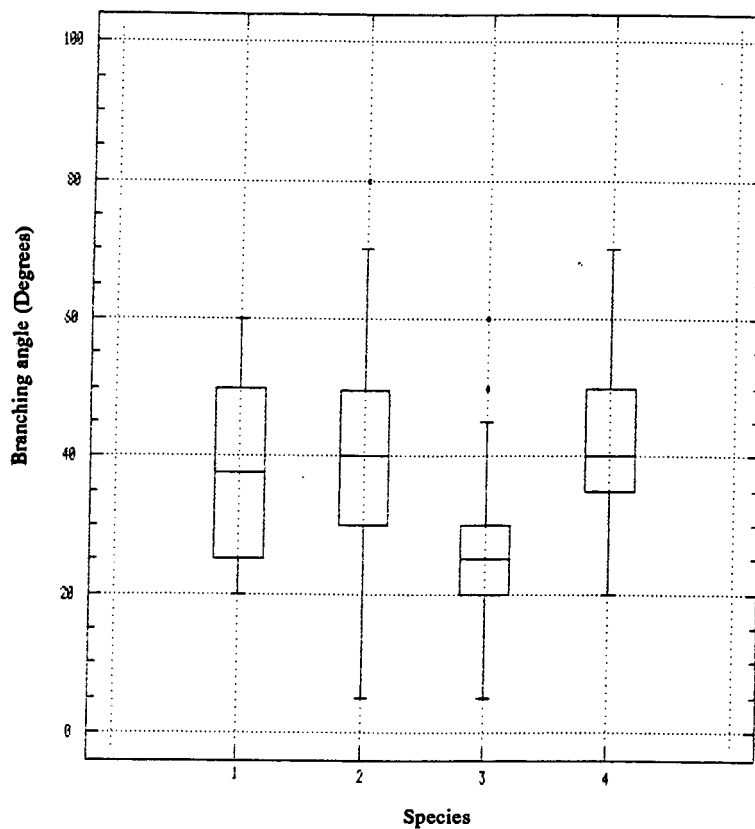


Fig 19: The variation in branching angle distribution in *Phylica costata* and associates. 1. *Phylica lucens*, 2. *P. wildenowiana*, 3. *P. costata*, and 4. *P. diocia*

Pentameris swartbergensis

The phylogeny constructed by Barker (1993) isolated *P. thuarii* as the low altitude relative of *P. swartbergensis*. *P. thuarii* is geographically widespread occurring from Stellenbosch to Montagu pass over a broad altitudinal range, from 300m.

Fig 20 illustrated the changes in the states of the relevant characters (Barker 1993). The culm length of the high altitude species falls into the lower part of the range of the low altitude relative (Fig 21).

The leaves of *P. swartbergensis* have a significantly smaller mean blade width than *P. thuarii* (Fig 22). The blades of *P. swartbergensis* are also significantly smaller than those of *P. thuarii* (Fig 23).

There are two different types of hairs on the adaxial surface of the blades of *P. swartbergensis*, macro hairs and conventional types (Barker 1993). The length of the prickles on the adaxial surface are slightly smaller, while the adaxial microhairs are longer. The leaf sheath is glabrous in the high altitude species but near the leaf base it is sparsely pubescent.

While the culms tend to be shorter in the high altitude species, both species have the same decumbent or caespitose habit. There are also similarities in the leaf structure of the two species. Both have wide shallow furrows between the ribs. The sclerenchyma cap at the

margin is poorly developed and discrete with the edges of the leaf being unswollen. The abaxial epidermal cell width is similar and there are no macrohairs on the abaxial surface of the leaf.

Inspection of the herbarium specimens drew attention to the fact that the inflorescence of the high altitude species was more compact and possibly slightly smaller than that of the low altitude relative.

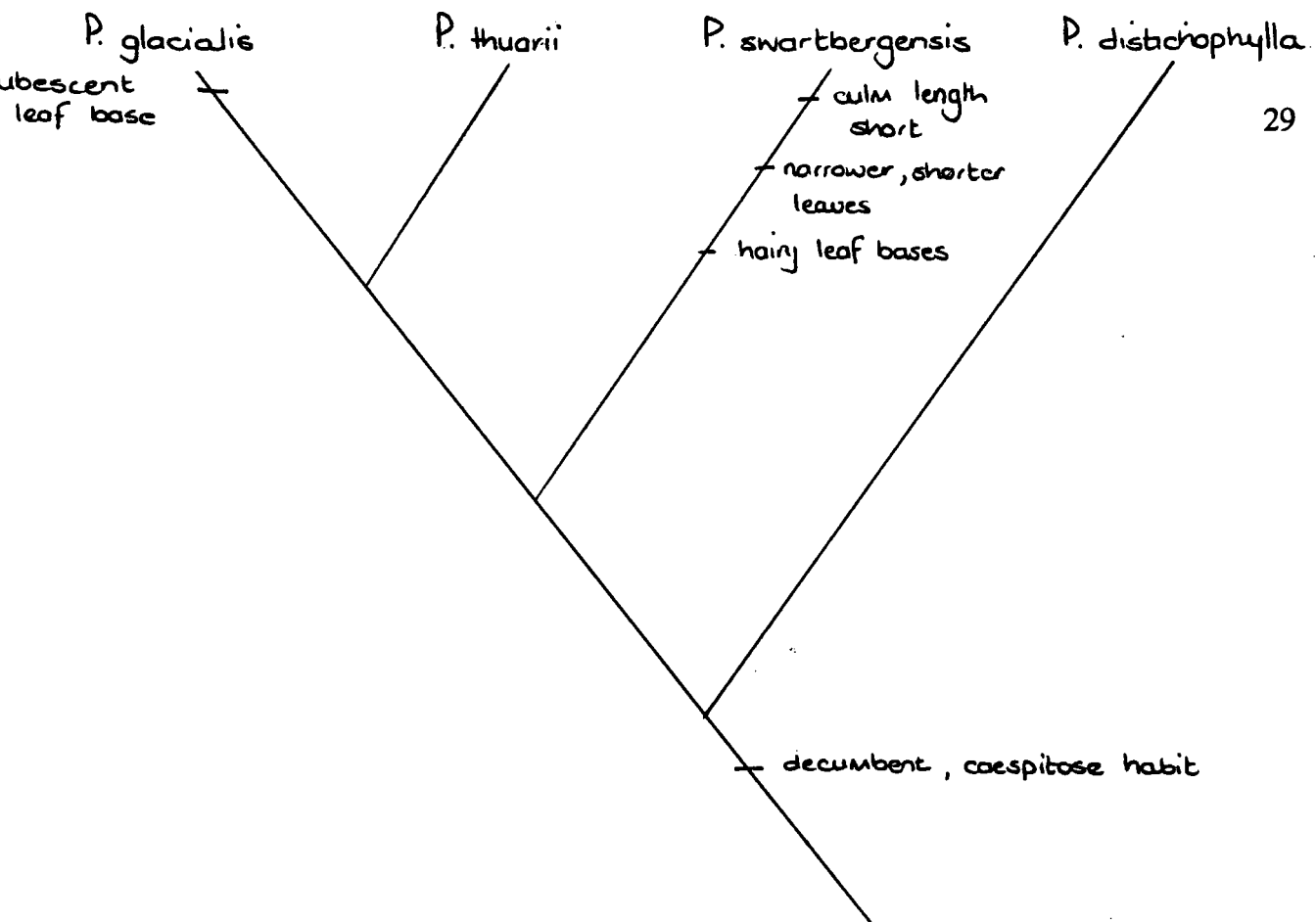


Fig 20: A cladogram illustrating the character state changes in two *Pentameris* species.

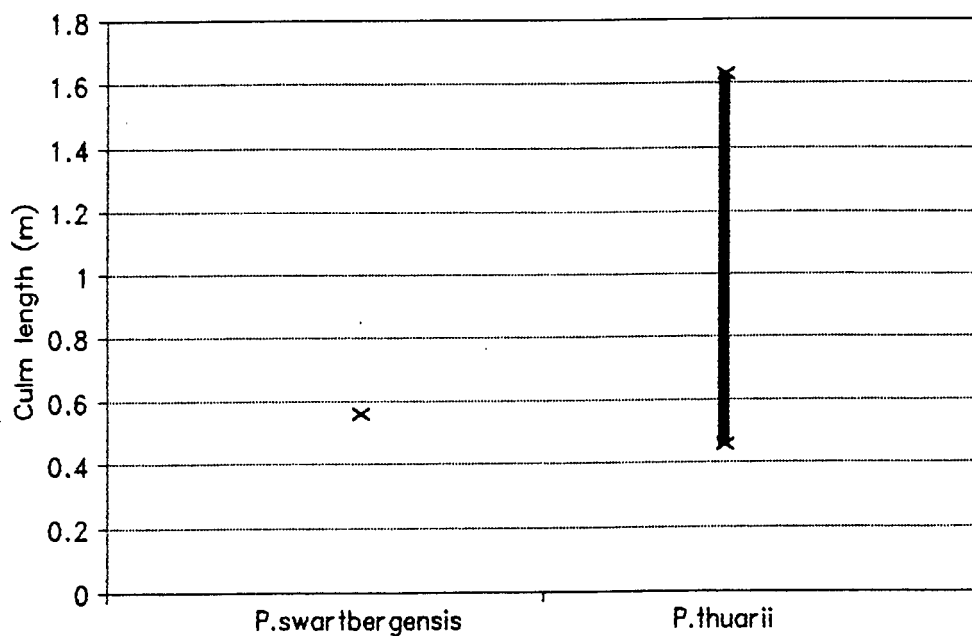


Fig 21: Culm length variation of *Pentameris swartbergensis* and *P. thuarii*.

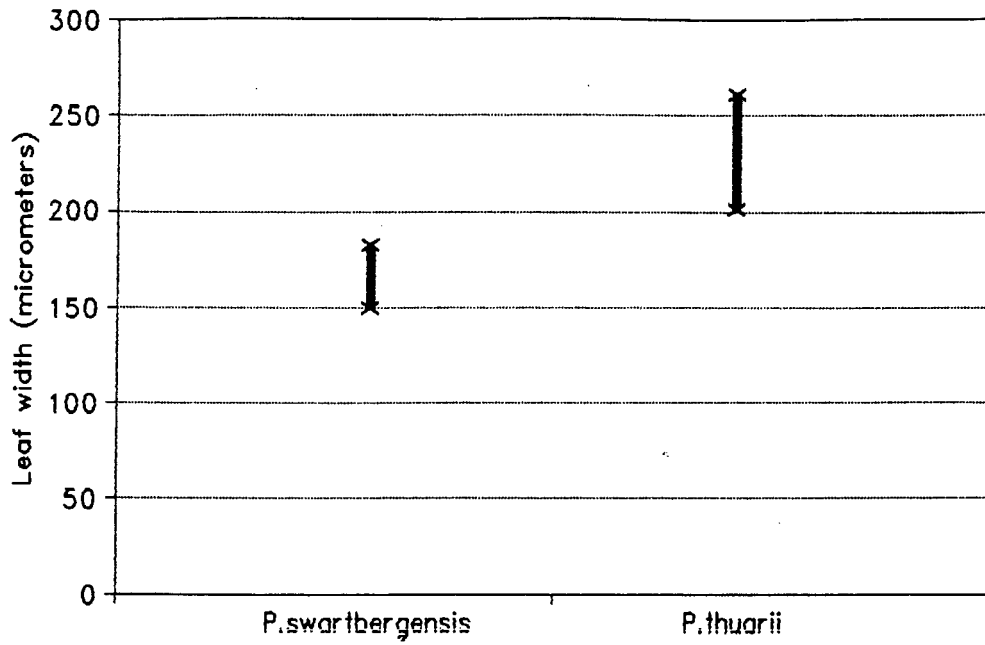


Fig 22: Leaf width variation in *Pentameris swartbergensis* and *P. thuarii*.

