

# A biosystematic study of *Pentameris* (Arundineae, Poaceae)

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**Keywords:** Arundineae, Arundinoideae, cladistics, conservation status, cytology, leaf anatomy, *Pentameris*, phylogeny, systematics

This paper is dedicated to the memory of Lucy K.A. Crook (née Chippindall)

## ABSTRACT

A biosystematic study of the endemic southwestern Cape grass genus *Pentameris* Beauv. is presented. Results of studies on the macro- and micromorphology, leaf blade anatomy and cytology are discussed and illustrated. The results of a cladistic study indicate that the genus is monophyletic, united by the synapomorphies of ovary and fruit characters. The conservation status of the taxa in the genus is assessed, and conservation status codes allocated. A key to the taxa in the genus is presented, and each species is described. Five new species, *Pentameris glacialis* N.P. Barker, *P. hirtiglumis* N.P. Barker, *P. oreophila* N.P. Barker, *P. swartbergensis* N.P. Barker and *P. uniflora* N.P. Barker, and one new subspecies, *P. longiglumis* (Nees) Stapf subsp. *gymnocolea* N.P. Barker, are described and illustrated.

## UITTREKSEL

'n Biosistematiese ondersoek van die endemiese Suidwes-Kaapse grasgenus *Pentameris* Beauv. word aangebied. Resultate van ondersoek op die makro- en mikromorfologie, blaarskyfanatomie en sitologie word bespreek en geïllustreer. Die resultate van 'n kladistiese ondersoek dui daarop dat die genus monofileties is, verenig deur die afgeleide kenmerke van die vrugbeginsel en vrug. Die bewaringstatus van die taksons in die genus word geraam en bewaringstatuskode toegeken. 'n Sleutel tot die taksons in die genus word aangebied, en elke spesie word beskryf. Vyf nuwe spesies, *Pentameris glacialis* N.P. Barker, *P. hirtiglumis* N.P. Barker, *P. oreophila* N.P. Barker, *P. swartbergensis* N.P. Barker en *P. uniflora* N.P. Barker, en een nuwe subspesie, *P. longiglumis* (Nees) Stapf subsp. *gymnocolea* N.P. Barker, word beskryf en geïllustreer.

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## INTRODUCTION

The genus *Pentameris* Beauv. occurs in the winter rainfall region of the Cape Province, South Africa, where it is restricted to soils derived from Table Mountain Sandstone or the shale bands associated with this geology. It may therefore be considered an endemic of the Cape Flora (Goldblatt 1978). All known species of the genus are perennial C<sub>3</sub> plants.

The genus was erected by Palisot de Beauvois in 1812 on the basis of a specimen sent to him by Du Petit-Thouars. No collection number or locality is provided in this description. However, it is known that Du Petit-Thouars,

a French traveller and botanist, obtained material from the Cape during a visit in February 1793 (Gunn & Codd 1981). The genus name is Greek, meaning 'five parts', probably a reference to the apical region of the lemma which is divided into what Palisot De Beauvois (1812) described as four bristles (two of which may be more accurately described as lemma lobes) and a central awn.

Only one species is mentioned under the generic description: *P. thuarii* Beauv. (Palisot de Beauvois l.c.). This single species was subsequently placed in *Danthonia* DC. by a number of early taxonomists (Desvaux 1831; Nees 1841; Steudel 1855; Durand & Schinz 1895), whereas others retained it in the genus *Pentameris* (Roemer & Schultes 1817; Kunth 1833, 1835). Stapf (1897) expanded the genus *Pentameris* to include four other taxa, all characterised by fruit with a free pericarp. Chippindall (1955) retained the genus in this format, but incorporated two nomenclatural corrections published by Schweickerdt (1938). Gibbs Russell *et al.* (1985) list these five taxa as *Pentameris dregeana* Stapf, *P. longiglumis* (Nees) Stapf, *P. macrocalycina* (Steud.) Schweick., *P. obtusifolia* (Hochst.) Schweick. and *P. thuarii* Beauv.

However, the unusual leaf blade anatomy (Ellis 1985d; Barker 1990) and fruit morphology (Barker 1986, 1989, 1990) of *P. obtusifolia* places this species within the genus *Pseudopentameris* Conert (Barker in prep.a). *Pentameris obtusifolia* is therefore not further considered in this study.

## MORPHOLOGY

The basal parts of all the species are woody, but the woolly and/or swollen underground parts that occur in certain species of *Pentastichis* (Nees) Spach and *Merxmüllera* Conert are absent. The species are generally tufted, with stems sometimes branching, but generally only

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in the basal quarter. In older plants branching results in a cushion or a bush-like growth form. These branched structures are referred to here as 'culms', although they do not possess typical culm anatomy. Instead, the anatomy resembles that of a rhizome (H.P. Linder pers. comm.). The term 'aerial culm' will be used here to denote the annually produced, few-noded structure which terminates in an inflorescence.

In *P. thuarii*, branching can occur at any node on the culm, and some specimens comprise long, decumbent, scandent or vertical culms with many shorter vegetative and reproductive branches arising from the upper regions. Such branching from cauline innovation shoots results in an 'evergreen', perennial plant, which takes the form of a divaricate herb. This branching pattern might allow the plant to grow taller than species possessing only basal innovation shoots (Linder & Ellis 1990a). Branching and growth from cauline innovation shoots is also found in a few species of *Pentaschistis*, *Chaetobromus* Nees and *Pseudopentameris*. In the latter genus the branched condition may approximate the extreme development found in *Pentameris thuarii*.

The leaf structure of *Pentameris* is typical of the Arundineae. The leaf sheaths are persistent, although the leaf blades may not be. The older culms are thus frequently covered in the remains of sheaths from previous years of growth. These sheaths may be appressed to or free from the culm. The sheath indumentum varies between the species, ranging from glabrous to pubescent along the margins to uniformly pubescent (and sometimes woolly). These sheath characters are also found in other arundinoid genera. The ligule is, as in many other arundinoid genera, a fringe of hairs. The sheath mouth may be bearded in some species, but this, too, is not unusual. Two species, *P. thuarii* and *P. longiglumis* have fairly well-developed auricles. In the former species these are a characteristic purple or brown colour. The leaf blade varies in its internal and epidermal anatomy. Many characters are shared, although not consistently so, with taxa of *Pentaschistis*, and (to a lesser extent) *Merxmuellera*. Ellis (1985c, 1986; Ellis & Linder 1992), on the basis of leaf anatomical studies, is of the opinion that *Pentameris* is closely allied to *Pentaschistis*.

The inflorescence is a panicle which varies from compactly lanceolate to laxly globose. It must, however, be noted that the panicles of all the species are open and somewhat lax during the period of pollination. Before and after this period, the panicles contract to a lanceolate shape. Panicle shape is therefore difficult to describe as it depends on the reproductive phase of the plant at the time of observation or collection. This variation is also found in numerous other arundinoid taxa, for example *Pentaschistis* (Linder & Ellis 1990b). No spicate panicles are known from this genus.

The spikelets are two-flowered (one exception; *P. uniflora*), and the partially developed remains of a third floret may sometimes be present, particularly in *P. macrocalycina*. The two-flowered state is shared with the vast majority of the species in *Pentaschistis* (Linder & Ellis 1990b). When two florets are present, the basal floret is sessile, the apical floret pedicellate. The florets are otherwise morphologically identical, and both are hermaphroditic and fertile, as in *Pentaschistis*.

The lemma is generally nine- to eleven-nerved. The majority of the veins anastomose in the basal region of the central awn and the two lateral bristles. The lemma lobes on the outside of the bristles are variously adnate to the bristle, ranging from free (in *P. thuarii*) to almost completely adnate (in *P. macrocalycina*). The shape of this lobe is also variable, being acuminate, acute or dentate. Similar variation is found in *Pentaschistis* (Linder & Ellis 1990b). The central awn is geniculate in all species, the basal portion is flattened but twisted and shorter than the attenuating apical portion. The margin of both the basal and apical regions of the awn are finely serrated. This awn structure is shared with genera such as *Pentaschistis*, *Pseudopentameris*, *Merxmuellera* and *Chaetobromus* as well as the non-African genus *Danthonia*.

The palea is bicarinate, apically bilobed and pubescent between the veins. It exceeds the lemma body in length, but seldom exceeds the lemma lobes, a situation also found in species of *Pentaschistis*, *Pseudopentameris* and *Merxmuellera*.

The lodicules in certain arundinoid genera have been examined and used for taxonomic purposes (Tomlinson 1985). The lodicules of *Pentameris* are generally glabrous and cuneate, but differences have been noted in some specimens of *P. swartbergensis* and *P. distichophylla*. The lodicules in these species are generally apically ciliolate, and sometimes an arm-like extension arising from one of the lateral margins is present. Ciliolate lodicules are also known from species of *Pseudopentameris*, *Merxmuellera* and *Pentaschistis* (Linder & Ellis 1990b).

All species of the genus have three anthers, which are usually purple in colour. These vary in size in relation to the size differences of the florets, but this has not been incorporated as a taxonomically meaningful character.

The above morphological features can therefore not be used to clearly differentiate *Pentameris* from several other southern African arundinoid genera, notably *Pentaschistis*. There are, however, two micromorphological features which have, in the past, been used to distinguish *Pentameris* from all other southern African arundinoids. Both features are characters of fruit and ovary. Firstly, the fruit is an achene, and secondly, the fruit of all taxa possesses a dense tuft of hairs at the apex of the ovary. These hairs are retained in developing and mature fruit where they become reluctantly deciduous.

Stapf (1897: 512) separated *Pentameris* from *Pentaschistis* on the basis of fruit morphology: the crustaceous pericarp and free seed. He described the structure of the ovary as being '... so alike in the five species of this genus that it is very probable that they agree in the peculiarities of the ripe fruit which is known only in *P. thuarii*' and further stated that '... there is in *Pentaschistis* no approach to the characteristic structure of the ovary and the fruit of *Pentameris*.'

This unusual fruit type, the achene, is described by Clayton & Renvoize (1986) as a fruit with a thin, hard, free pericarp attached to the ovule in the region of the hilum. It is unusual in the tribe Arundineae, and is found in only three of the approximately 40 arundinoid genera worldwide. The fruits of the remaining arundinoid genera are described as caryopses or as caryopses with a variably separable pericarp (Clayton & Renvoize *l.c.*).