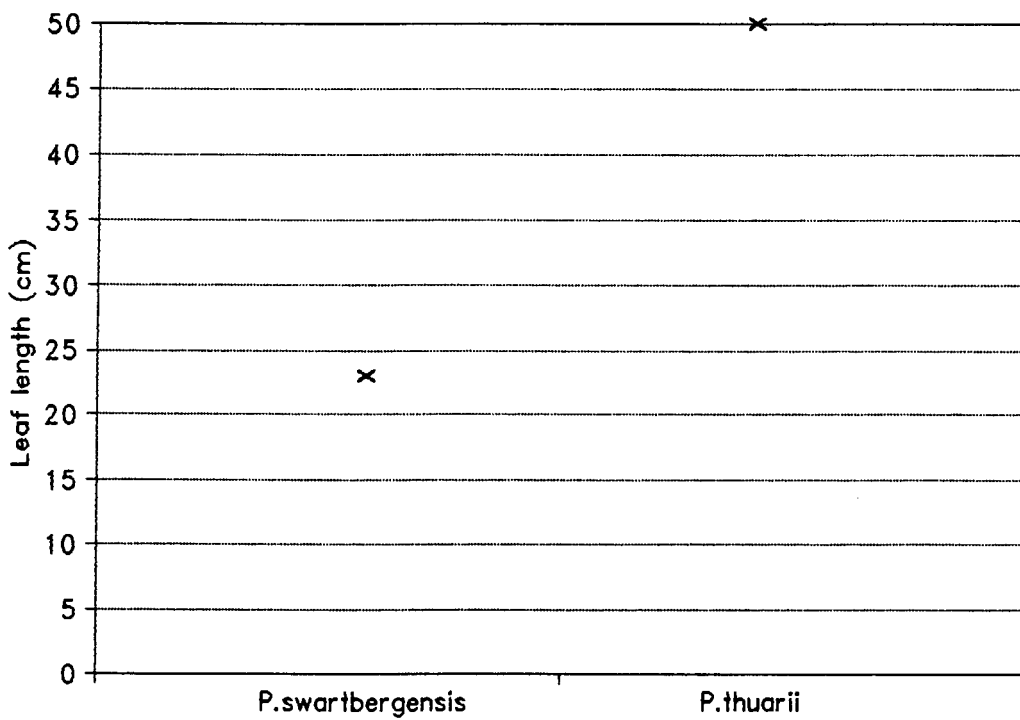


Fig 23: Blade length variation of *Pentameris swartbergensis* and *P. thuarii*

Thamnochortus papyraceus

The low altitude relative of *T. papyraceus* is *T. amoena* (Linder 1990). *T. amoena* is a low altitude species from the Langeberg.

The most striking difference is that the high altitude *T. papyraceus* is half as tall as the low altitude *T. amoena* (Fig 24). The flower spikelets are smaller and no sterile branches develop on the post-flowering stems. The floral bracts and flowers of the two species are identical.

Examination of the culm anatomy (Linder 1993) highlighted differences in the relative thickness of the cell layers. In *T. papyraceus* the chlorenchyma is wider than the epidermal layer and the sclerenchyma layer is narrow. In *T. amoena* all cell layers are approximately the same width.

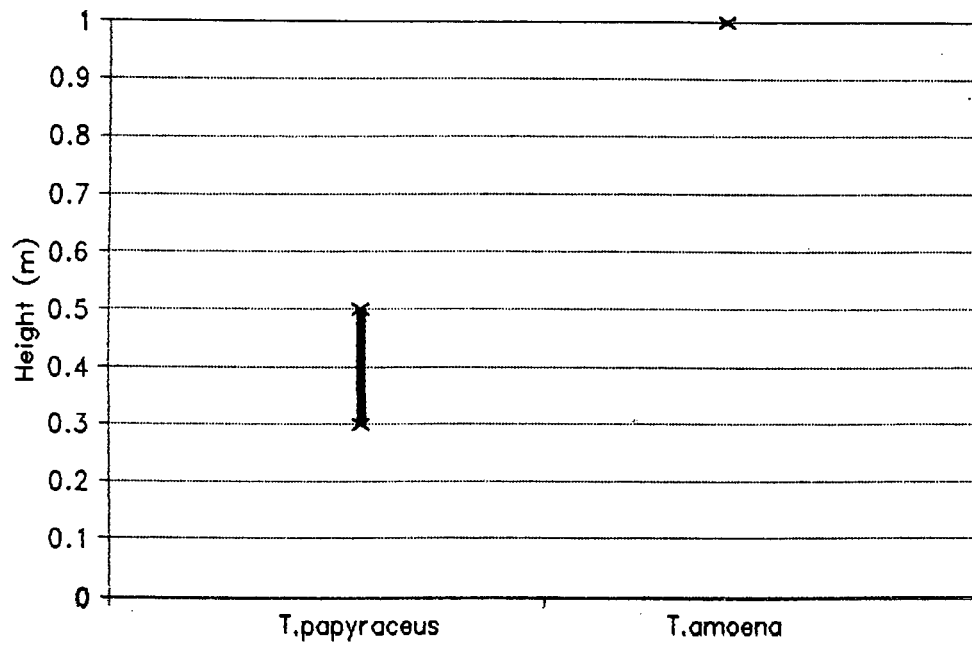


Fig 24: Plant height variation in *Thamnochortus papyraceus* and *T. amoena*

Cliffortia setifolia

According to Weimarck (1937) *C. setifolia* is most similar to the low altitude *C. subsetacea*. *C. subsetacea* is a widespread species which occurs in the Cape Peninsula and in the Caledon district (Weimarck 1934). Weimarck (1937) also stated that *C. paucistaminea* was very similar to *C. setifolia*, this species ranges from George in the Eastern Cape to the Drakensberg in Natal (Weimarck 1934).

The branchlets of *C. setifolia* appear thicker but it is difficult to justify this statement without sectioning the branchlets. While the branches of both species are hairy the hairs appear more dense in *C. setifolia*. In addition to the denser hair covering the bark seems rougher and broken.

Fig 25 illustrates the change of state in characters. The internode length appeared to be less with the branch nodes being more frequent. A count of the number of nodes indicated that this is the case (Fig 26), although the amount of variation in node number in *C. setifolia* means that it is not significantly different. There was, however, no difference in branching angle, *C. setifolia* being exactly the same as *C. subsetacea* (Fig 27).

Inspection of the herbarium specimens indicated that the leaves of *C. setifolia* were narrower than those of *C. subsetacea*, unfortunately no measurements were available for the leaf width of *C. subsetacea* so they cannot be compared graphically. However, the range of leaf width of *C. setifolia* is much smaller than that of *C. paucistaminea* the other species which it was similar to (Weimarck 1937). The leaves of *C. setifolia* are also shorter than those of *C.*

paucistaminea, but they fall within the same range as *C. subsetacea* (Fig 28). The range of length is much smaller in *C. setifolia* than in the low altitude species.

The leaves of the high altitude species have rough margins and a prominent round keel. An attempt was made to count the number of leaves at each leaf node but the manner in which the specimens had been pressed made it impossible to have any confidence in the counts and so this was not continued.

In terms of differences in flower structure *C. setifolia* differs to *C. subsetacea* by having four stamens in the male flowers, as opposed to eight. The bracteoles of the flowers of *C. setifolia* are two to three times as long as those of *C. subsetacea* (Fig 29).

Both species generally have short plants. The leaves of *C. setifolia* and *C. subsetacea* are curved on the upper side. Both the male and female flowers are sessile in both species.

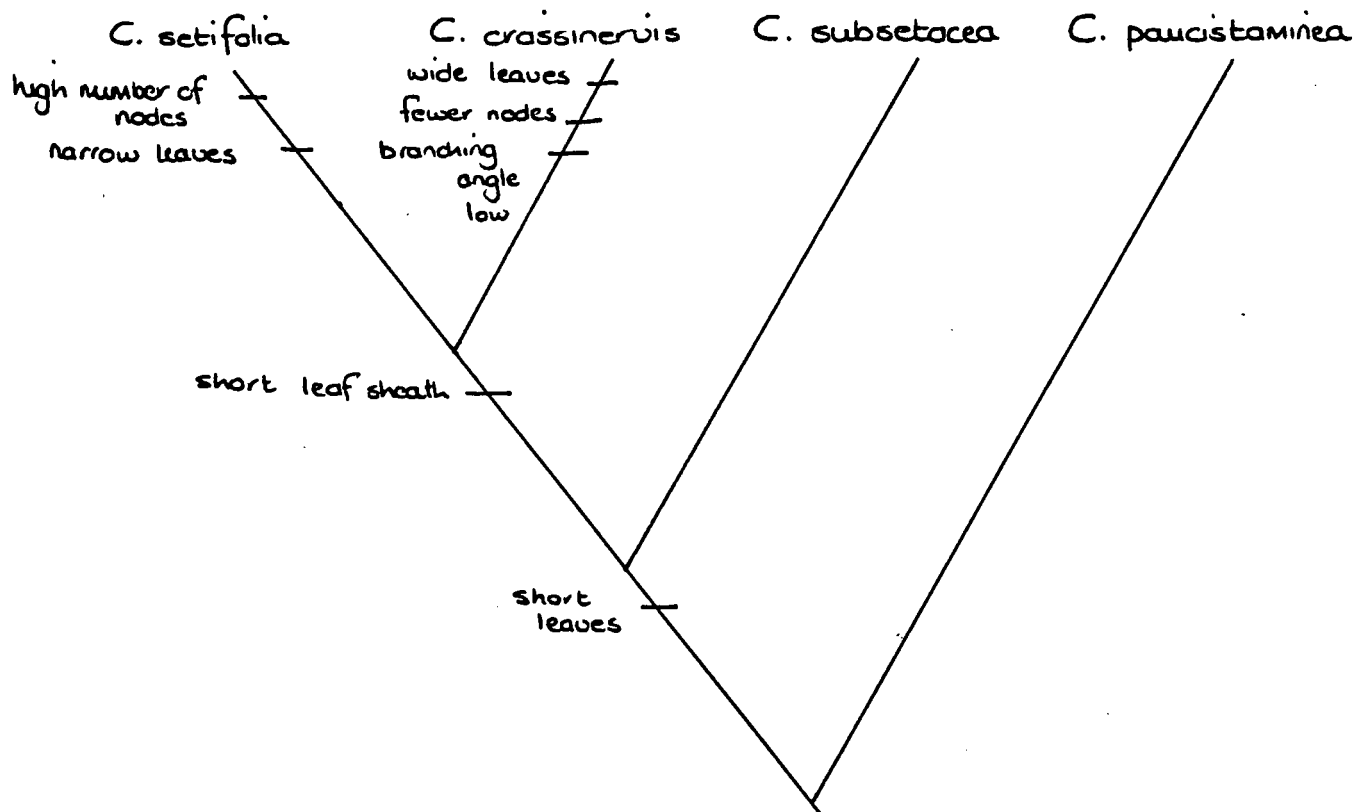


Fig 25: Cladogram showing the character state changes in *Cliffortia setifolia*, *Cliffortia crassinervis* and associates.

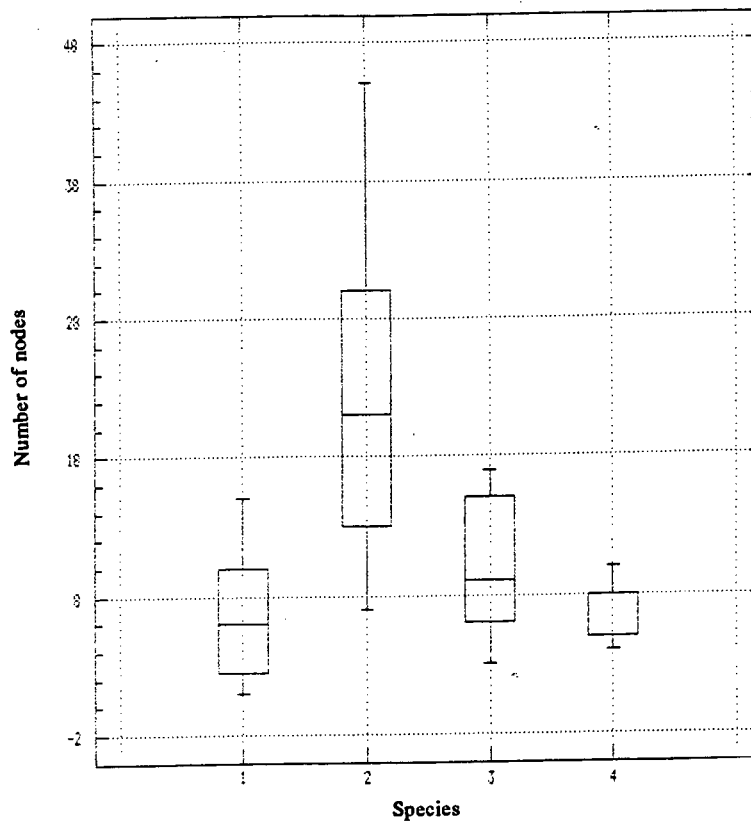


Fig 26: The variation in the number of nodes in *Cliffortia setifolia* and *Cliffortia crassinervis* and associates. 1. *Cliffortia paucistaminea*, 2. *C. setifolia*, 3. *C. subsetacea*, 4. *C. crassinervis*