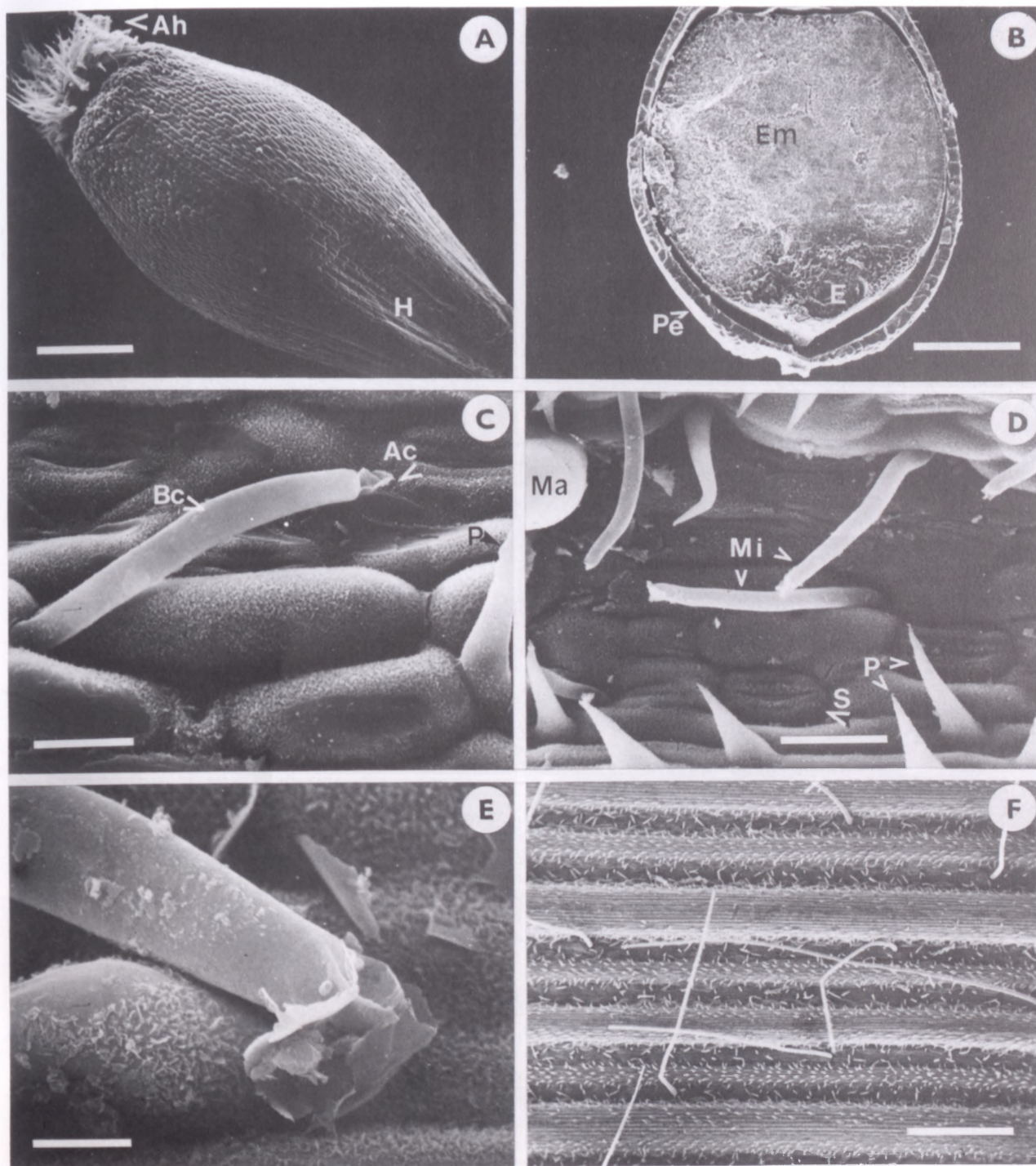


FIGURE 1.—*Pentameris*: A, B, SEM of fruit; C–F, SEM of leaf blade. A, *P. hirtiglumis* N.P. Barker, whole fruit, note colliculate surface features and apical hairs. B, D, F, *P. thuarii* Beauv.: B, longitudinal section; D, furrow on adaxial surface; F, adaxial surface showing ribs over vascular bundles and open furrows between ribs. Note abundance of conventional macrohairs and slightly inclined, sparsely distributed prickles. C, *P. distichophylla* (Lehm.) Nees, adaxial microhair. E, *P. oreophila* N.P. Barker, magnified view of deflated apical cell of adaxial microhair. Ac, small deflated apical cell; Ah, apical hairs; Bc, long basal cell; E, embryo; Em, endosperm; H, hilum; Ma, macrohair, basal portion; Mi, microhair; P, prickles; Pe, free crustaceous pericarp, seed within; S, stomata. Scale bars: A, 390  $\mu\text{m}$ ; B, 541  $\mu\text{m}$ ; C, 19  $\mu\text{m}$ ; D, 33  $\mu\text{m}$ ; E, 6  $\mu\text{m}$ ; F, 550  $\mu\text{m}$ .

Scanning electron microscope (SEM) studies on the fruit of *Pentameris* have shown the pericarp to be sculptured (Barker 1986, 1989, 1990) as illustrated here in Figure 1A, and partly or almost completely free from the seed coat when viewed in section (Barker 1990) as shown here in Figure 1B. The colliculate surface sculpturing is also unique among the fruit of the southern African genera of the Arundineae (Barker in prep. b).

The second feature that characterises the genus is the presence of hairs on the apical region of the ovary and fruit. This was first observed by Palisot de Beauvois (1812), who described the fruit as being crowned with stellate hairs. Nees (1841) also noted this feature in his descriptions of *P. thuarii* and the taxon now known as *P. macrocalycina*. Phillips (1931) considered these hairs to be characteristic of the genus, using this feature in his



TABLE 1.—Salient anatomical characters differentiating the species of *Pentameris*. All measurements in micrometres

Character	<i>distichophylla</i>	<i>glacialis</i>	<i>hirtiglumis</i>	<i>longiglumis</i>	<i>macrocalycina</i>	<i>oreophila</i>	<i>swartbergensis</i>	<i>thuarii</i>	<i>uniflora</i>
Rib shape in T/S	1' & 3' squared	1' & 3' round	1' squared, 3' rounded	1' squared, 3' rounded	1' rounded, 3' conical	1' rounded, 3' conical	1' & 3' rounded	1' & 3' rounded	1' squared, 3' rounded
Relative depth of 1' and 3' ribs	1' = 3'	1' = 3'	1' > 3'	1' > 3'	1' > 3'	1' > 3'	1' = 3'	1' = 3'	1' = 3'
Leaf shape in T/S	rolled	rolled	rolled	'U'-shaped	acicular	permanently rolled	rolled	flat, 'V'-shaped or rolled	rolled
Depth of furrows between ribs	shallow	shallow	deep	deep	deep	deep	shallow	shallow	shallow
Width of furrows	narrow	wide	narrow	narrow	narrow	narrow	wide	wide	narrow
Shape and nature of abaxial 1' VB sclerenchyma girdler	trapezoid and discrete	trapezoid and discrete	trapezoid, continuous with hypodermal band	trapezoid, continuous with hypodermal band	trapezoid, continuous with hypodermal band	trapezoid, continuous with hypodermal band	equidimensional, discrete	equidimensional—trapezoidal, discrete	trapezoid, discrete
Nature of sclerenchyma cap at leaf margin	poorly developed, discrete	poorly developed, discrete	well developed, continuous with hypodermal band	well developed, continuous with hypodermal band	poorly developed, continuous with hypodermal band	well developed, continuous with hypodermal band	poorly developed, discrete	poorly developed, discrete	poorly developed, continuous with hypodermal band
Nature of leaf blade near edges	unswollen	unswollen	swollen	swollen	unswollen	unswollen	unswollen	unswollen	unswollen
Abaxial epidermal cell width:									
mean	21.9	25	29.6	40.0	30.4	19.6	23.7	20.8	36.5
std. deviation	4.39	n/a	4.03	5.02	5.24	3.17	4.49	4.42	3.57
range	12–29	n/a	24–35	32–48	22–44	14–25	20–30	13–28	32–42
sample size	19	1	7	8	21	10	3	10	4
Mean blade width at midrib	201	171	250	345	366	301	166	231	165
std. deviation	25.0	n/a	28.7	47.5	57.1	48.4	16.5	29.6	5.6
range	142–236	n/a	200–289	274–444	307–506	185–385	153–189	188–282	156–171
sample size	19	1	7	8	21	10	3	10	4
Abaxial macro-hairs	sometimes present	sometimes present	sometimes present	absent	absent	absent	absent	absent	absent
Adaxial macro-hair presence and type	conventional and filament types	conventional type	conventional type	filament type	filament type	filament type	conventional and filament types	conventional type	filament type
Adaxial prickle type; structure; orientation and density	needle-like; knobbed; erect; sparse	inflated; erect with tips bent over; dense	inflated; with basal collar; appressed to surface; dense	inflated; appressed to surface; dense	inflated; tips curling over; erect; dense	long, needle-like; erect with basal collar; dense	inflated; erect with tips bent over; sparse	inflated; erect with tips slightly bent; sparse	inflated; erect with tips slightly bent; dense
Adaxial prickle length	33	32–39	52–64	79–83	44	122	32–39	37–45	44
Mean adaxial micro-hair length	72	95.7	122	142	109	105	88	71	45
ranges	68–76	71–116	105–145	129–156	101–118	103–108	75–101	68–75	45
sample size	5	4	3	3	2	2	2	3	1

1' = primary vascular bundles; 3' = tertiary vascular bundles.

key to the grass genera. Chippindall (1955) describes *Pentameris* as having an ovary which is hairy on top, the hairs being deciduous. This character was also used in the key to the genera of the tribe Danthoneieae. The nature of these unusual structures has been clarified to a certain extent by Barker (1986, 1989, 1990), but their ontogeny and function is not known. These structures, visible on the apex of the fruit (Figure 1A) appear to be unicellular, and arise from the apex of the ovule around the base of the styles.

#### LEAF BLADE ANATOMY

Leaf blade anatomy has contributed much to the tribal and subfamilial classification of the grass family. However, within the tribe Arundineae, the variation of observed anatomical characters led Renvoize (1981) to comment that the arundinoid genera could not be readily divided into the tribal groups on the basis of their leaf anatomy, and he concluded that other characters such as spikelet morphology would have to be used to divide the subfamily further.

The leaf blade anatomy of many of the southern African arundinoid genera has been documented (Schweickerdt 1942; De Wet 1956; Conert & Tuerpe 1969; Ellis 1980; 1981; 1985a–d).

Ellis (1985a–d, 1986) examined many specimens of the then five known and one undescribed species of *Pentameris*. Additional anatomical information for the new and undersampled species was obtained by sectioning a small portion of leaf material obtained from herbarium specimens. This material was heated in a soapy solution prior to sectioning by means of a sledge microtome. Sections thus obtained were 30 to 50 microns thick. The sections were stained in safranin and fast green and mounted in Euparal.

To complement the data obtained from the work of Ellis (1985a–d, 1986) and additional sections, leaf material from 95 of these previously studied specimens was prepared from herbarium specimens, mounted on two-sided tape, coated in gold-palladium and examined using a ISI-SX-25 scanning electron microscope. The salient anatomical features obtained from the SEM and light microscope studies are presented in Table 1.

The abaxial surface is relatively uniform throughout the genus. It is generally smooth, with ribs observed only occasionally. No abaxial microhairs or stomata are present, and the silica bodies are usually rounded, but are tall and narrow in *P. thuarii* (Ellis 1985b–d, 1986). Abaxial macrohairs were occasionally present in specimens of some taxa (Table 1). The adaxial epidermis is far better endowed with micromorphological structures, including prickles, microhairs and macrohairs. These epidermal features are discussed in some detail below.

#### Microhairs

The genus *Pentameris* has a 'festucoid' type of leaf epidermis and leaf anatomy (implying the absence of abaxial microhairs), a poorly differentiated parenchyma sheath and evenly distributed chlorenchyma sheath (De Wet 1956). However, Renvoize (1986) places *Pentameris*

in the 'core' of the arundinoids, a group possessing microhairs, and describes the lower epidermis of *Pentameris* and *Pseudopentameris* as possessing long slender papillae which occasionally bear the remains of a small thin-walled apical cell. Clayton & Renvoize (1986) note that these structures distinguish these genera (and certain others such as *Cortaderia* Stapf and *Centropodia* Reichb. f.) from the rest of the Arundineae.

These 'papillae', as described by Renvoize (1986) and Clayton & Renvoize (1986), appear to differ from those described by Ellis (1979), who considers papillae to be protuberances of the cell wall rather than structures consisting of separate cells. From observations discussed below, it appears that Renvoize is using the term 'papillae' to describe what others, such as De Wet (1956) and Ellis (1979), call microhairs.

In addition to their structure and appellation, the recorded distribution of these microhairs is also controversial. Renvoize (1986, discussed above) reported them from the lower (abaxial) surface of specimens of *Pentameris*. However, Ellis (1985a–d, 1986) has found no evidence of abaxial microhairs on any of the specimens he has examined. Microhairs were however found on the sides and bottoms of the furrows of the adaxial surfaces of many specimens in all the taxa observed (Ellis *l.c.*). My observations on material examined, using the SEM, corroborate Ellis's observations, and it is clear that there are no abaxial microhairs present in any of the species of *Pentameris*.

As illustrated in Figure 1C, D and E, these microhairs are indeed bicellular, with a minute, deflated apical cell (shown at high magnification in Figure 1E). The length of the basal cell varies, but it is always very much longer than the apical cell. Microhairs with this structure were found on the adaxial surface of all specimens of all taxa in *Pentameris* (Barker 1990), and were also reported from certain species of *Pentaschistis* (Ellis & Linder 1992).

In addition to their distribution and morphology, variation in the size of the microhairs is taxonomically useful. The microhairs were measured from a number of SEM micrographs in order to determine whether or not there was any measurable size difference. These varying sizes are recorded in Table 1. Unfortunately, the limited sample size does not allow a statistically meaningful comparison to be carried out on this potentially very valuable taxonomic character.

The definite bicellular nature of these microhairs is comparable to those reported and illustrated by Amarasinghe & Watson (1988, 1989). However, microhairs with such unequal cell sizes have not been previously documented, and perhaps merit recognition as a separate type of microhair, the 'pentameroid' type.

#### Abaxial macrohairs

Abaxial macrohairs were only observed on the abaxial surface of some specimens of *Pentameris distichophylla*, *P. hirtiglumis* and *P. glacialis*. In all these taxa, the hairs were long, usually produced from the intercostal regions, had a distinctly swollen base and were surrounded by four or more cells, termed 'modified cells' by Ellis (1986). The taxonomic value of these structures is limited, as it



appears that they are not universally present throughout all specimens examined of all taxa. Inconsistent sampling (variation in the region of the leaf from which the samples were taken, or the age of the leaf blade) may explain the lack of macrohairs in some samples.

#### Adaxial macrohairs

Two different hair-like structures were found on the adaxial leaf surface in some of the taxa of *Pentameris*, sometimes both occurring on the same leaf. Conventional macrohairs, those which have a distinct basal structure comprised of modified cells, were frequently observed on the adaxial epidermis in *Pentameris thuarii*, *P. glacialis* and *P. distichophylla*, but were only occasional in *P. swartbergensis*. Figure 1F illustrates these hairs on the adaxial leaf blade surface in *P. thuarii*.

The second type of macrohair, termed here a 'filament', is a long, unicellular hair without any obvious basal differentiation or associated cells. Although no measurements were taken, the filament type of macrohair appeared to be shorter than the conventional type. Filaments were frequently observed in the bottom of the adaxial furrows in specimens of *P. macrocalycina* and occasionally in *P. distichophylla* and *P. swartbergensis*. In *P. oreophila*

filaments were only found in the furrow nearest the edge of the lamina. One of these filaments observed in *P. distichophylla* is shown in Figure 2A.

Adaxial macrohairs are of slightly greater taxonomic significance than abaxial macrohairs. The presence and type of macrohair are useful characters in *Pentameris*, although some variability within the species exists. It appears that the species with open or folded leaves (*P. thuarii*, *P. distichophylla* and *P. swartbergensis*) possess conventional macrohairs, whereas those taxa with permanently rolled or folded leaf blades have the second type of macrohair (*P. macrocalycina*, *P. oreophila*, *P. distichophylla* and *P. swartbergensis*). *P. swartbergensis* and *P. distichophylla* thus have both types of macrohair. It is possible that the filament macrohairs are conventional macrohairs that have lost the modified cells around the hair base. The loss of these modified cells may be related to the evolution of the permanently rolled leaf blade, where the adaxial surface is not as exposed to the environment.

#### Prickles

The adaxial surfaces of all the specimens examined had prickles of one form or another. These different prickle types (Table 1) are invariant within the taxa of the genus.

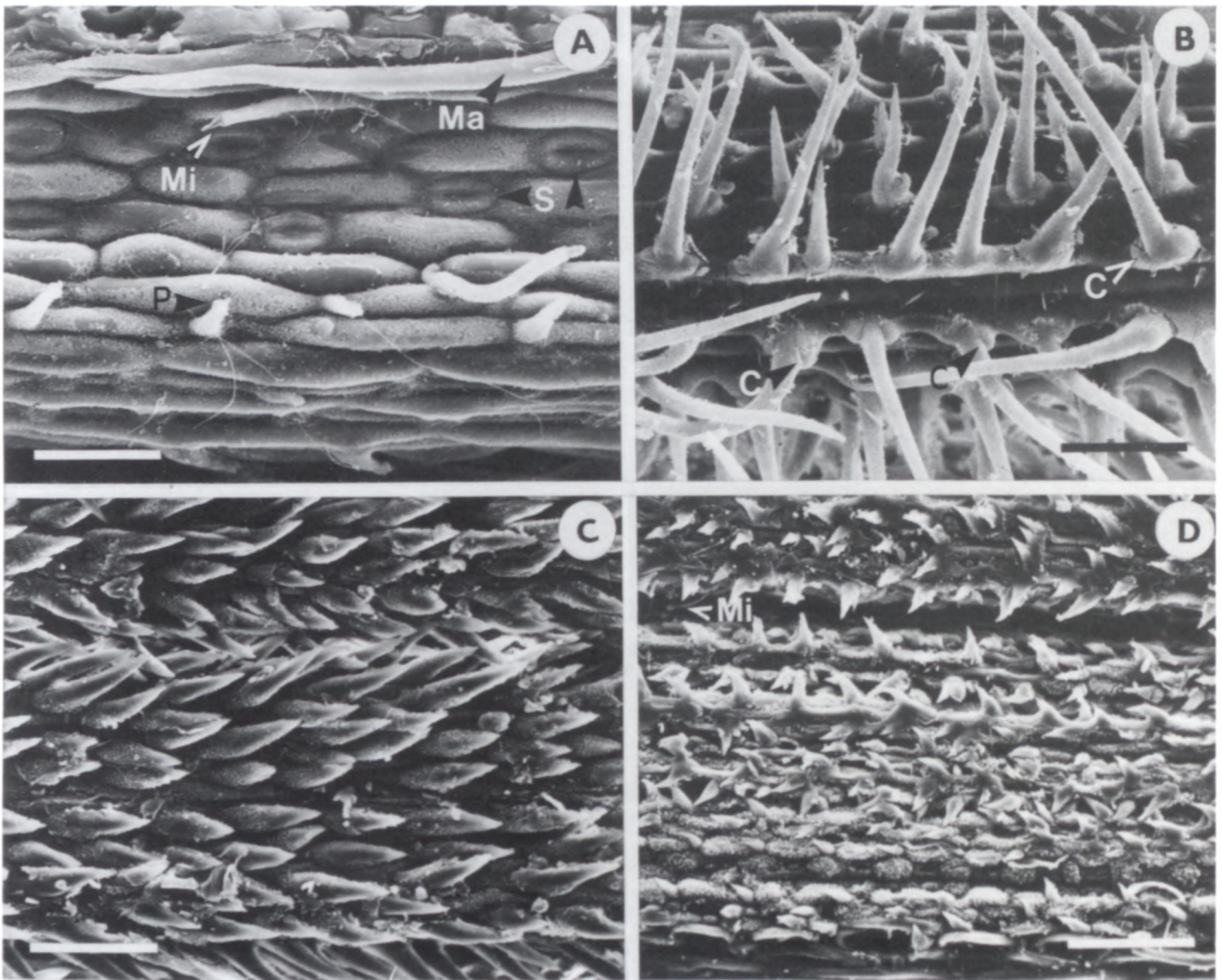


FIGURE 2.—Leaf blade SEM of *Pentameris*. A, *P. distichophylla* (Lehm.) Nees, adaxial surface; B, *P. oreophila* N.P. Barker, adaxial surface, note extreme length of prickles and presence of collar at base of each prickle; C, *P. longiglumis* (Nees) Stapf subsp. *gymnocolea* N.P. Barker, adaxial surface, note extreme density and inclination of prickles; D, *P. uniflora* N.P. Barker, adaxial surface showing prickles and small microhairs. C, collar; P, prickles; Ma, macrohairs; Mi, microhairs; S, stomata. Scale bars: A, 48  $\mu\text{m}$ ; B, 50  $\mu\text{m}$ ; C, 87  $\mu\text{m}$ ; D, 120  $\mu\text{m}$ .