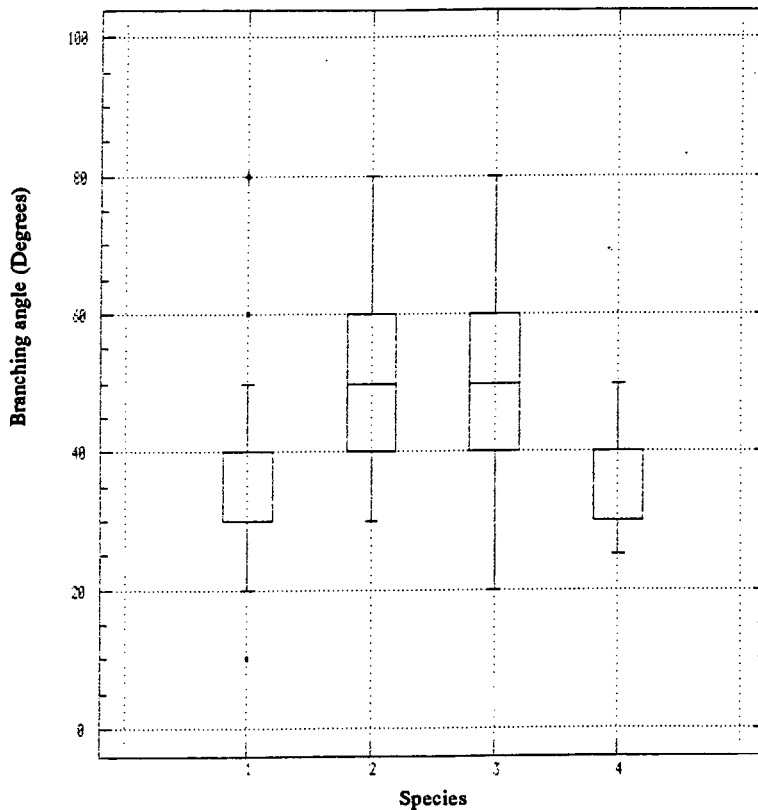


Fig 27: The variation of branch angle in *Cliffortia setifolia* and *C. crassinervis* and associates. 1. *Cliffortia paucistaminea*, 2. *C. setifolia*, 3. *C. subsetacea*, 4. *C. crassinervis*

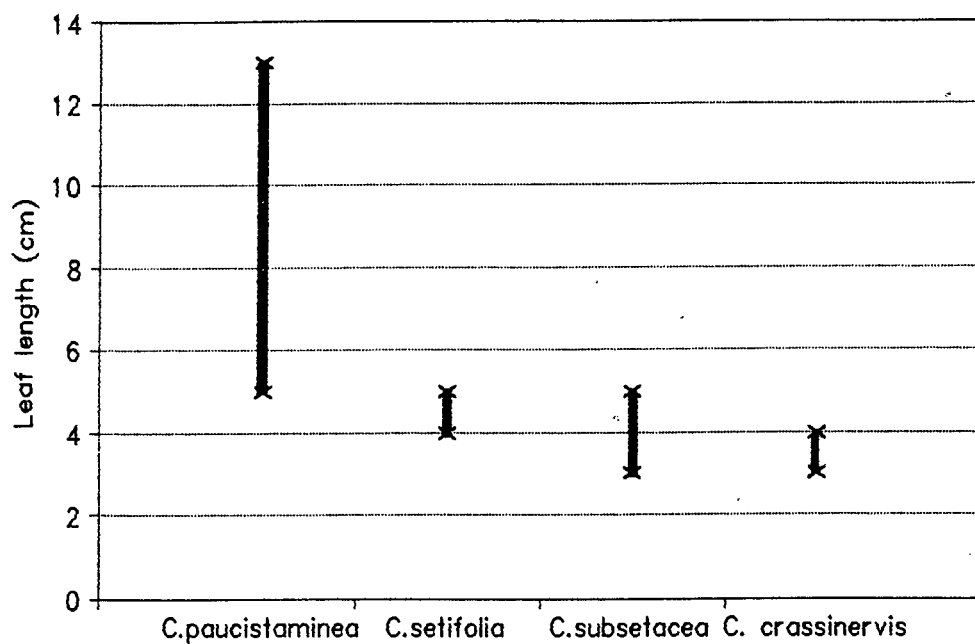


Fig 28: Leaf length variation in *Cliffortia setifolia* and *C. crassinervis* and associates

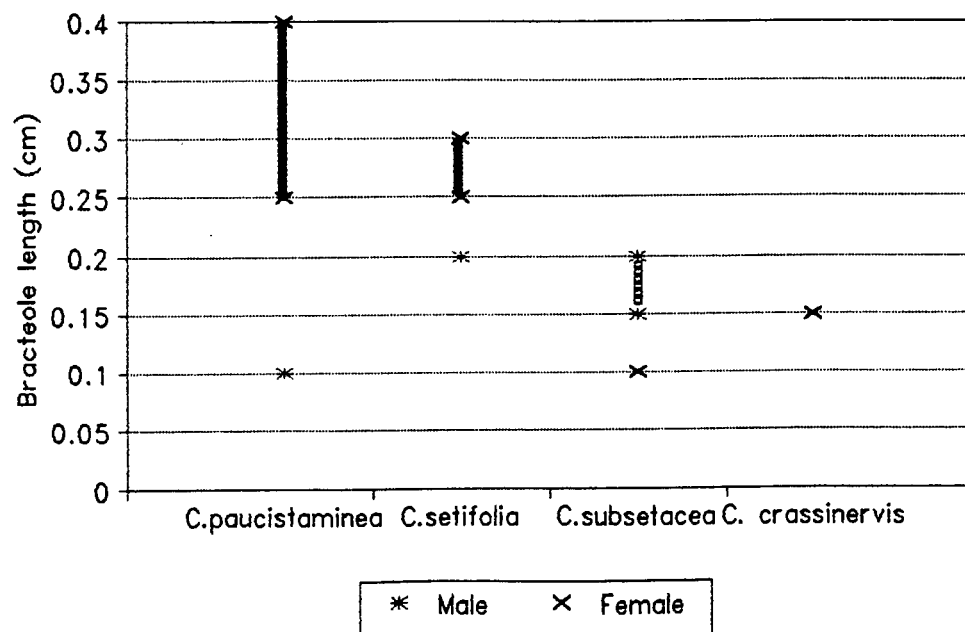


Fig 29: Bracteole length variation in *Cliffortia setifolia* and *C. crassinervis* and associates.

Cliffortia crassinervis

Weimarck did not specify which species *C. crassinervis* was associated with but it appears that this high altitude species is, like *C. setifolia*, closely related to *C. subsetacea* and *C. paucistaminea* (Fehling pers com).

The changes in character state are illustrated in Fig 30. Unfortunately Weimarck (1959) does not describe the habit of *C. crassinervis* comprehensively. However, counting the number of nodes and measuring branch angle gives an indication of architecture of the plant. Fig 26 indicates that *C. crassinervis* has fewer nodes than *C. subsetacea* but similar numbers to *C. paucistaminea*. Similarly, *C. crassinervis* has smaller branching angles than *C. setifolia* but they are virtually the same as those in *C. paucistaminea* (Fig 27).

The leaves of *C. crassinervis* are slightly shorter than those of *C. subsetacea*, although they fall into the same length range (Fig 28), and they are significantly shorter than *C. paucistaminea*. The range of leaf width, however, does overlap with that of *C. paucistaminea* so that they are significantly wider than the leaves of the other high altitude *Cliffortia* species, *C. setifolia* (Fig 31).

The leaf sheath of *C. crassinervis* is shorter than that of *C. subsetacea* (Fig 32). The upper surface of the leaf in *C. crassinervis* is convex, as opposed to flat-concave in *C. subsetacea* and the leaf of the high altitude species is characteristically shiny green.

The bracteoles and sepals of the female flowers are shorter in *C. crassinervis* than in *C. subsetacea*, as is the ovary (Fig 29 and Fig 33).

In both species the young branches are hairy, on the leaves are bumpy and the female flowers are sessile.

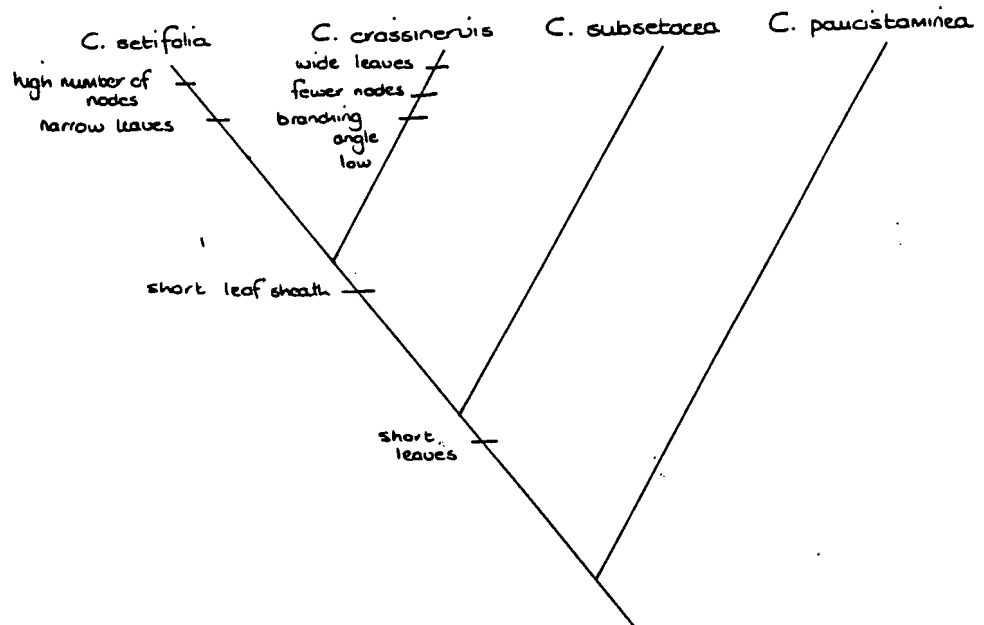


Fig 30: A cladogram illustrating the character state changes for *Cliffortia crassinervis*.

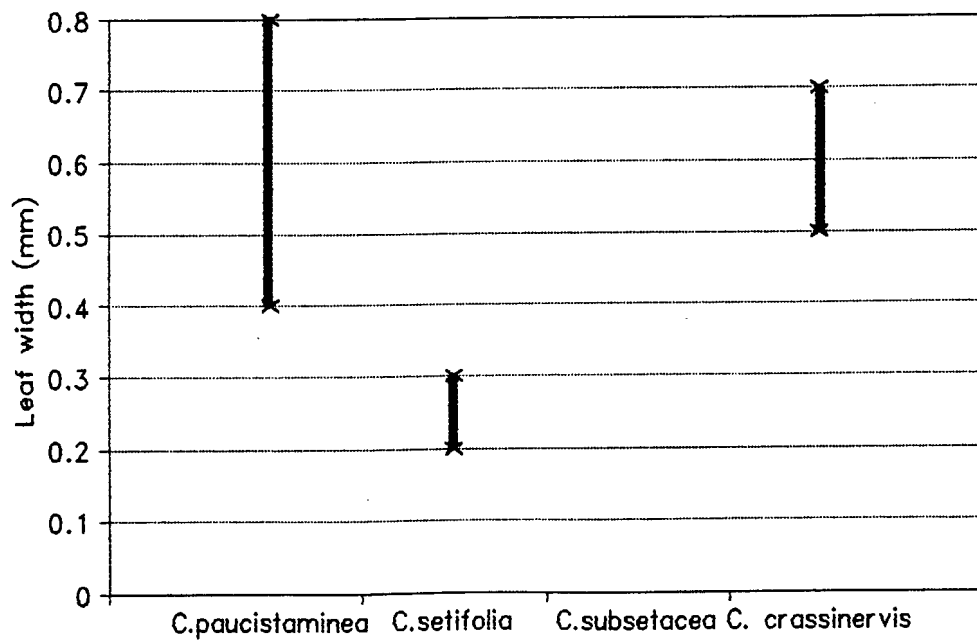


Fig 31: Leaf width variation in *Cliffortia crassinervis* and *C. setifolia* and associates.