Characters such as prickles density, distribution, orientation, length and structural differences are all taxonomically useful for distinguishing taxa within *Pentameris* (Figure 2A–D).

The prickles of *P. oreophila* are long and erect, with the tips sometimes bent or recurved. In addition to their unusual length, the prickles possess a basal collar-like structure (Figure 2B), a character shared with *P. hirtiglumis*. The prickles of the latter species are, however, much shorter, and are almost appressed to the surface of the leaf, a character shared with *P. longiglumis* (Figure 2C).

Of the remaining species, *P. macrocalycina*, *P. thuarii*, *P. glacialis* and *P. swartbergensis* have short, erect prickles, the tips of which may be bent or curved; are swollen basally, and the sides are convexly shaped; are densely distributed, particularly so in *P. macrocalycina*. The prickles of *P. uniflora* are also quite densely distributed and almost erect, as indicated in Figure 2D.

In contrast to the above, *P. distichophylla* has erect prickles that are almost straight-sided (as opposed to the slightly inflated convex sides of the prickles of the other taxa); they appear to have knobbed tips (Figure 2A) and are sparsely distributed over the adaxial surface, usually only on the edges of the ribs. Both the short, inflated prickle type and the erect, knobbed prickle type have also been observed in species of *Pentaschistis*, for example *P. colorata* (Ellis & Linder 1992). The long, collared prickles observed in *P. oreophila* are unique among the African Arundineae.

#### CYTOLOGY

Preliminary cytological studies have shown that *Pentameris distichophylla* has a chromosome count of  $2n=36$ , whereas *P. thuarii* has a count of  $2n=12$ . The latter figure has been corroborated by H. du Plessis (pers. comm.). Both these counts were obtained from meiotic material. *P. distichophylla* is therefore hexaploid. Such polyploidy is not unusual in the southern African Arundineae (see for example counts for *Merxmuellera*, *Pentaschistis* and other genera given by Du Plessis & Spies 1988; Spies & Du Plessis 1988; Spies *et al.* 1990).

These counts further support the contention that the base chromosome number for the Arundineae appears to be  $x=6$  (Davidse 1988), and not  $x=12$  as proposed by Clayton & Renvoize (1986). Despite the apparent similarities between *Pentameris* and *Pentaschistis*, the different base chromosome number of the latter genus ( $x=7$  in many of the known instances) does not suggest a close relationship between these two taxa. It is, however, possible that *Pentameris* evolved by means of aneuploidy from a pentaschistoid ancestor.

#### PHYLOGENY

The data presented in Table 1 were converted into a data set suitable for cladistic analysis. The anatomical characters were augmented by a few morphological characters, resulting in a data set of 26 characters (presented in Tables 2 & 3). Four of these characters are

TABLE 2.—Characters used in the cladistic analysis. 1' = primary vascular bundles, 3' = tertiary vascular bundles

#### Leaf blade characters (t/s)

1. Leaf blade shape in t/s: 0 = flat to curled, 1 = rolled, 2 = permanently rolled
2. 1' rib shape: 0 = squared, 1 = round
3. 3' rib shape: 0 = squared, 1 = round, 2 = conical
4. Relative rib depth: 0 = 1' = 3', 1 = 1' < 3'
5. Furrow depth: 0 = shallow (< 1/2 lamina thickness) 1 = deep
6. Furrow width: 0 = narrow, 1 = wide
7. 1' Abaxial sclerenchyma girder: 0 = discrete, 1 = continuous with hypodermis
8. Sclerenchyma cap on leaf margin: 0 = discrete, 1 = continuous with hypodermis
9. Leaf blade thickness: 0 = uniform thickness, 1 = swollen near margin
10. Abaxial epidermal cells: 0 = small (< = 25  $\mu$ m wide), 1 = inflated
11. Silica body shape: 0 = round, 1 = dumbbell-shaped

#### Adaxial epidermal characters

12. Conventional macrohair type: 0 = absent, 1 = present
13. Filament macrohair type: 0 = absent, 1 = present
14. Prickle type: 0 = inflated basally, 1 = markedly elongated, 2 = apically knobbed
15. Prickle orientation: 0 = erect, 1 = inclined/appressed
16. Prickle base: 0 = unornamented, 1 = collar present
17. Prickle density: 0 = sparse, 1 = dense
18. Microhair type: 0 = basal cell length >> apical cell length  
1 = basal cell length = apical cell length
19. Microhair length: 0 = short (< 60  $\mu$ m), 1 = long
20. Papillae: 0 = absent, 1 = present

#### Morphological characters

21. Growth form: 0 = unbranched, 1 = branched
22. Glands: 0 = absent, 1 = present
23. Lodicule margin: 0 = entire, 1 = ciliolate
24. Achene surface: 0 = rugose, 1 = colliculate, 2 = reticulate
25. Fruit type: 0 = caryopsis, 1 = achene
26. Ovary appendages: 0 = absent, 1 = present

multistate, and are treated as undirectional in the analysis. The 'ie' option of the cladistic package HENNIG86 version 1.5 was used to analyse the data. Using this method, the complete set of most parsimonious trees is found (Platnick 1989).

#### Choice of outgroup

*Pentaschistis* is the obvious outgroup, although the recognition of a particular species or group of species within this genus as the closest to the study group is not possible on an *a priori* basis. Six species of *Pentaschistis* were therefore chosen as possible outgroup taxa. These taxa were chosen on the basis of inferences made by Ellis in his anatomical papers (1985c, 1986), and after discussions with Dr H. P. Linder. The taxa chosen were *P. aspera* (Thunb.) Stapf, *P. colorata* (Steud.) Stapf, *P. curvifolia* (Schrad.) Stapf, *P. eriostoma* (Nees) Stapf, *P. glandulosa* (Schrad.) Linder and *P. tortuosa* (Trin.) Stapf.

Two of these taxa, the glandular *P. glandulosa* and *P. aspera*, were included because they were considered to be most dissimilar to the study group. Following the outgroup substitution method of Donoghue & Cantino (1984), these two least related glandular taxa were used as the initial outgroup to determine the relationships between the remaining taxa. Using this method, the single

TABLE 3.—Data used in cladistic analyses. Characters marked by asterisks above the data set were removed in the data set where *Pentaschistis curvifolia* was used as the outgroup (data set delimited below the dashed line). Characters appear in the order presented above. The question mark (?) indicates absent data

	Characters										26																
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25		
<i>Pentaschistis:</i>																											
<i>aspera</i>	0	1	1	1	0	0	0	0	0	0	1	0	0	0	0	0	0	1	1	0	1	1	0	2	0	0	0
<i>glandulosa</i>	0	0	1	1	0	0	0	0	0	0	1	1	0	0	1	0	0	1	1	0	0	1	0	2	0	0	0
<i>colorata</i>	1	0	0	1	0	0	0	0	0	1	1	0	1	2	0	0	0	1	0	1	?	0	1	2	0	0	0
<i>tortuosa</i>	1	0	0	1	0	0	0	0	0	1	1	0	0	0	1	0	0	1	0	1	0	0	0	2	0	0	0
<i>eriosoma</i>	1	0	2	0	0	0	1	1	0	0	0	0	0	0	1	0	1	0	1	0	0	0	1	2	0	0	0
<i>curvifolia</i>	0	0	1	0	1	0	0	0	1	0	0	0	0	0	1	0	0	0	1	0	1	0	1	2	0	0	0
<i>Pentameris:</i>																											
<i>distichophylla</i>	1	0	0	0	0	0	0	0	0	0	0	1	1	2	0	0	0	0	1	0	1	0	1	0	1	1	1
<i>glacialis</i>	1	1	1	0	0	1	0	0	0	0	0	1	0	0	0	0	1	0	1	0	1	0	0	1	1	1	1
<i>hirtiglumis</i>	1	0	1	1	1	0	1	1	1	1	0	0	0	0	1	1	1	0	1	0	1	0	0	1	1	1	1
<i>longiglumis</i>	1	0	1	1	0	0	1	1	1	1	0	0	0	0	1	0	1	0	1	0	1	0	0	1	1	1	1
<i>macrocalycina</i>	2	1	2	1	1	0	1	1	0	1	0	0	1	0	0	0	1	0	1	0	1	0	0	1	1	1	1
<i>oreophila</i>	2	1	2	1	1	0	1	1	0	0	0	0	1	1	0	1	1	0	1	0	1	0	0	1	1	1	1
<i>swartbergensis</i>	1	1	1	0	0	1	0	0	0	0	0	1	1	0	0	0	0	0	1	0	1	0	1	1	1	1	1
<i>thuarii</i>	0	1	1	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	1	0	1	0	0	1	1	1	1
<i>uniflora</i>	1	0	1	0	0	0	0	0	0	1	0	0	1	0	0	0	1	0	0	0	1	0	0	?	1	1	1

or few non-study group taxa found to be most closely related to the study group were then used to perform the final cladistic analysis on the data set from which the other outgroup taxa had been removed.

When the two distantly related taxa are used as the outgroup, one shortest length tree (l. = 60, c.i. = 50, r.i. = 67) is generated. In this tree (not presented), *P. curvifolia* is the taxon most closely related to the study group, and was used as the outgroup (the other *Pentaschistis* species were removed from the data set); the data were re-analysed after the autapomorphies and invariant characters had been removed. Once again, HENNIG86 found one shortest tree, presented in Figure 3 (l. = 34, c.i. = 64, r.i. = 70). The phylogeny of the study group in this tree is identical to that obtained in the initial tree (not presented) where the two glandular taxa are used as an outgroup.

#### Character distribution

In discussing the distribution of the characters on the tree, the characters from the complete database are used, although in the smaller data set (where *Pentaschistis curvifolia* is the outgroup) some are excluded because they are constant or autapomorphic. The distribution of the characters is shown on this tree (Figure 3).

The genus *Pentameris* is a monophyletic clade supported by the ovule and fruit characters; the apical appendages and the achene fruit type (char. 25 and 26, represented by the star in Figure 3).

Within *Pentameris*, two smaller clades are recognised. The first clade comprising *P. distichophylla*, *P. thuarii*, *P. glacialis* and *P. swartbergensis* is supported by the presence of conventional macrohairs on the adaxial surface (char. 12). Within this group, *P. distichophylla* is basal to the other three taxa and is characterised by the autapomorphies of knobbed prickles (char. 14), the rounded ribs of the tertiary vascular bundles (char. 3) and the rugose pericarp surface (char. 24). *P. thuarii*, *P. glacialis* and

*P. swartbergensis* share a flat leaf blade with wide furrows between the adaxial ribs (char. 6). *P. glacialis* and *P. thuarii* share a character that has arisen in parallel elsewhere: entire lodicule margins (char. 23).

The other clade within the genus is supported by the presence of dense prickles (char. 17), as well as other characters which undergo reversals in some of the lower

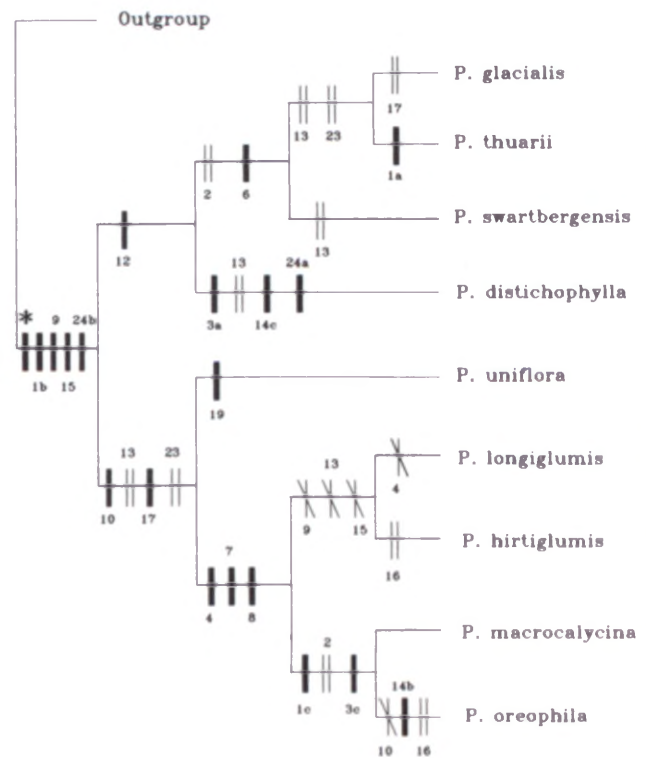


FIGURE 3.—Shortest cladogram produced by HENNIG86 using the 'ie' option. The outgroup used was *Pentaschistis curvifolia* (Schrad.) Stapf. Length = 34, c.i. = 64, r.i. = 70. Numbers represent characters (given in Tables 2 & 3; 'a' = state 0, 'b' = state 1 and 'c' = state 2). Solid bars represent apomorphies, parallel lines represent parallelisms and crosses represent character state reversals. Star at base of *Pentameris* clade represents apomorphic fruit characters: achene fruit type and presence of apical hairs on ovary.



clades (char. 10 and char. 13: abaxial epidermal cell width and presence of filament macrohairs respectively). *P. uniflora* is basal to this clade, characterised by the presence of one floret (data not included in data set) and short microhairs (char. 19). The remaining four taxa are united by the presence of a continuous hypodermal band of sclerenchyma which connects to the abaxial girders and cap on the leaf margin (char. 7 and 8), and primary ribs which are deeper than the tertiary ribs (char. 4). *P. longiglumis* and *P. hirtiglumis* both have enlarged or swollen leaf blade margins (char. 9), as does the outgroup. *P. macrocalycina* and *P. oreophila* share conical tertiary ribs (char. 3) and permanently rolled leaf blades (char. 1). The latter species is distinguished by the autapomorphy of long prickles (char. 14).

The low consistency index obtained from the analysis of the complete data set (c.i.=50) indicates the homoplasy present within the data set. This is further demonstrated by the increase in the value of the consistency index with the removal of all but the closest outgroup taxa (c.i.=64). Characters which are synapomorphies in the reduced data set are often homoplastic in the complete data set. For example, the unequal primary and tertiary vascular bundle thicknesses (char. 4) is a synapomorphic character for the *P. longiglumis*, *P. hirtiglumis*, *P. macrocalycina* and *P. oreophila* clade in the analysis based on the reduced data set. However, in the large data set, this character is also present in *Pentaschistis aspera*, *P. glandulosa*, *P. colorata* and *P. tortuosa*. Similar situations are found in other characters. Such homoplasy has probably been one of the root causes bedevilling the efforts of taxonomists, both past and present, to find an equitable classification for this group.

#### Taxonomic implications

The monophyletic status of *Pentameris* is supported by the fruit and ovary characters. However, as *Pentameris* is undoubtedly closely related to *Pentaschistis* (at least the eglandular taxa), the possibility that the latter genus is paraphyletic ought not to be ruled out. The observation that *Pentameris* was placed within, and terminal to, the *Pentaschistis* clade in the analysis of the complete data set provides some evidence as to this possibility. If this is the case, the name *Pentameris* would be retained for the monophyletic assemblage containing the taxa with the unique fruit characters, while other genera may have to be erected to accommodate monophyletic groups within the *Pentaschistis* assemblage. Only a detailed phylogenetic study of both *Pentaschistis* and *Pentameris* can provide sufficient data to properly test any hypothesis of paraphyly.

#### CONSERVATION STATUS

Of the previously known taxa of *Pentameris*, only *P. obtusifolia* is listed in the Red Data Book as a rare, threatened or extinct species, where it is listed under the synonym '*P. squarrosa*' (Hall & Veldhuis 1985). The conservation status for this taxon is given as 'uncertain'. However, as discussed above, the nomenclature of this taxon has been found to be confused, and *P. obtusifolia* is not included in the genus *Pentameris*.

Certain species of *Pentameris* nonetheless require consideration and recognition as taxa requiring conservation. Most of the new taxa described below are known from only a few localities, and should perhaps be regarded as 'rare'. However, as many of these taxa are found in inaccessible and thus rarely collected areas, the true distribution is not fully known. In addition to the problem of varying collecting intensity, the effects of fire on the germination, growth and re-establishment of fynbos grass species are poorly known. Linder & Ellis (1990a) discuss the various strategies that fynbos grasses have evolved to escape or adapt to fire. These authors note that grasses appear in abundance in the first few years after fire, but are then almost inevitably outcompeted by members of the Restionaceae and woody fynbos elements. The collection of fynbos grasses is therefore best carried out in areas that have been burnt within the previous few years. Such areas are not always attractive to collectors intent on obtaining other woody or non-graminoid taxa. Mature, woody fynbos may therefore hide many new or apparently rare grass species which are present as dormant seeds or underground vegetative structures. Actual species distributions may therefore be wider than presently known.

In assessing conservation status of the taxa of *Pentameris*, the categories proposed by Rabinowitz (1981) and modified by Karron (1987) will be used. These categories record the geographic distribution, demographic structure and habitat requirements in a two-state form: restricted or widespread, sparse or abundant, wide or narrow respectively. The demographic component can thus reflect, to a certain extent, the biological aspects of rarity of the taxa.

As the category of geographic distribution is scale dependent, it is used here at the level of magisterial districts or mountain ranges, whichever is more geographically homogeneous. The allocations of the species of *Pentameris* to these categories is presented in Table 4. Detailed descriptions of distributions and habitats are provided under individual species descriptions.

#### TAXONOMY

Taxonomic descriptions of all the taxa are presented. The dimensions given below for the lemma body, lemma

TABLE 4.—The modified Rabinowitz conservation categories allocated to each taxon of *Pentameris*. The allocation of these codes is based on field observations and data obtained from labels on herbarium specimens

<i>Pentameris</i>	Geographic distribution	Demographic structure	Habitat requirements
<i>distichophylla</i>	WS	A	W
<i>glacialis</i>	R	A	N
<i>hirtiglumis</i>	R	A	N
<i>longiglumis</i>			
subsp. <i>gymnocolea</i>	R	S	N
subsp. <i>longiglumis</i>	R	S	N
<i>macrocalycina</i>	WS	A	W
<i>oreophila</i>	WS	A	N
<i>swartbergensis</i>	R	A	N
<i>thuarii</i>	WS	A	N
<i>uniflora</i>	WS	A	N

A = abundant; N = narrow; R = restricted; S = sparse; W = wide; WS = widespread.



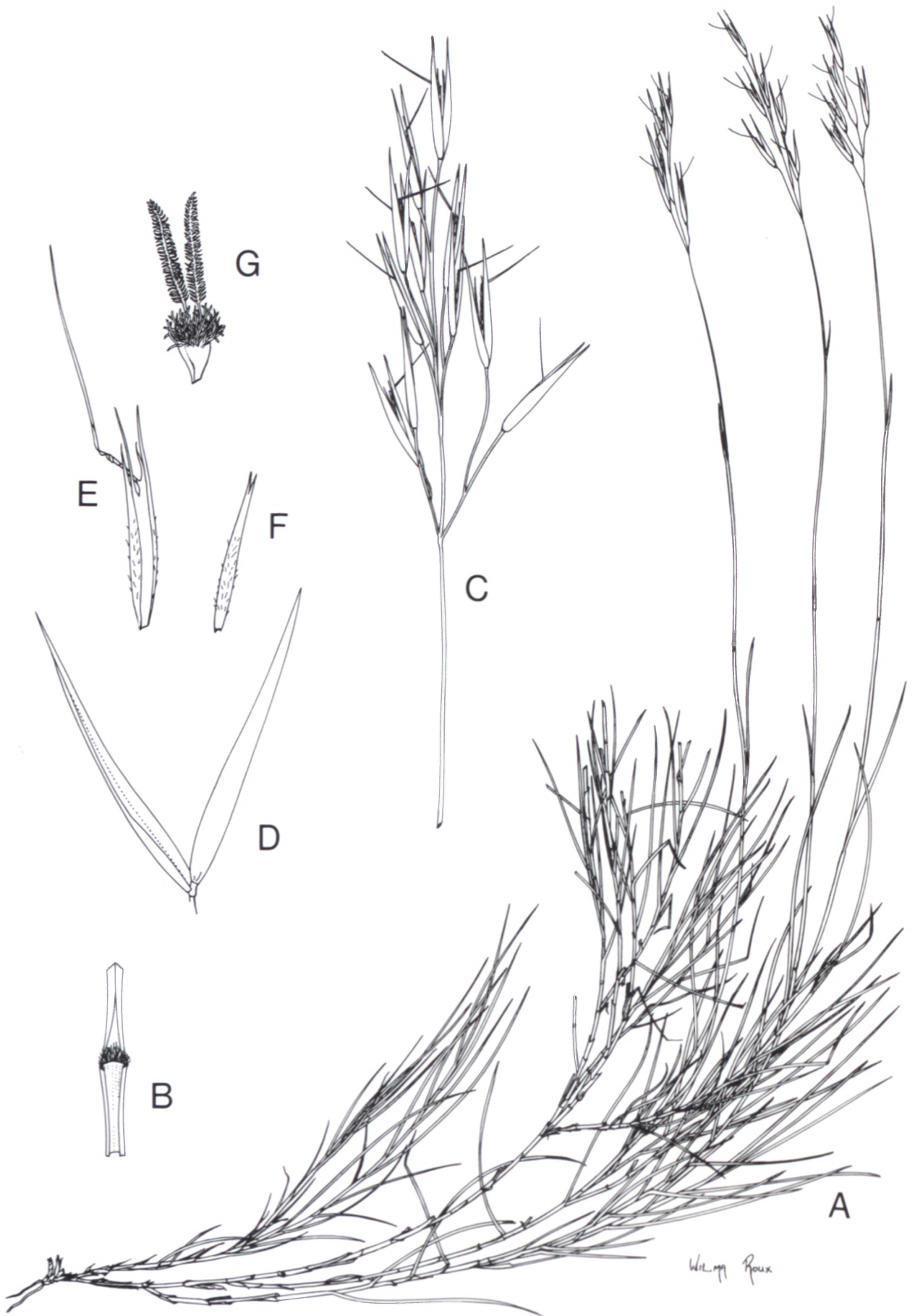


FIGURE 4.—*Pentameris uniflora* N.P. Barker. A, habit with decumbent, branching culm basally covered in dead, appressed leaf sheaths; B, ligule, which is a row of hairs, and surrounding leaf parts; C, panicle subcontracted to lax, with few spikelets. D–G, parts of spikelet and florets: D, glumes; E, lemma (in its normal conformation) showing lemma bristles, lobes (which are adnate to the bristle for most of their length) and geniculate awn; F, palea; G, ovary with apical hairs and stigmas. A,  $\times 0.5$ ; B, D–F,  $\times 4.7$ ; C,  $\times 1.6$ ; G,  $\times 11.8$ .