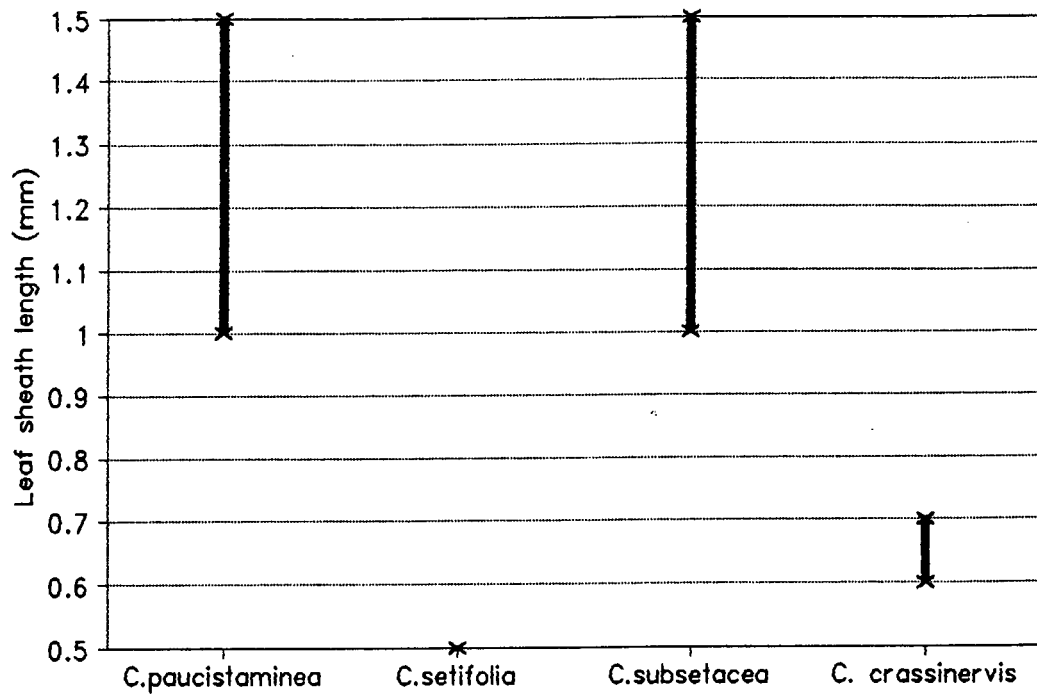


Fig 32: Leaf sheath length variation in *Cliffortia setifolia* and *Cliffortia crassinervis* and associates

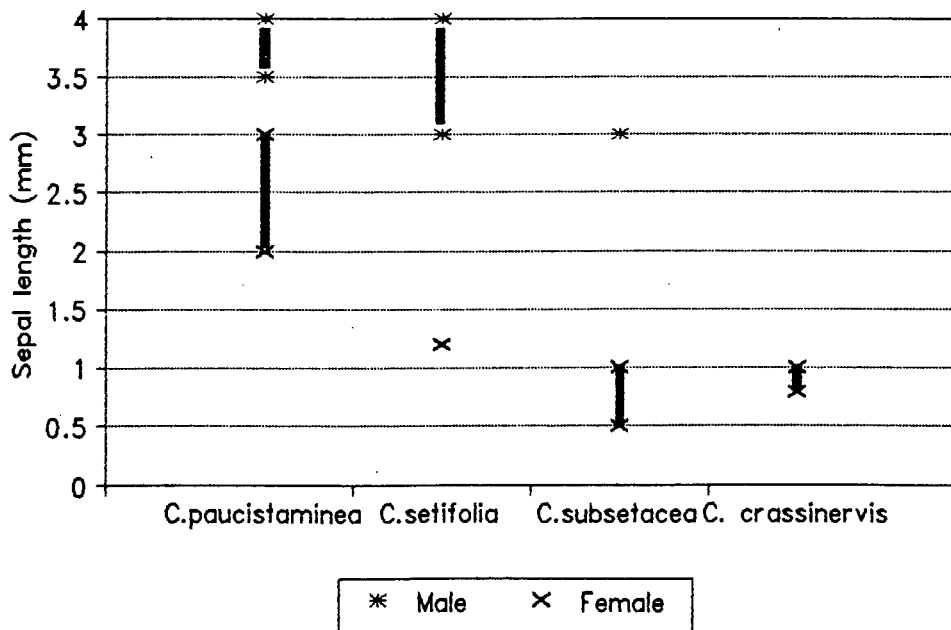


Fig 33: Sepal length variation in *Cliffortia setifolia* and *Cliffortia crassinervis* and associates

Euryops glutinosus

No closely related species was mentioned so the three species situated either side of *E. glutinosus* in the descriptions were used. The three species are *E. thunbergii*, *E. oligoglossus* and *E. nodosus*. *E. thunbergii* is a fairly widespread low altitude species occurring in the Van Rhynsdorp, Clanwilliam, Piketberg, Tulbagh, Malmesbury, Belville and Worcester divisions. The highest altitude that *E. oligoglossus* has been collected from is 8325 ft in Lesotho, in terms of its geographical range it has been collected from Laingsburg, Richmond, Hanover, Murraysburg, Graaf Reniet-Middleburg, Steynsburg, Aliwal North and Lady Grey divisions. *E. nodosus* has been collected from an altitude of 5400 ft in the Sutherland division. It is also known from Carnarvon and Beaufort West divisions (Nordenstam 1968)

Fig 34 illustrates the character state changes for *Euryops* sp. *E. glutinosus* has several features which distinguish it from the other three other species. These features all have the potential to be adaptations. One of the most interesting is the fact that chromosome counts in *E. glutinosus* gave $2n=40$, while those for *E. oligoglossus* gave $2n=20,40$ and *E. nodosus* $2n=20$

In terms of leaf structure *E. glutinosus* is the only species where the adaxial side of the leaf is keeled. It is peculiar in that it is the only species to have resin on the leaves and a resiniferous vein on each leaf margin. Unlike the other species it does not have fleshy leaves, however, the peduncles of *E. glutinosus* are slightly thicker than any of the other species (Fig 35).

Cliffortia crassinervis

Weimarck did not specify which species *C. crassinervis* was associated with but it appears that this high altitude species is, like *C. setifolia*, closely related to *C. subsetacea* and *C. paucistaminea* (Fehling pers com).

The changes in character state are illustrated in Fig 30. Unfortunately Weimarck (1959) does not describe the habit of *C. crassinervis* comprehensively. However, counting the number of nodes and measuring branch angle gives an indication of architecture of the plant. Fig 26 indicates that *C. crassinervis* has fewer nodes than *C. subsetacea* but similar numbers to *C. paucistaminea*. Similarly, *C. crassinervis* has smaller branching angles than *C. setifolia* but they are virtually the same as those in *C. paucistaminea* (Fig 27).

The leaves of *C. crassinervis* are slightly shorter than those of *C. subsetacea*, although they fall into the same length range (Fig 28), and they are significantly shorter than *C. paucistaminea*. The range of leaf width, however, does overlap with that of *C. paucistaminea* so that they are significantly wider than the leaves of the other high altitude *Cliffortia* species, *C. setifolia* (Fig 31).

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The bracteoles and sepals of the female flowers are shorter in *C. crassinervis* than in *C. subsetacea*, as is the ovary (Fig 29 and Fig 33).

In both species the young branches are hairy, on the leaves are bumpy and the female flowers are sessile.

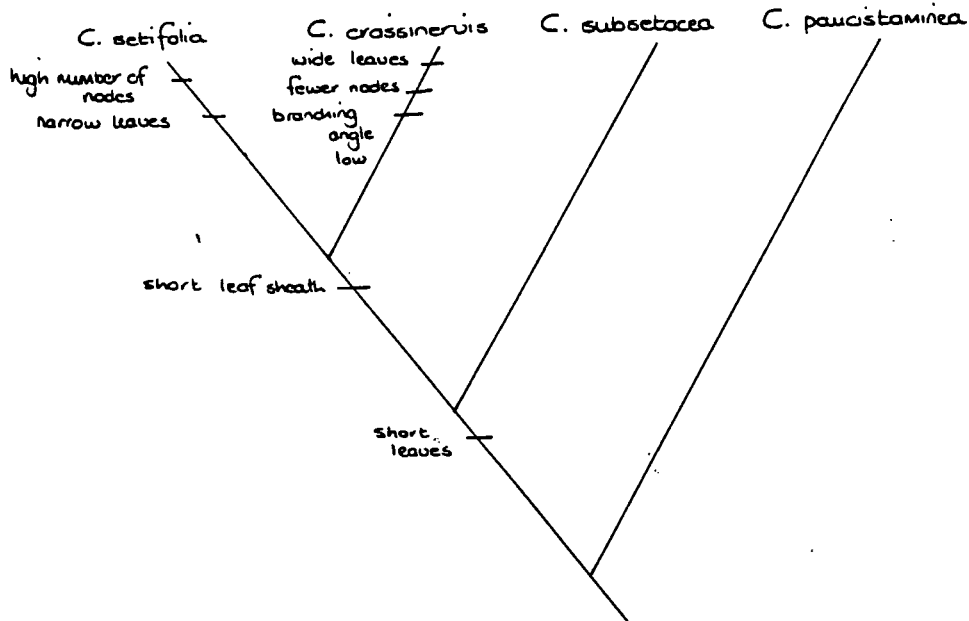


Fig 30: A cladogram illustrating the character state changes for *Cliffortia crassinervis*.

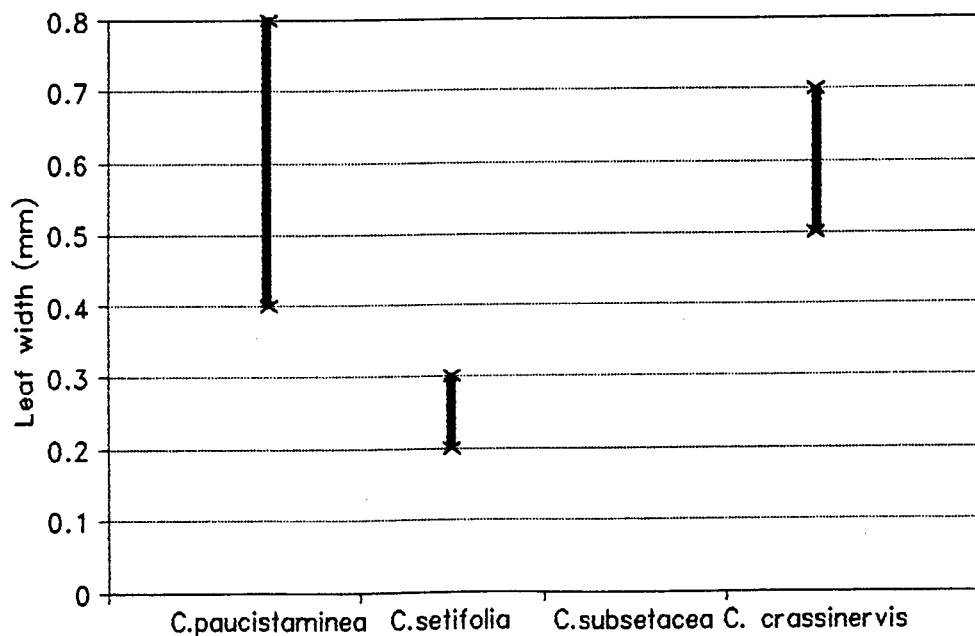


Fig 31: Leaf width variation in *Cliffortia crassinervis* and *C. setifolia* and associates.