lobes and lateral bristles are measured as follows: the lemma body is measured from the base to the lowermost point of insertion of the central awn, whereas the lobes and bristles are measured from this same insertion point to the apex of the lobe or bristle. The full length of the lemma (either from base to lobe apex or base to bristle tip) can be obtained by adding the lemma body length to the length of the lobe or bristle. The term 'culm' is used in the descriptions below to describe all aerial parts (branched stems and reproductive culms) despite the anatomical discrepancies discussed in the introduction.

**Pentameris Beauv.**, Essai d'une Nouvelle Agrostographie: 92, t.18, fig.8 (1812); Kunth: 107 (1829); Kunth: 315 (1833); Nees: 336 (1841); Stapf: 512 (1897); Chippindall: 251 (1955); Clayton & Renvoize: 174 (1986); Gibbs Russell *et al.*: 251 (1990). Type species: *Pentameris thuarii* Beauv.

Perennial; caespitose, cushion-like or decumbent, sometimes branched. Culms 250–2 000 mm in length; woody and persistent from a woody base; leaf sheaths appressed to culm or free, persistent; sheath mouth sometimes auriculate; ligule a fringe of hairs; leaf blades linear, 50–550

mm long, rigid or filiform, open and flat, rolled or acicular; inflorescence paniculate, lanceolate and somewhat contracted to globose and lax; spikelets solitary, 13–25 mm long, laterally compressed, 1–2-flowered, highly reduced third floret rarely present; glumes two, more or less equal, 1-nerved, membranous to chartaceous, minutely scabrid, sometimes hirsute; lemma body uniformly pubescent, 7–9(–11)-nerved, 2.2–6.0 mm long, pubescent, the hairs arising from between the nerves, nerves anastomosing into the awn base and a 2.5–12.0 mm long lateral bristle; lemma lobes 0.4–4.0 mm long, acute to acuminate, sometimes lacerated, partly to fully adnate to the bristles; central awn geniculate, scabrid, contorted basally, 2–11 mm long from base to knee, 6–21 mm long from knee to tip; palea longer than lemma body, bifid at apex, pubescent between the keels; lodicules two, glabrous or ciliolate, sometimes with arm-like extensions; stamens three; ovary apically hairy, these hairs retained until maturity; fruit an achene with free pericarp, fusiform, subglobose to globose or cuneate, surface colliculate or rugose, hilum up to two thirds the length of the fruit, embryo small.

A genus of nine species, endemic to the southwestern region of the Cape Province, South Africa.

#### Key to species

- 1a Spikelets with one floret ..... 1. *P. uniflora*  
 1b Spikelets with two florets, occasionally with a rudimentary third floret:  
 2a Leaves with purple to dark brown auricles at base of blade; lemma lobes truncate, apically dentate .. 2. *P. thuarii*  
 2b Leaves without auricles, or if present then not coloured as above; lemma lobes acute to acuminate:  
 3a Panicle lax at anthesis, globose, 170–300 mm long; basal leaf sheaths 120 mm or longer, clustered at, and free from culm base; culm, including inflorescence, usually taller than 1.2 m:  
 4a Leaf sheaths densely covered in short hairs; glumes 15–18 mm long; lemma body 3.0–3.5 mm long; known only from Table Mountain ..... 3a. *P. longiglumis* subsp. *longiglumis*  
 4b Leaf sheaths glabrous; glumes 21–24 mm long; lemma body 5.0–5.5 mm long; known only from the Kogelberg ..... 3b. *P. longiglumis* subsp. *gymnocolea*  
 3b Panicle subcontracted to contracted at anthesis, lanceolate, up to 150 mm long; basal leaf sheaths seldom longer than 120 mm, partially free or appressed to culm; culm, including inflorescence, seldom taller than 1.2 m:  
 5a Glumes 14–24 mm long; leaf blades acicular or permanently rolled, rigid, sometimes pungent:  
 6a One or both glumes pubescent ..... 4. *P. hirtiglumis*  
 6b Glumes never pubescent:  
 7a Leaf blades acicular, usually straight but sometimes curling toward apices, occasionally pungent; leaf sheaths glabrous, but sheath mouth may be bearded; sheaths closely appressed to culm . 5. *P. macrocalycina*  
 7b Leaf blades permanently rolled, usually falcate, strongly pungent; leaf sheaths not appressed to culm, always pubescent, if only at margins ..... 6. *P. oreophila*  
 5b Glumes usually 14 mm or shorter; leaf blades usually soft, rolled (not permanently), folded or flat in cross section, never pungent:  
 8a Lateral bristle of lemma 5.5–10.0 mm long; leaf sheaths pubescent to densely woolly, especially near sheath mouth ..... 7. *P. distichophylla*  
 8b Lateral bristle of lemma 2.5–5.5 mm long; leaf sheaths glabrous or pubescent at margin only:  
 9a Leaves 200 mm long or longer, up to 5 mm wide; panicle with 25 or more spikelets ..... 8. *P. swartbergensis*  
 9b Leaves usually shorter than 100 mm, thin and rolled, narrower than 2 mm; panicle with fewer than 15 spikelets ..... 9. *P. glacialis*

#### 1. *Pentameris uniflora* N.P. Barker, sp. nov.

A aliis omnibus speciebus *Pentameridis* flosculo singulari differt.

*Pentameris* sp. 2. in Gibbs Russell *et al.*: 253 (1990).

TYPE.—Cape, Riversdale, Sleeping Beauty Peak. Along edges of overgrown ledges or on steep south slopes. Dense. 4200ft (1 275 m), 29 Oct. 1967, Esterhuysen 31771 (PRE, holo.!; BOL, iso.!).

Plants soft, decumbent; culms thin and flexuous, up to

650 mm long; leaf sheaths glabrous or only pubescent along margins, appressed to culm; leaf blades soft, filiform, short, up to 125 mm long, open or folded to somewhat rolled; panicle lanceolate, delicate, 40–60 × 10–20 mm, lax; spikelets 5–20, one-flowered; glumes 11–12 × 0.9–1.0 mm; lemma body 5.5–6.0 mm long; lemma lobes acuminate, 1.5–3.0 mm long, adnate to 2.5–4.5 mm long lateral bristle for most of their length; awn geniculate, 2.0–3.5 mm from base to knee, 6.5–7.0 mm from knee to tip; palea 5.5–6.0 mm long; lodicules cuneate, glabrous; anthers 4 mm long; fruit not known; flowering time September to December. Figures 2D; 4.



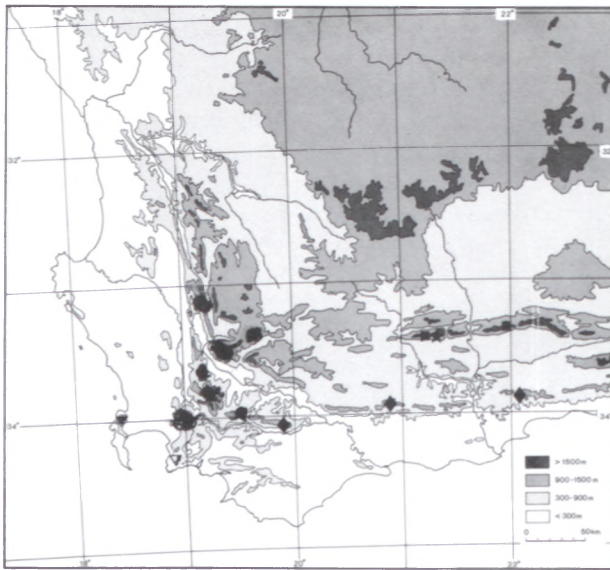


FIGURE 5.—Distribution of *P. glacialis* N.P. Barker, ■; *P. hirtiglumis* N.P. Barker, ○; *P. longiglumis* (Nees) Stapf subsp. *longiglumis* N.P. Barker, ▼; *P. longiglumis* (Nees) Stapf subsp. *gymnocolea* N.P. Barker, ▽; *P. oreophila* N.P. Barker, ●; *P. swartbergensis* N.P. Barker, ★; *P. uniflora* N.P. Barker, ◆; neighbouring locality of *P. hirtiglumis* and *P. oreophila*, ⊙.

This species is the only taxon in the genus with one-flowered spikelets. Mature fruit have not been seen, but stylar hairs on the apex of the ovary confirm the position of this species in the genus *Pentameris* (Barker 1990).

*P. uniflora* is known from only three localities which are quite widely separated (Figure 5). Populations at these localities appear to be quite abundant, but the habitat of this species (damp, rocky, southern aspects of the Cape fold mountains), habit (decumbent, hidden under taller plants), and small, somewhat inconspicuous inflorescences may account for the paucity of herbarium specimens.

Vouchers: Bond 1581 (SAAS); Ellis 2546 (PRE); Esterhuysen 25025, 32718a (BOL); Esterhuysen 31771 (BOL, PRE).

2. *Pentameris thuarii* Beauv., Essai d'une Nouvelle Agrostographie: 92, t. 18, fig. 8 (1812); Roem. & Schult.: 693 (1817); Kunth: 107 (1829) as 'thouarsii'; Kunth: 315 (1833) as 'thouarsii'; Kunth: 270 (1835) as 'thouarsii'; Stapf: 513 (1897); N.P. Barker in Gibbs Russell *et al.*: 253. (1990). Type: Du Petit-Thouars *s.n.* (P, lecto!). Lectotype here designated.