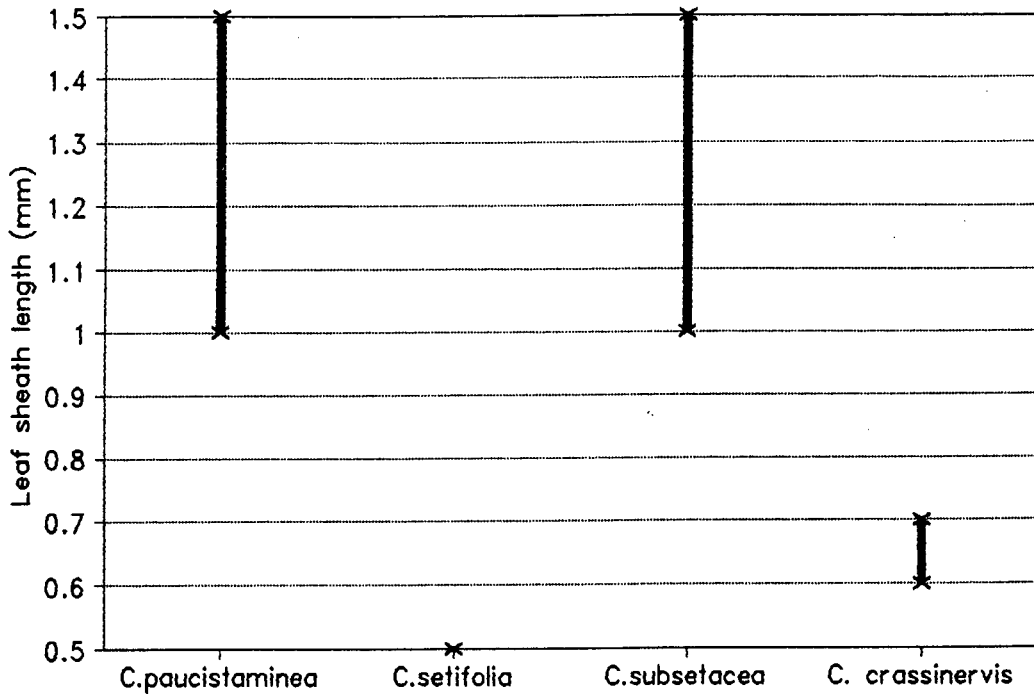


Fig 32: Leaf sheath length variation in *Cliffortia setifolia* and *Cliffortia crassinervis* and associates

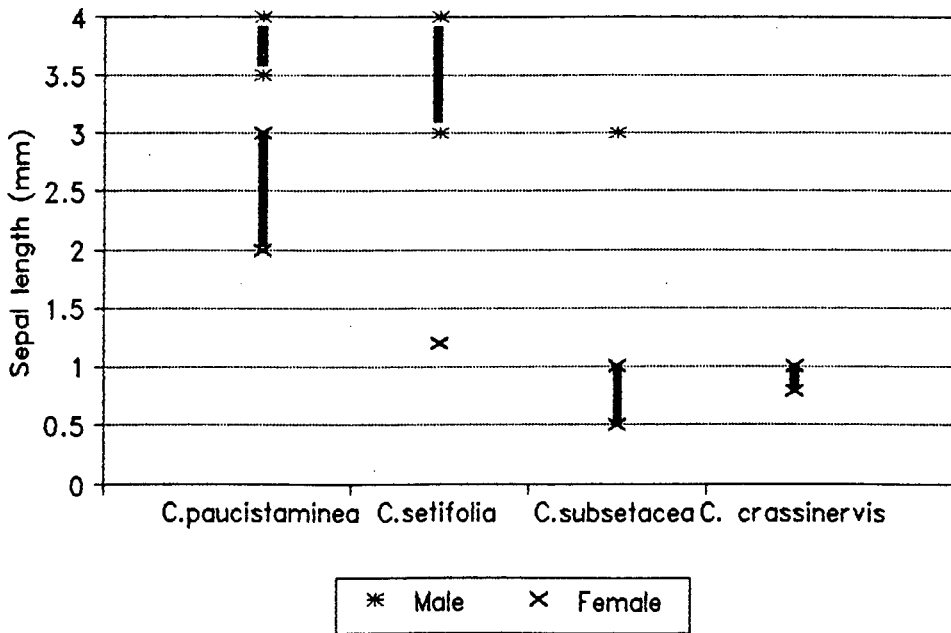


Fig 33: Sepal length variation in *Cliffortia setifolia* and *Cliffortia crassinervis* and associates

Euryops glutinosus

No closely related species was mentioned so the three species situated either side of *E. glutinosus* in the descriptions were used. The three species are *E. thunbergii*, *E. oligoglossus* and *E. nodosus*. *E. thunbergii* is a fairly widespread low altitude species occurring in the Van Rhynsdorp, Clanwilliam, Piketberg, Tulbagh, Malmesbury, Belville and Worcester divisions. The highest altitude that *E. oligoglossus* has been collected from is 8325 ft in Lesotho, in terms of its geographical range it has been collected from Laingsburg, Richmond, Hanover, Murraysburg, Graaf Reniet-Middleburg, Steynsburg, Aliwal North and Lady Grey divisions. *E. nodosus* has been collected from an altitude of 5400 ft in the Sutherland division. It is also known from Carnarvon and Beaufort West divisions (Nordenstam 1968)

Fig 34 illustrates the character state changes for *Euryops* sp. *E. glutinosus* has several features which distinguish it from the other three other species. These features all have the potential to be adaptations. One of the most interesting is the fact that chromosome counts in *E. glutinosus* gave $2n=40$, while those for *E. oligoglossus* gave $2n=20,40$ and *E. nodosus* $2n=20$

In terms of leaf structure *E. glutinosus* is the only species where the adaxial side of the leaf is keeled. It is peculiar in that it is the only species to have resin on the leaves and a resiniferous vein on each leaf margin. Unlike the other species it does not have fleshy leaves, however, the peduncles of *E. glutinosus* are slightly thicker than any of the other species (Fig 35).

In terms of flower structure *E. glutinosus* has the shallowest and widest involucre for the measurements given, no width measurement was given for *E. nodosus*. The floral bracts of *E. glutinosus* change shape, from uniserate to subuniserate, with the development of the flower. In *E. thunbergii* they are uniserate, and in the other two species they are subuniserate.

E. glutinosus has a much higher number of disc florets than the other species of *Euryops* which were examined (Fig 36). The number of ray florets present on the inflorescence of *E. glutinosus* falls into the same range as *E. thunbergii*, however it does seem to be slightly higher (Fig 37). Similarly the length and the width of the florets of *E. glutinosus* are longer and wider than those of any of the other species. The achenes of *E. glutinosus* are also longer and wider than those of the other species (Fig 38).

E. glutinosus also has a number of features in common with one or more of the other species which were examined. Due to the lack of resolution regarding the relationship between the species it is not possible to say whether these are preadaptations to the alpine conditions or not. *E. glutinosus* falls into the same height range as *E. nodosus*. The other two species both grow slightly higher (Fig 39).

The young branches of the low altitude species, *E. thunbergii*, and the high altitude *E. glutinosus* are both relatively densely hairy.

The leaves of *E. glutinosus* are in the same size category as *E. thunbergii*, that is much longer than the leaves of the other two species (Fig 40). However, the leaves of *E.*

glutinosus are much wider than *E. thunbergii* and *E. nodosus* and slightly wider than *E. oligoglossus* (Fig 41). Both *E. glutinosus* and *E. oligoglossus* have prominent midribs.

The peduncles *E. glutinosus* and *E. thunbergii* are also of similar length much longer than those of the other two species (Fig 42).

E. glutinosus, *E. thunbergii* and *E. nodosus* have fairly high numbers of involucre bracts (Fig 43). These three species all have puberulous tips to the bracts. The bracts of *E. glutinosus*, *E. oligoglossus* and *E. nodosus* all have distinct nerves, with *E. glutinosus* and *E. oligoglossus* having similar numbers of nerves, 3-5, while *E. nodosus* has 1-3 and *E. thunbergii* has none.

The bracts of all four species have a range of lengths the maximum of which is virtually the same. In *E. glutinosus* and *E. oligoglossus* the bracts tend to be wider than in the other two species.

Corolla length falls within the same range in all species as does anther length.

The achenes of *E. glutinosus*, *E. oligoglossus* and *E. nodosus* have dense hairs all over the achene, but in *E. thunbergii* the hairs are restricted to in between the ribs. The achenes of *E. thunbergii* and *E. glutinosus* both have thick distinct ribs (Fig 38).

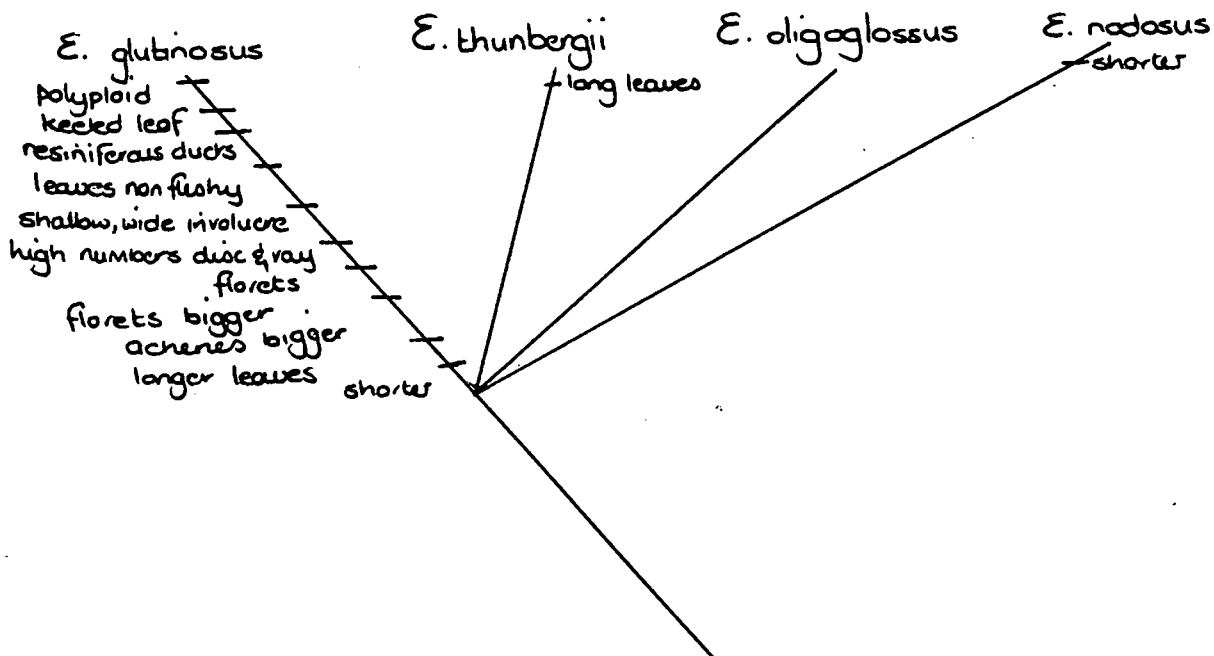


Fig 34: Cladogram illustrating the character state changes for *Euryops glutinosus*.

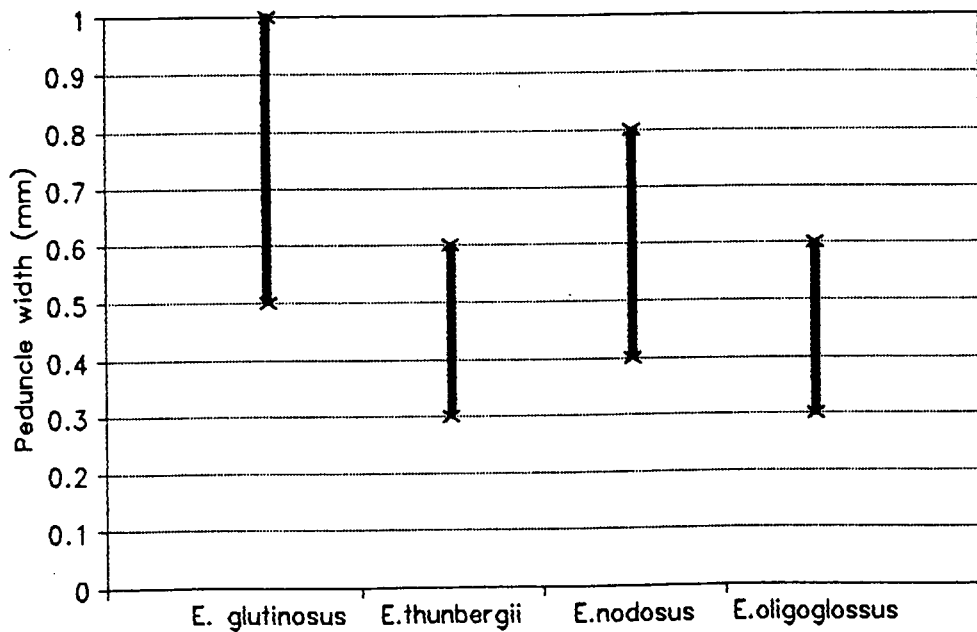


Fig 35: Peduncle width in *Euryops glutinosus* and associates

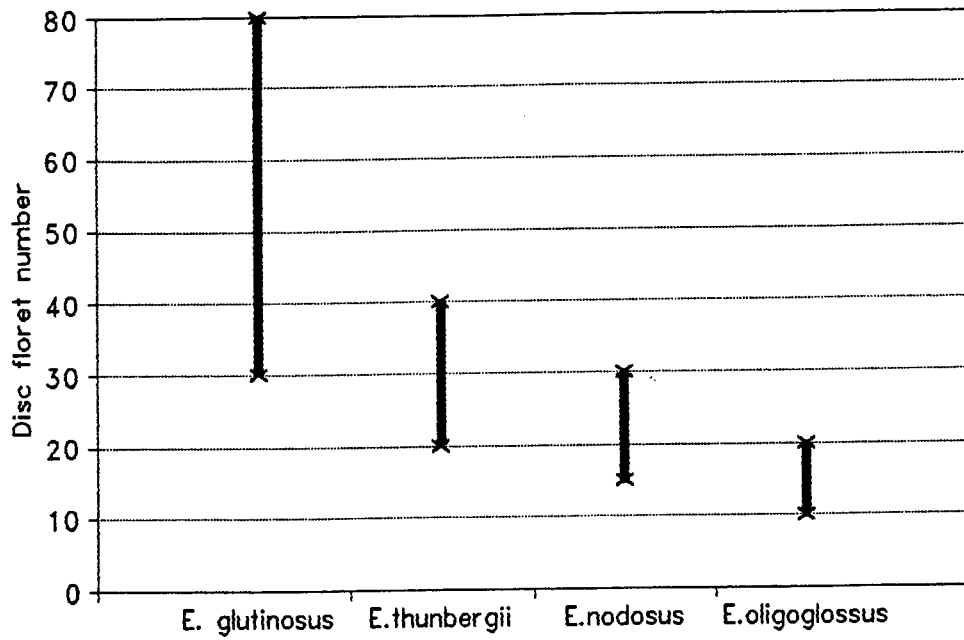


Fig 36: Number of disc florets in *Euryops glutinosus* and associates

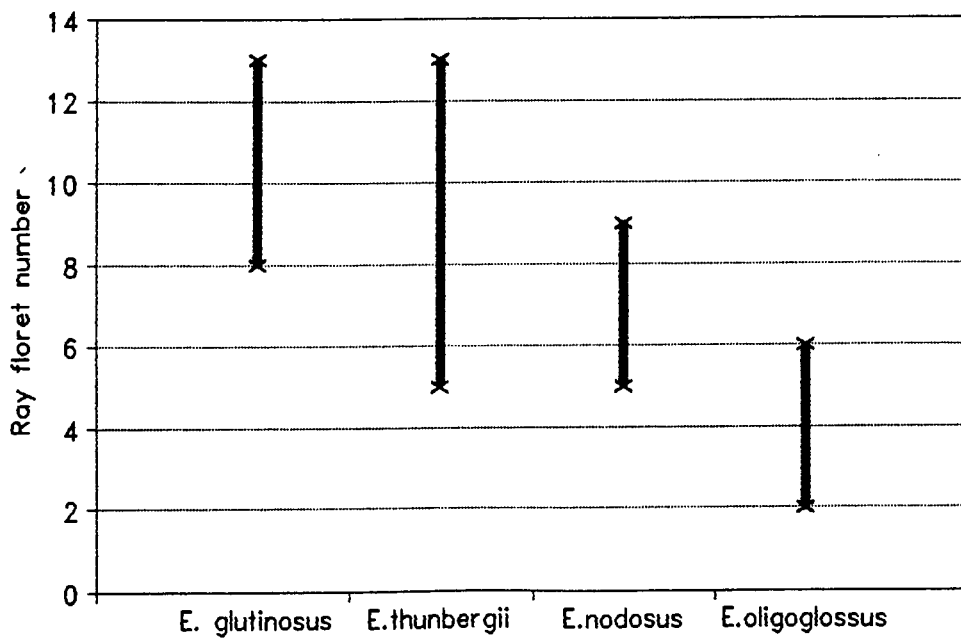


Fig 37: The number of ray florets in *Euryops glutinosus* and associates.



Fig 38: *E. glutinosus* (A-C), *E. thunbergii* (D-F), *E. nodosus* (G-I) and *E. oligoglossus* (J-L).
 Plant- x1 (Or 1/2 for *E. glutinosus* and *E. thunbergii*), Florets- x5, Achenes- x10. (after Nordenstam 1968)

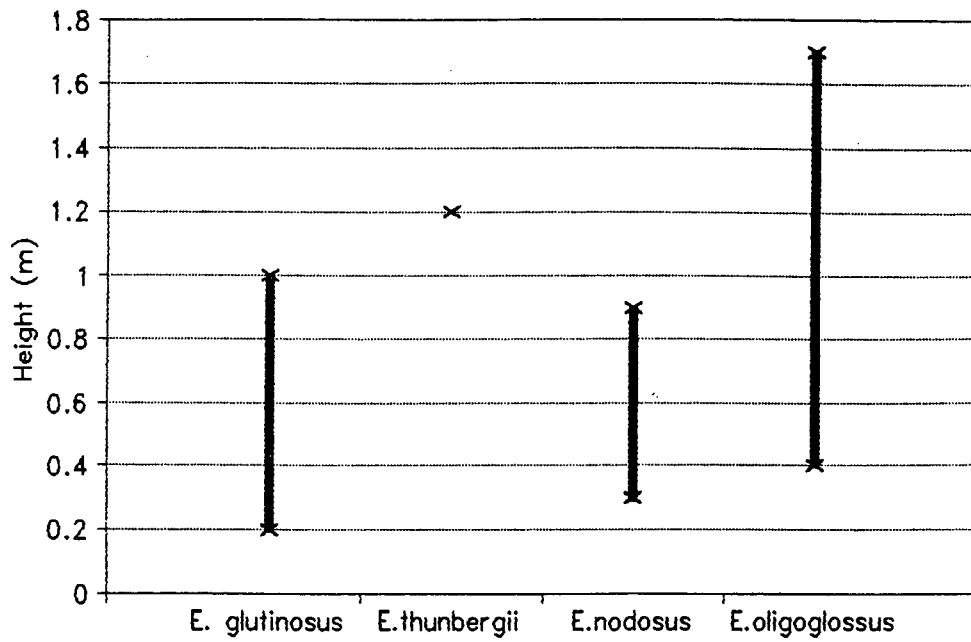


Fig 39: Height variation in *Euryops glutinosus* and associates.

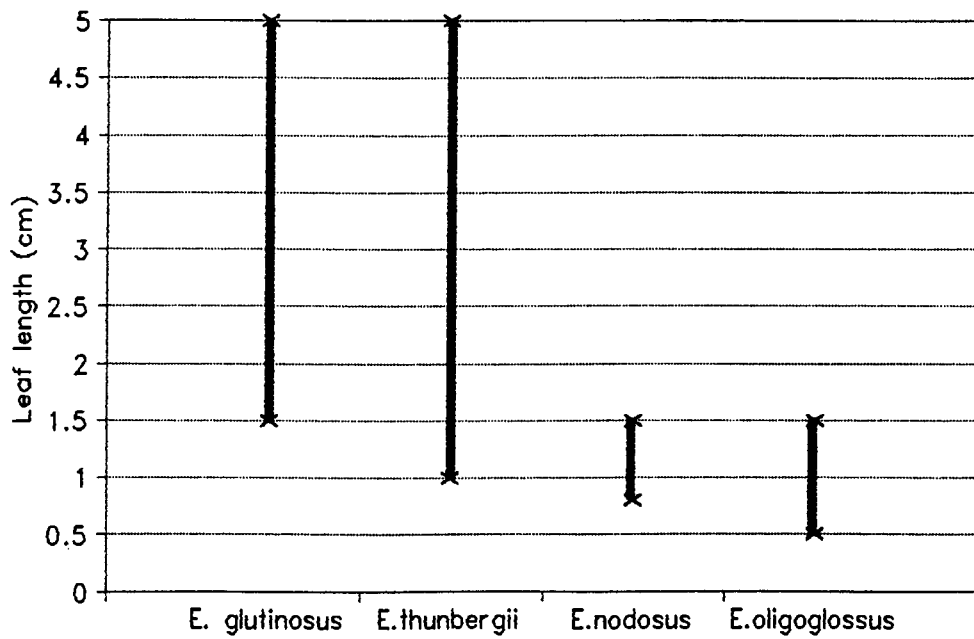


Fig 40: Leaf length variation in *Euryops glutinosus* and associates.

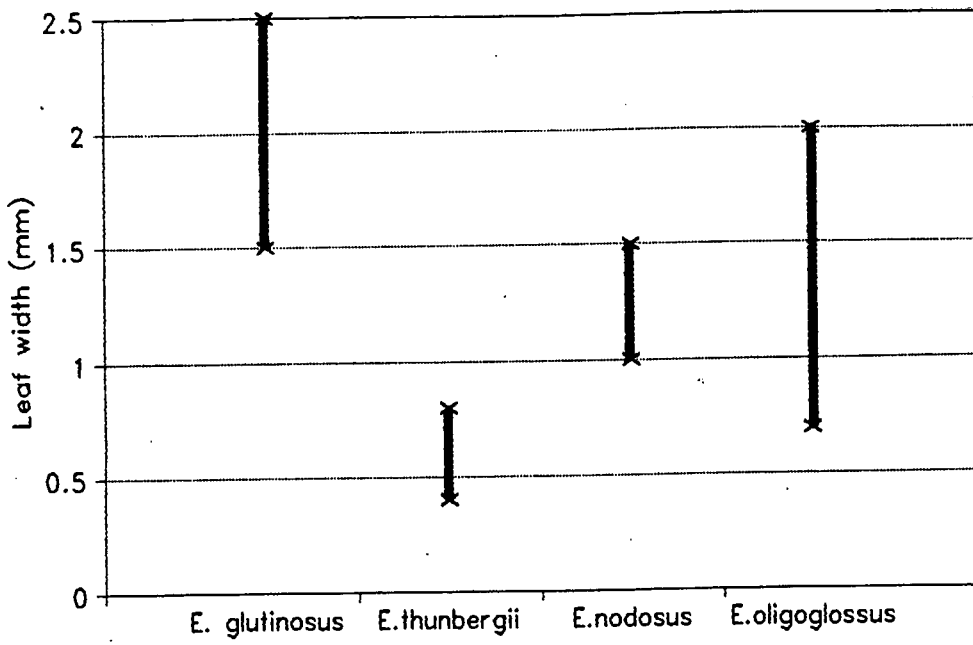


Fig 41: Leaf width variation in *Euryops glutinosus* and associates

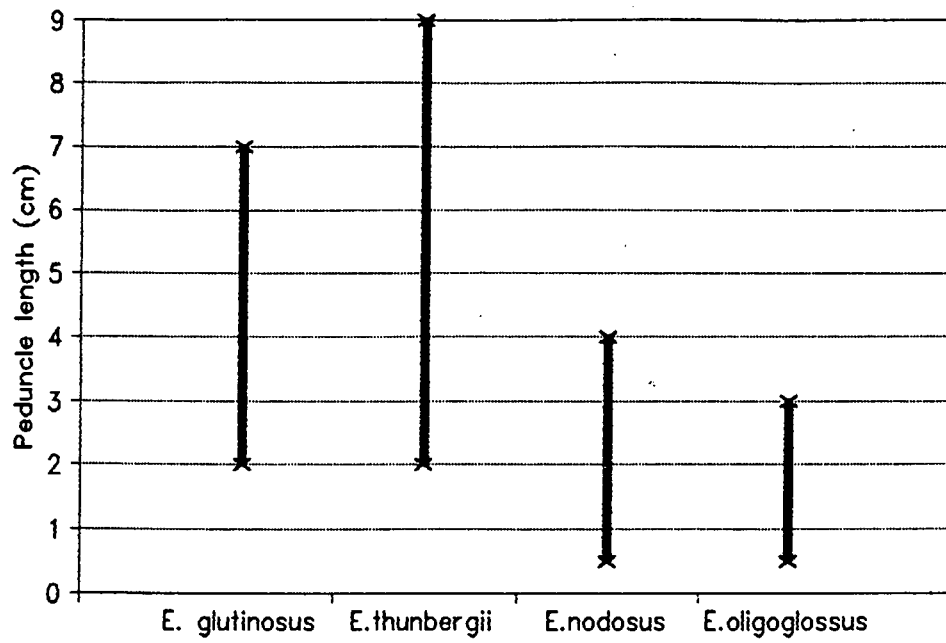


Fig 42: Peduncle length in *Euryops glutinosus* and associates

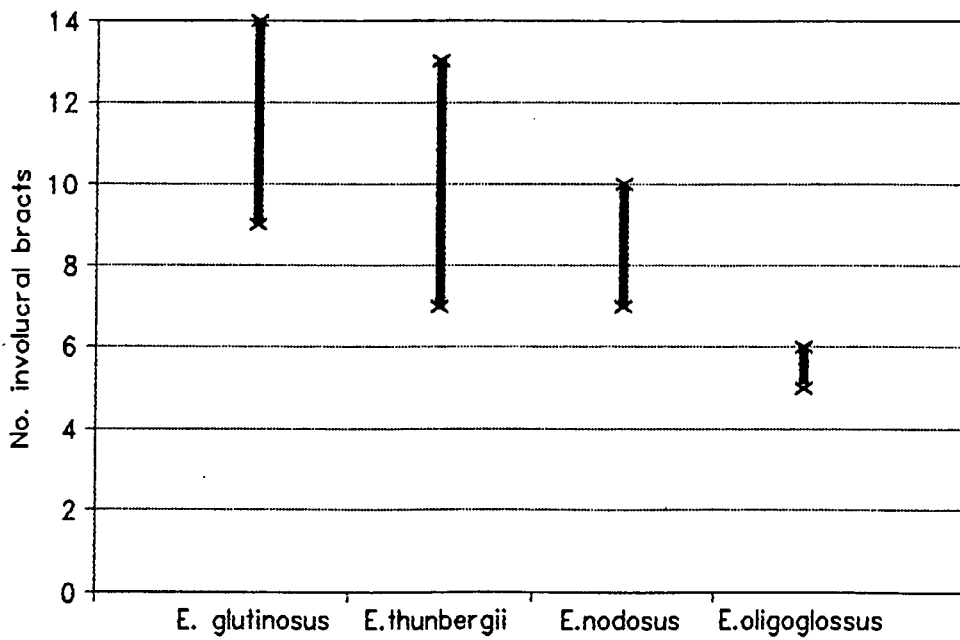


Fig 43: Number of involucre bracts in *Euryops glutinosus* and associates

Erica costatisepala

E. costatisepala is closely related to two other species which grow at fairly high altitudes, *E. keerombergensis* and *E. blesbergensis*, and together these three species are related to the widely spread *E. calycina* (Oliver pers com).