*Danthonia thuarii* Desv.: 99 (1831); Nees: 337 (1841) as 'thouarsii'; Steudel: 243 (1855) as 'thouarsii'; Durand & Schinz: 854 (1895) as 'thouarsii'; Durand & Schinz: 854 (1895).

*P. thuarii* Beauv. var. *burchellii* Stapf: 513 (1897). Type: Riversdale Div., lower part of the Lange Bergen, near Kampsche Berg, Burchell 6964 (K, holo.!, GRA, iso.!, PRE (fragment), iso.!).

Plants caespitose or decumbent; culms 0.46–1.63 m long; leaf sheaths pubescent, appressed to culm, with purple auricle at mouth, persistent; leaf blades up to 500 mm long, folded or flat (rarely rolled); panicle globose, lax, 70–220 × 40–170 mm; spikelets 16–90, two-flowered; glumes 15.5–21.5 × 1.8–3.0 mm; lemma body 2.2–3.3 mm long; lemma lobes 0.4–0.7 mm long, acute, apically lacerate-dentate, almost free from a 4.0–5.5 mm

long lateral bristle; awn geniculate, 4.5–7.0 mm from base to knee, 9.5–12.5 mm from knee to tip; palea 2.8–3.5 mm long; lodicules cuneate, glabrous; anthers 3–4 mm long; fruit an achene, globose, 2.5 × 1.7–2.0 mm, surface colliculately sculptured; flowering time September to December. Figure 1B, D, F.

The spelling of the epithet *thuarii*, as used in the protologue, differs so obviously from that of the name of the collector, Du Petit-Thouars, that it is not considered a typographic error. The epithet *thouarsii*, used in a number of subsequent accounts, is therefore not adopted. It is plausible that Palisot de Beauvois wished to maintain the phonetic pronunciation of the French name 'Thouars', and thus spelt it 'thuarii' in latinised form.

No locality or specimen number of the type specimen was cited by Palisot de Beauvois. However, two specimens of *P. thuarii* were obtained from the Paris herbarium (P). One of these specimens is annotated with 'Herb. Du Petit Thouars', which is written on the bottom of the label. The identity of the handwriting is not known. That one (or both) of these specimens are type material is further supported by the observation that the illustration accompanying the original description includes a representation of a mature fruit, a description of which also appears in the text (Palisot de Beauvois 1812). The type specimen must therefore have borne mature fruit. This deduction is compatible with the historical record which indicates that Du Petit Thouars visited the Cape in February 1793. February is the time of year when many fynbos grasses, including *P. thuarii*, are in fruit (pers. obs.). As the annotated specimen from Paris is in full fruit, this specimen is regarded as type material. However, this evidence is considered to be insufficient to warrant holotype status for this specimen, which is therefore selected as a lectotype.

Stapf (1897) distinguished two varieties of *P. thuarii*: var. *thuarii*, was described as being only 1–2 ft. (300–600 mm) tall with a woody, sometimes branched, suffrutescent base, with leaves only 1 lin. (approximately 2 mm) wide and with a lax, open or contracted panicle; var. *burchellii* Stapf was considered to be taller, simple basally

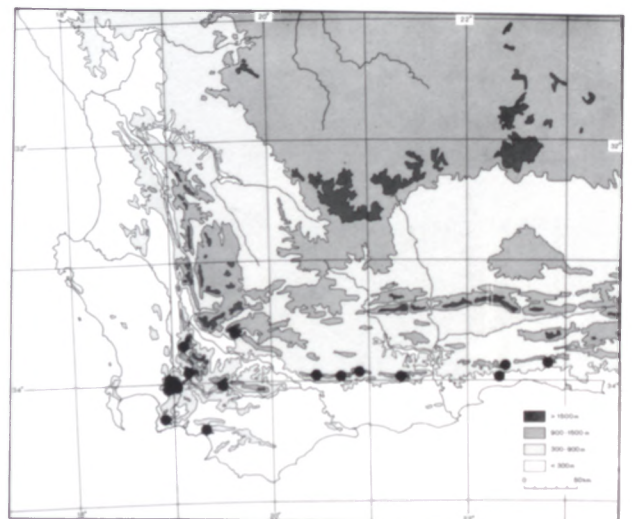


FIGURE 6.—Distribution of *P. thuarii* Beauv.



and branching after 1 ft. (300 mm), with leaves 2 lin. (approximately 4–5 mm) wide and with an effuse panicle. Stapf added that this latter variety has the appearance of a robust annual. Chippindall (1955) considers the characters on which these distinctions are made to be too variable, and rejects the two varieties, a conclusion supported by Barker (1990).

This species grows abundantly in moist environments, and is usually found alongside streams, seeps and drainage lines. Geographically widespread, it occurs from Stellenbosch in the west to Montagu Pass in the east (Figure 6).

Vouchers: *Ellis 2221* (PRE); *Compton 7494* (BOL, NBG); *Levy's 693* (BOL, STE); *Parker 4465* (BOL, NBG, SAM); *Schlechter 9282* (BOL, GRA, PRE).

### 3. *Pentameris longiglumis* (Nees) Stapf

The following description is based on all the specimens seen, and the variation reported includes that for both known subspecies, described below.

Plants densely tufted from a woody base; *culms* erect, up to 1.4 m tall, unbranched or branched close to woody base; *leaf sheaths* loose and free from culm, wide, persistent, clustered at base of plant, shortly pubescent or glabrous, straw-coloured or purple, sheath mouth sometimes with green auricles; *leaf blades* rigid, rolled, up to 550 mm long; *panicle* lax, globose, up to 300 × 140 mm; *spikelets* 30–100 or more, two-flowered; *glumes* 15.0–24.0 × 1.1–2.4 mm; *lemma body* 3.0–5.5 mm long; *lemma lobes* 2.4–4.0 mm long, long-acuminate, almost completely adnate to a 3.5–11.0 mm long lateral bristle; *awn* geniculate, 3.5–10.0 mm from base to knee, 7.5–21.0 mm from knee to tip; *palea* 3.0–9.5 mm long; *lodicules* cuneate, glabrous; *anthers* 3.6–5.5 mm long; *fruit* broadly fusiform, 3.5 × 1.3 mm, surface colliculately sculptured; *flowering time* September to December. Figures 8 & 9.

Two subspecies are recognised on the basis of a number of floral and vegetative characters, as listed in Table 5. The significance of these differences is demonstrated by the results of a principal components analysis (PCA)

TABLE 5.—A statistical summary of the variation in characters differentiating the two subspecies of *P. longiglumis* (Nees) Stapf. Measurements in mm

Character	subsp. <i>longiglumis</i>	subsp. <i>gymnocolea</i>
Sheath indumentum	pubescent	glabrous
Panicle dimensions	170 × 105	300 × 140
No. of spikelets	30–95	70–100
Glume length	15.0–19.5	21–24
Lemma body length	2.7–3.5	5.0–5.5
Lemma lobe length	2.4–3.0	3.5–4.0
Bristle length	3.5–8.0	8–11
Awn length:		
base to knee	3.5–5.0	8–10
knee to tip	7.5–10.0	14–21
Palea length	5.5–6.5	7.5–9.5

carried out on data obtained for 11 characters from 10 herbarium specimens. The PCA was done using the numerical taxonomy package NT-SYS, version 1.4 (Rohlf 1988).

The first three axes resulting from the PCA accounted for 94.2% of the variation in the data, with the first axis contributing 75.7%. The first two axes (Figure 7) account for 88.3% of the variation in the data. The two groups comprise specimens from two geographically distinct localities, Kogelberg and Table Mountain. On the basis of this evidence, the allocation of the rank of subspecies to these two groups is considered to be justified.

### 3a. *Pentameris longiglumis* (Nees) Stapf subsp. *longiglumis*

*Danthonia longiglumis* Nees in Flora africana australioris I: 306 (1841).

TYPE.—Cape, In summo monte tabulare (Dist. Cap.), *Bergius s.n.* (B, holo.!; fragment and photo in PRE, iso!).

Note: *Pentameris longiglumis sensu* Stapf: 514 agrees with neither Nees's description nor the type (see discussion below).

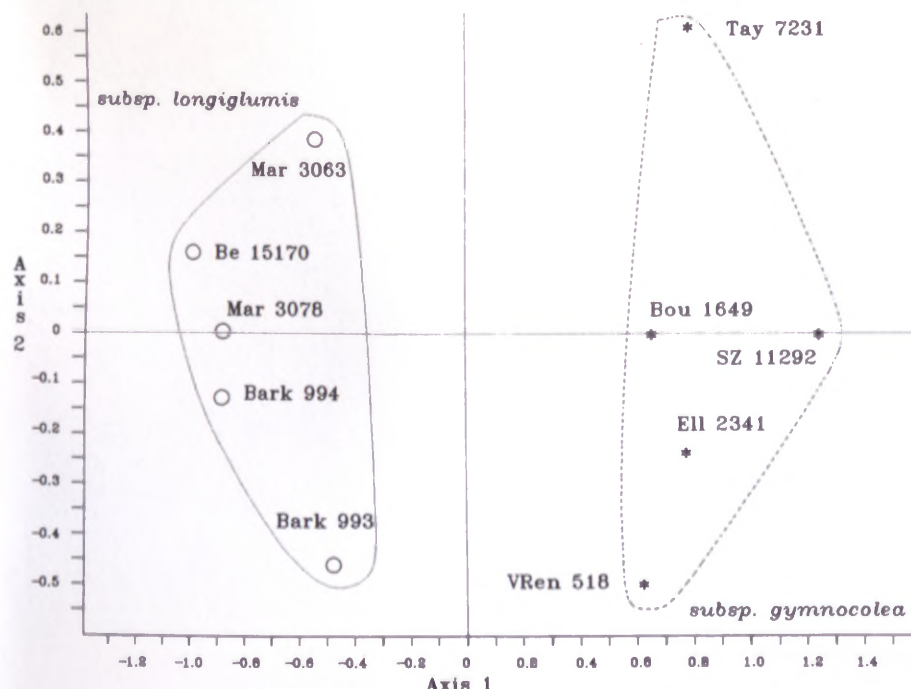


FIGURE 7.—First two axes of the principal components analysis on data of eight specimens of *Pentameris longiglumis* (Nees) Stapf. Axis 1 accounts for 75.7% of variation in data, axis 2, 12.6%. Points represent specimens, annotated as follows: Bark = Barker, Be = Bews, Ell = Ellis, Mar = Marloth, SZ = Stirton & Zantovska, Tay = Taylor, VanR = Van Rensburg. Specimens from BOL, PRE and STE.