The change in character states is illustrated in Fig 44. All three high altitude species have a fairly low habit compared to *E. calycina*. *E. costatisepala* is approximately half as tall as *E. calycina* (Fig 45) (Baker 1971). Unlike *E. calycina* and *E. blesbergensis*, *E. costatisepala* does not have hairs on the branches. The leaves of *E. costatisepala* are approximately half as long as those of *E. calycina* (Fig 46).

All of the high altitude species have only a few flowers. These vary in shape and size among all of the species (Fig 47). Two consistent differences between *E. costatisepala* and the other species which were examined are firstly, in the bracts, which are lanceolate in *E. costatisepala* and ovate in all the other species and secondly in the flower shape, narrow in *E. costatisepala* and campanulate in *E. calycina*. In addition to this the anthers of *E. costatisepala* have large crests.

The flowering time of *E. costatisepala* is much narrower than for *E. calycina*. *E. costatisepala* flowers in December and January while *E. calycina* flowers is recorded as flowering from June until December.

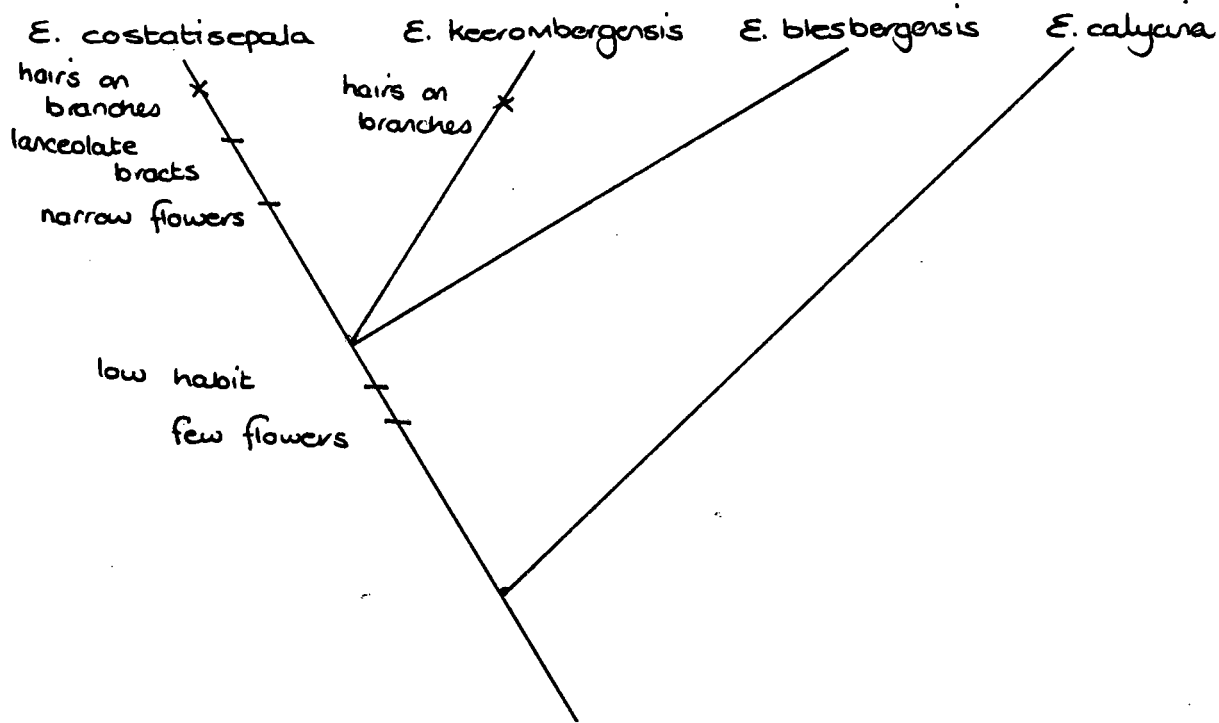


Fig 44: A cladogram illustrating the character state changes for *Erica costatisepala*, *E. keerombergensis*, *E. blesbergensis* and *E. calycina*.

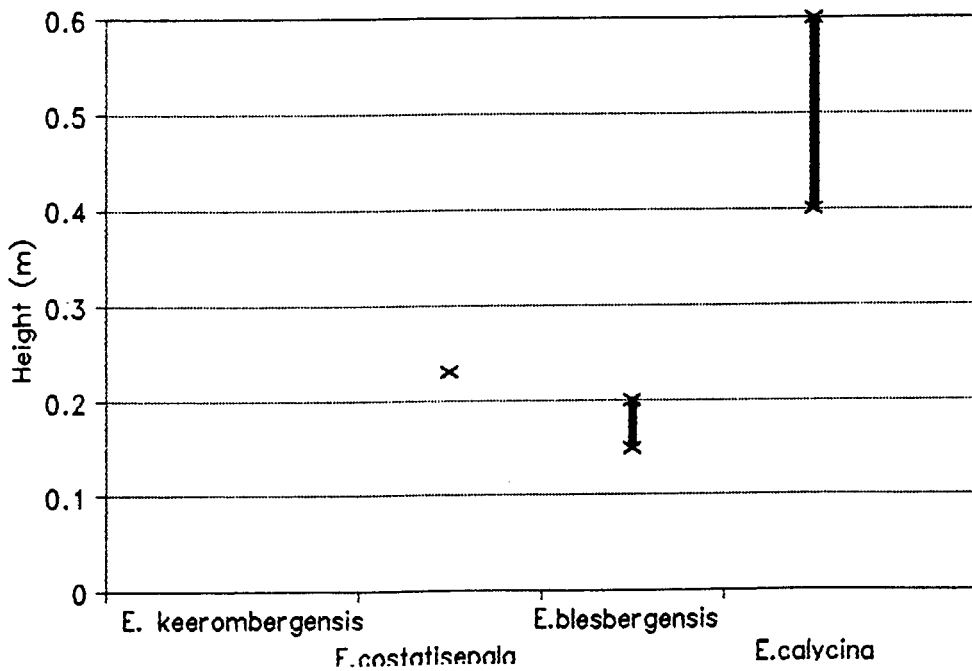


Fig 45: Height variation in *Erica costatisepala* and associates

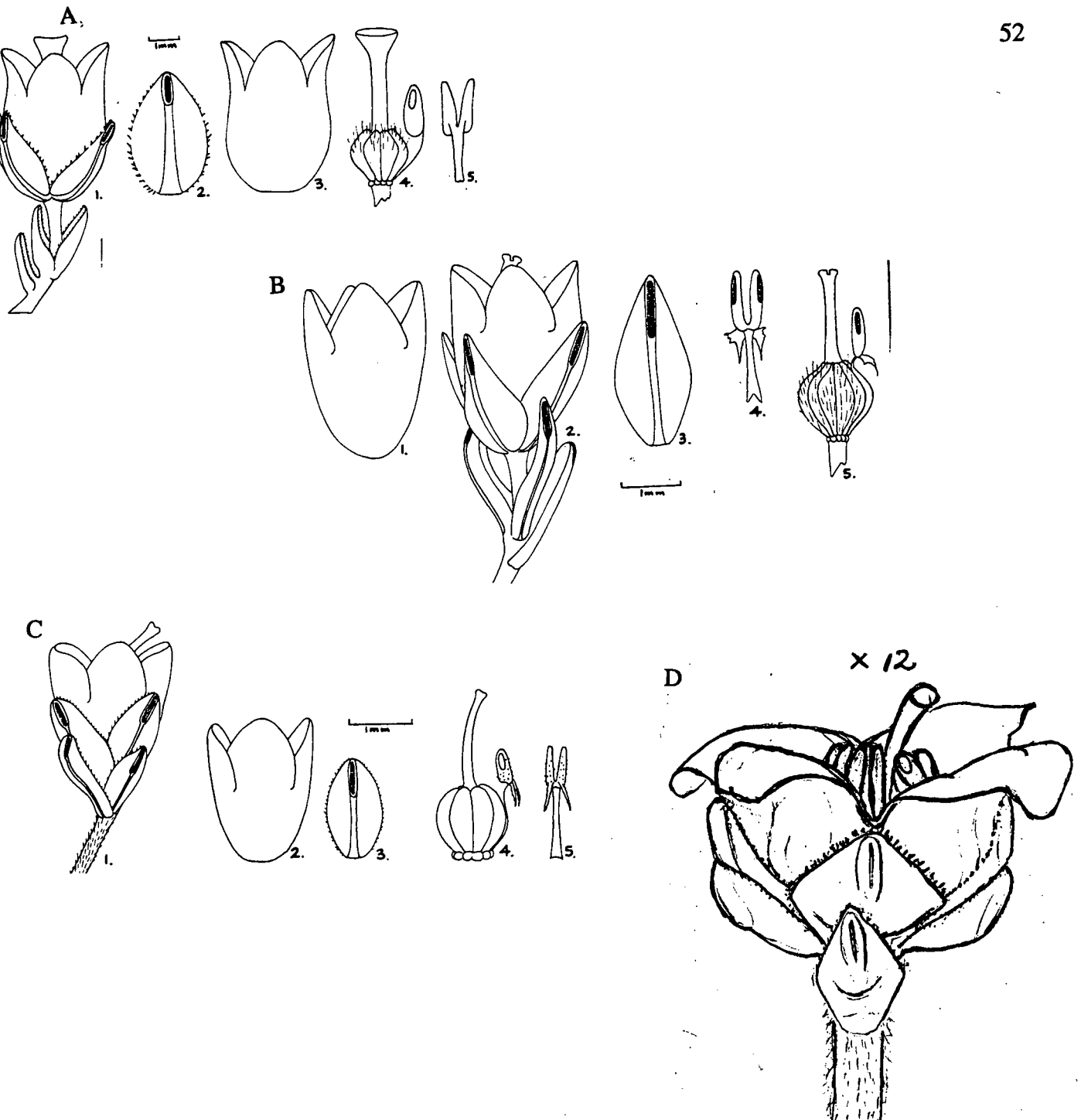


Fig 47: A, *Erica blesbergensis*, 1. Flower, 2. Sepal, 3. Corolla, 4. Gynoecium and stamen, 5. anther back view. B, *Erica costatisepala*, 1. Corolla, 2. Flower, 3. Sepal, 4. Anther, front view, 5. Gynoecium and stamen. C, *Erica keerombergensis* 1. Flower, 2. Corolla, 3. Sepal, 4. Gynoecium, 5. Anther, back view. (Baker 1971) D, *Erica calycina*, flower (herbarium specimen 3602 drawn by Esterhuysen 1939).

Erica torinbergensis

This high altitude species is thought to be a variation of *E. incarnata* (Oliver pers com). *E. incarnata* is a widespread species with an altitude range of 900-1500m.

E. torinbergensis is a tall seemingly spindly plant, compared to *E. incarnata* which is about half as tall (Fig 48) and a fairly well branched plant. The branches of *E. torinbergensis* are hairy with persistent leaf cushions.

The only other information that was available for *E. incarnata* described the leaves as small and tightly placed around the branches. The leaves of *E. torinbergensis* are approximately 3-3,5mm long on a petiole which is approximately 1,5-2mm long.

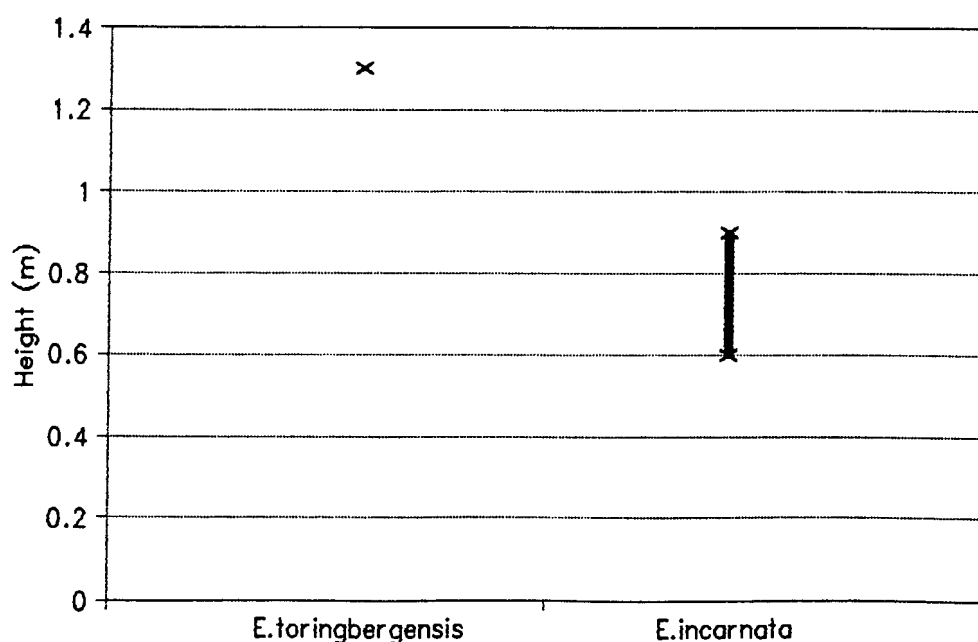


Fig 48: Height variation in *Erica torinbergensis* and *E. incarnata*

DISCUSSION

There are a few general trends which occur in most of the species (Table 1). The first of these is in plant height. Almost all of the alpine species are shorter, or fall into the lower height range of the nearest low altitude relatives (Figs 5, 11, 16, 17, 24, 36, 45). There is, however, one interesting exception which *Erica toringbergensis* which is considerably taller (Fig 48) and more spindly, than it's low altitude associate. While the difference in plant height is clear between the different species the range of heights makes it very difficult to classify them even roughly in a similar manner to that used by Squeo et al (1991).

An attempt at this identifies three of the species, namely the *Phyllica's* and *Erica costatisepala*, as small shrubs. The grass, *Pentameris swartbergensis* and the restio, *Thamnochortus papyraceus* fall into a similar height category as these shrubs. However, while *Erica toringbergensis* could be classified as a tall shrub, *Leucadendron dregei* falls somewhere in between this and the height category of the small shrubs. Similarly, *Euryops glutinosus* is difficult to classify, varying in stature from a small shrub to verging on a small tree.

Related to height and growth form are the branching angles and number of nodes on a plant. Once again among the species which were examined, the *Phyllica's* and *Cliffortia's*, the majority followed the expected trend, more branches with a smaller or similar branching angle to the low altitude relatives (Figs 13, 14, 18, 19, 26, 27). However, there was one exception, *Cliffortia crassinervis*, which had virtually the same number of branches and branch angle as the low altitude associate *P. subsetacea*. From the herbarium specimens and

the description it appeared that this species tended to have a more sprawling habitat than the other species. In other words this species exhibited a different type of low growth form to the other shrub species having a more open habit close to the ground.

The second trend which is evident can be found in leaf length and width. Leaf length shows a relatively more robust trend. All of the species which were evaluated had smaller leaves than their relatives (Figs 6, 12, 17, 23, 28, 40) with only one exception, *Euryops glutinosus* (Fig 40). Similarly, *E. glutinosus* was the only species, of those for which measurements were available (Fig 7, 22 and 31), to have wider leaves than its low altitude relatives (Fig 41). The large leaves of *E. glutinosus* suggests that there is another factor or factors which are capable of overriding the effects of an alpine climate.

It could be argued that while smaller, narrower leaves are consistent with other alpine floras, they are in this case a preadaptation to the nutrient limited nature of the fynbos, especially since six of the ten species are ericoids. A group which by definition has sclerophyllous leaves. However, those species which are ericoids had smaller leaves than their ericoid relatives. In addition to this the small leaf size of *Leucadendron dregei*, a genus which usually has relatively broad leaves, and the grass, *Pentameris swartbergensis*, indicates that alpine conditions may play a role in determining leaf size.

In two of the ericoid species, *Cliffortia crassinervis* and *Cliffortia setifolia*, the leaf sheath length was substantially smaller than those of the low altitude relatives (Fig 32). It does not seem likely that this structure is directly affected by alpine conditions although it is possible, rather the size of the leaf sheath is may be connected to the size of the leaves and thus

reduction in leaf size leads to a reduction in leaf sheath size.

Unfortunately very little information is available for leaf thickness. In the descriptions of the *Phyllica* species it is suggested that the leaves of the high altitude species were thicker, "terete", than those of the low altitude relatives. In contrast the leaves of *Euryops glutinosus* were said to be less fleshy than the low altitude relatives. It would be interesting to discover which of the cell layers, if any, were different in the high and low altitude species.

Indication that they may differ is provided by information on the arrangement of the cell layers in the culms of *Thamnochortus papyraceus*. The culms of the restio are similar to the leaves of the shrubs in that they are the site of photosynthesis. In the low altitude relative of *T. papyraceus*, *T. amoena*, the epidermis, chlorenchyma and sclerenchyma layers are all approximately the same width (Linder 1993). However, in the high altitude species the chlorenchyma layer is wider than the epidermis while the sclerenchyma layer is narrower. It is not possible to say that this directly related to the impact of the alpine environment, but it is possible that it is related to the high levels of irradiance which are believed to exist. In leaves an adjustment in the size of certain layers may also be related to strengthening or temperature control.

General trends in leaf shape can also be observed amongst the species with several of them having concave, revolute or keeled leaves. Surprisingly, only the leaves of the two *Phyllica* sp. were evidently more hairy than those of the low altitude relatives, although the base of the leaf of *Pentameris swartbergensis* was sparsely pubescent while that of the low altitude relative was not. Other interesting characters in the leaves of *Cliffortia crassinervis* and

Euryops glutinosus may also be adaptations to cope with high levels of solar radiance. The leaves of *Cliffortia crassinervis* were characteristically shiny, while those of *Euryops glutinosus* were exceptional in that they had resiniferous vein on the margins.

Information of floral characteristics is also limited. There is an indication that the flowers, or parts of the flowers do tend to be hairier than those of the low altitude relatives. For example, the male flower bud of *Leucadendron dregei* is densely tomentose while that of the low altitude relative is not. Certain parts of female flowers are also hairier in the high altitude species (Williams 1972). Parts of the flowers, i.e the corolla and the ovary, of the *Phyllica* sp. are also hairy.

Limited data on the size of floral parts indicates that while dimensions may be restricted by alpine conditions, other environmental and inherent biological factors probably play a greater role. For example, one would expect that large flowers would be energetically expensive to produce in a cold and nutrient poor environment, thus floral parts would remain the same size, or could become reduced possibly accompanied by a change in pollination mechanism.

In certain cases this was indeed true, the sepal size of the *Cliffortia* sp. was the same length as those of the low altitude relative (Fig 33), while the bracteoles of the alpine species, *Cliffortia crassinervis*, were smaller than those of the relative (Fig 29). The inflorescence of *Pentameris swartbergensis* illustrates this point as well being more compact than that of *P. thuarii*. Similarly, the female inflorescence of *Leucadendron dregei*, is clearly shorter than the low altitude *L. rubrum*, although they do have similar widths (Fig 8 and 9). However, the male inflorescence of *Leucadendron dregei* is larger than those of the low altitude species

(Fig 8 and 9), but the nectar found in these flowers and their strong scent, indicates that they are entomophilous (Williams 1972).

Likewise, *Euryops glutinosus*, has a much wider and shallower inflorescence than any of the associates. These are situated on peduncles which are longer (Fig 42) and wider (Fig 35) than those of the low altitude relatives. Within the inflorescence there is a greater number of disc florets (Fig 36) and ray florets (Fig 37). The variation in disc floret number tends to be greater in *Euryops glutinosus*.

Interestingly enough the shape of the flowers of the high altitude species is fairly consistent with that of the low altitude species. There is, of course, one exception and that is *Erica costatisepala* and associates which show considerable variation from one another and especially from the low altitude relative *E. calycina* (Fig 47). The extent of the influence of alpine conditions on flower shape is not known. Presumably it is related, indirectly, through environmental pressures on the pollinators or possibly more directly through energy budgets.

Genetics is one aspect of the alpine flora which has been neglected. The possibility that there are some interesting differences and scope for further study is given by the chromosome numbers of *Euryops glutinosus*. Low percentages of polyploidy expected in Mediterranean climates because of the high percentages of woody species which usually do not exhibit polyploidy, higher levels being found in herbaceous perennials (Stebbins 1950). Original theories hypothesised that polyploids were more tolerant of extreme ecological conditions than their diploid relatives, however, this has only be found to be true for those polyploids

which are the result of crossing between subspecies or races. Exactly how *Euryops glutinosus* fits into the present understanding of the relationship between polyploids and diploids is not clear, however, it appears to be the perfect opportunity to obtain information on the relative tolerance and success of diploids and polyploids. This could be achieved through careful analysis of morphological features and interrelationships in a closely related group of diploids and polyploids with particular reference to their climatic and ecological preferences.

CONCLUSION

This sub sample of Cape high altitude flora has highlighted a number of trends that may be present in this community. Firstly the plants do tend to be smaller than the low altitude relatives, but there are exceptions, *Erica toringbergensis*, which is much taller than its low altitude relative and *Euryops glutinosus* the height of which varies a great deal.

In terms of growth form certain of the shrubs tend to be compact with a high number of branches and a low branching angle, but there is an exception *Cliffortia crassinervis* which has fewer branches and a high branching angle indicating that it has a sprawling habit. Both these forms are in stark contrast to the spindly *Erica toringbergensis*.

The majority of the leaves of high altitude species follow the same pattern as that of plants from other high altitude areas, having smaller narrower leaves. Information on species such as *Phyllica* sp. and *Euryops glutinosus* indicates that there is a possible difference in the arrangement of the tissue layers. This information has important implications for gaining

understanding of cold tolerance and the effect of high irradiation levels. Connected with high irradiation levels are adaptations such as hair, shiny, waxy leaves and possibly resin. The relative effectiveness of each of these mechanisms would provide insight into the energy budgets of each of these species, and possibly others which may have similar or different mechanisms.

The trends detected in this study indicate that there may well be a classifiable alpine community within the fynbos biome. Further confirmation of this in terms of ecophysiological studies would be interesting and could lead to a wealth of information on how mediterranean sclerophylls and associated species cope with alpine conditions. In terms of the ecology of the community, the situation offers the perfect opportunity to investigate the interaction between nutrient limitations and extreme climatic conditions. Generally speaking there is much which remains to be learnt about the species which comprise this community.

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Table 1: General trends evident in the alpine species. + indicates that the feature in the alpine species is larger than in the relative, - indicates that it is smaller, / indicates that the measurements for the alpine species fall into the same range as the low altitude relative.

Species	Height	Node number	Branch angle	Leaf length	Leaf width	Flower size	Leaf thickness
<i>Leucadendron dregei</i>	-			-	-	m + f-	
<i>Phyllica stokoei</i>	-	+	-	-/	-		+
<i>Phyllica costata</i>	-	+	-	-/			+
<i>Pentameris swartbergensis</i>	-			-	-		stem +
<i>Thamnochortus papyraceus</i>	-					-	
<i>Cliffortia setifolia</i>	+/-	+	+/-	-/	-		
<i>Cliffortia crassinervis</i>		-	-	-/	+/-		
<i>Euryops glutinosus</i>	-/			+/	+	+	-
<i>Erica costatisepala</i>	-			-			
<i>Erica torinbergensis</i>	+			-			

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