FIGURE 8.—*Pentameris longiglumis* (Nees) Stapf subsp. *gymnocolea* N.P. Barker. A, habit: erect culms, basally covered in loose, dead leaf sheaths; note long leaf blades, which may be rolled or open, and large, globose, effuse panicle,  $\times 0.8$ ; B, ligule, which is a row of hairs, surrounding leaf parts, with hairs on leaf sheath, expanded auricles, and sparsely pubescent adaxial basal leaf surface,  $\times 4.7$ .



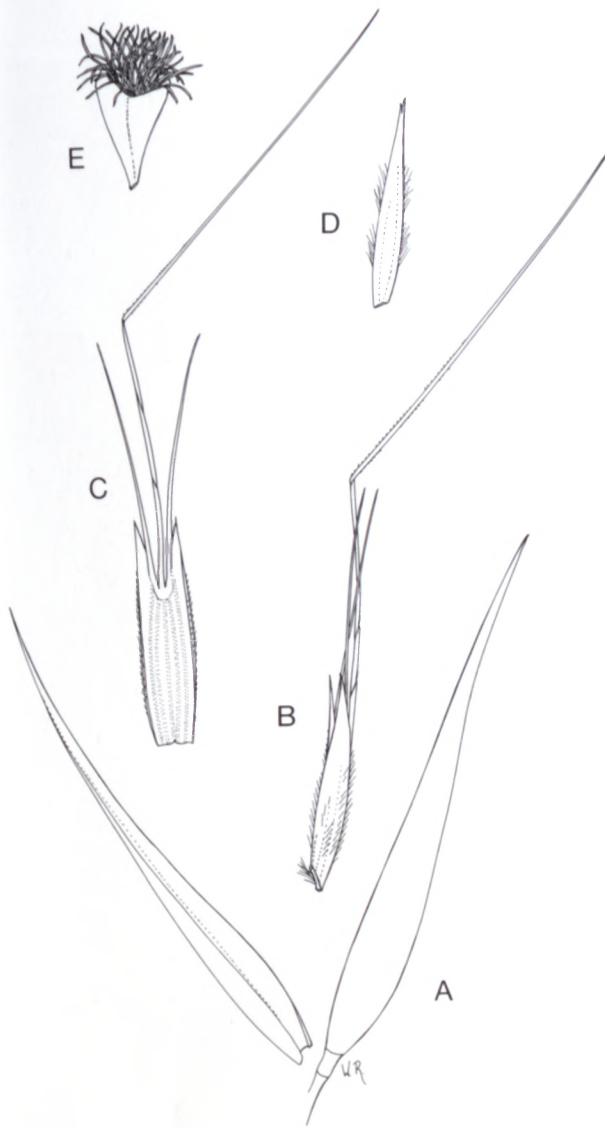


FIGURE 9.—*Pentameris longiglumis* (Nees) Stapf subsp. *gymnocolea* N.P. Barker. Parts of spikelet and florets: A, long, acuminate glumes; B, whole basal floret; C, lemma (opened, flattened and viewed from inside of floret) indicating venation, lemma bristles, lemma lobes (adnate to bristles for most of their length) and geniculate awn; D, palea; E, developing fruit, with apical hairs. A–D,  $\times 3.7$ ; E,  $\times 11$ .

Stapf (1897) describes *P. longiglumis* as only 1.5 to 2 feet (450–600 mm) tall. Nees does not give any indication of plant height, but all specimens of this taxon seen, including the type (*Bergius s.n.*), have far exceeded this height. Furthermore, Stapf describes the sheath as glabrous or sparsely hairy, whereas the type specimen has a distinctly pubescent sheath, as described by Nees (1841). In addition, Stapf describes the leaves as being filiform, 6–9 inches (150–220 mm) long. Nees does not provide leaf lengths in his description, but leaves on the type specimen were noted to be much longer than 6–9 inches, broad, rolled and somewhat rigid.

Furthermore, at least three of the four specimens cited by Stapf under his description of *P. longiglumis* do not match the *Bergius* specimen cited by Nees. The three specimens in question, *Burchell 542*, *Burchell 598* and *Milne 246* were obtained from The Herbarium, Royal Botanic Gardens, Kew (K). The fourth voucher cited by

Stapf, *Spielhaus s.n.*, was not traced. Unfortunately these three specimens are of poor quality. The spikelets (when present) are devoid of florets, and one specimen, *Burchell 542*, is entirely sterile. Uncertainty about the identity of the *Milne 246* specimen is further borne out by an annotation to the effect that the leaves resemble those of *Pentaschistis pallescens* (Schrad.) Stapf, whereas the inflorescence resembles that of *Pentameris thuarii*. The *Burchell 598* specimen may possibly be *Pentameris longiglumis* as it has floral parts of a size comparable to those observed in Nees's type specimen. However, the basal parts are absent, so the leaf and sheath characters cannot be compared.

It is therefore considered that Stapf's (1897) description and cited vouchers do not agree with Nees's description and type of *P. longiglumis*. Stapf's *Pentameris longiglumis* is therefore regarded as a misapplied name, and it appears that Stapf described a species of *Pentaschistis*.

This subspecies is known from a few specimens collected from Table Mountain, the distribution shown in Figure 5. Until recently, this taxon was thought to be extinct, as the most recent specimen seen among the holdings of eight South African herbaria is dated 1918. However, a small population has been located in a recently burnt area on Table Mountain. This population is growing in a slightly sloping seepage area. The moist habitat requirement matches that of the other subspecies, which is, however, found on steeper slopes.

Vouchers: *N. Barker 993, 994* (BOL, PRE); *Bews 15170* (BOL); *Marloth 3063, 3078* (PRE).

### 3b. *Pentameris longiglumis* (Nees) Stapf subsp. *gymnocolea* N.P. Barker, subsp. nov.

Differt a *P. longiglumis* subsp. *longiglumis* foliorum vaginis glabris et partibus floralibus grandioribus: glumae 21–24 mm longae, lemma 5.0–5.5 mm longum; subspecies tantum monte 'Kogelberg' nominato nota. Figures 2C; 8 & 9.

TYPE.—Cape, summit ridge of Platberg, Kogelberg, S side, edge of gully; culms 3–4 ft. (1.0–1.3 m), erect, coarse, loose tufts, 2650 ft (900 m), 27 Nov. 1967, *Taylor 7231* (PRE, holo.!; STE, iso.).

As shown in Table 5, this subspecies differs from *P. longiglumis* subsp. *longiglumis* in a number of features. The subspecific epithet chosen for this species describes one of these distinguishing characters: the glabrous leaf sheaths.

This subspecies is known only from the Kogelberg Forest Reserve (Figure 5). It inhabits south-facing mountain slopes in seepage areas where it forms large tussocks.

Vouchers: *Boucher 1649* (PRE); *Ellis 2341* (PRE); *Esterhuysen 13326* (BOL, PRE); *Stirton & Zantovska 11293* (STE); *Van Rensburg 518* (STE).

### 4. *Pentameris hirtiglumis* N.P. Barker, sp. nov.

*P. oreophila* similis sed glumis hirsutis facile distincta; lobis lemmae acutis, usque ad dimidium longitudinis ad setam adnatis.





FIGURE 10.—*Pentameris hirtiglumis* N.P. Barker, type specimen Kerfoot 6092. A, habit: decumbent, branching culm basally covered in dead leaf sheaths; note that flowering culm is not normally curved back upon itself, but appeared so on specimen. B–G, parts of spikelet and florets: B, hirsute glumes; C, whole basal floret; D, lemma (opened, flattened and viewed from inside of floret) showing venation, lemma bristles, lemma lobes (adnate to bristle for half or less of their length) and geniculate awn; E, palea; F, anthers, with no filaments; G, ovary with apical hairs and stigmas. A,  $\times 0.5$ ; B–F,  $\times 4.7$ ; G,  $\times 14$ .



TYPE.—Cape, Bosboukloof, Jonkershoek, locally very common, attractive, 980 ft (600 m), Oct. 1967, *Kerfoot 6092* (PRE, holo.!).

*Plants* cushion-like or densely bushy, branched; *culms* somewhat decumbent with numerous nodes, 200–750 mm long; *leaf sheaths* pubescent, at least along margins (rarely glabrous), persistent, not closely appressed to culm, loose when dead; *leaf blades* up to 200 mm long, permanently rolled, falcate; *panicle* lanceolate, somewhat lax, 75–110 × 20–35 mm; *spikelets* 15–50, two-flowered; *glumes* hirsute, 14.5–21.5 × 1.6–2.1 mm; *lemma body* 2.8–3.7 mm long; *lemma lobes* 1–2 mm long, acute, adnate to a 3.0–6.5 mm long lateral bristle for half or less of their length; *awn* geniculate, 4–6 mm from base to knee, 7.5–11.0 mm from knee to tip; *palea* 4.0–4.5 mm long; *lodicules* cuneate, glabrous; *anthers* 3.5–5.0 mm long; *fruit* broadly fusiform, 2.4 × 1.2 mm, surface colliculately sculptured (Figure 1A); *flowering time* September to October/November.

This species is similar in appearance to *P. oreophila*, but can be readily separated from that species by the presence of the hirsute glumes (Figure 10B). Additional differences between these two taxa are the acute lemma lobes (Figure 10D) and softer, non-pungent leaf apices in *P. hirtiglumis*. However, as is apparent from the cladogram discussed above (Figure 3), this species is sister to *P. longiglumis* on the basis of several anatomical features including swollen leaf margins, inflated abaxial epidermal cells and dense, strongly inclined adaxial prickles.

Like *P. oreophila*, this taxon has a geographically restricted distribution, and is known only from high montane regions of the Hottentots Holland Mts (Figure 5). Where found, this species is abundant and locally dominant. However, it appears to have narrow habitat requirements, and is restricted to shale bands.

Vouchers: *N. Barker 90* (PRE); *Ellis 4680* (PRE); *Kruger & Haynes 753* (JF, STE).

5. *Pentameris macrocalycina* (Steud.) Schweick. in Feddes Repertorium 43: 91 (1938); N.P. Barker in Gibbs Russell *et al.*: 252. (1990). Type: Cape, in summitate Montis Tabularis *Ecklon 932* (OXF, lecto.!, PRE isolecto.!, (fragments), S, isolecto.!). Lectotype here designated.

*Avena macrocalycina* Steud.: 482 (1829).

*Danthonia speciosa* Lehm. ex Nees: 307 (1841). Steud.: 241. (1855); Durand & Schinz: 854 (1895). Type: In apicis rupestribus montis ad Genadenthal solo sabuloso-humoso alt. 2000–3000 ft, (Stellenbosch), et in Dutoitskloof alt. 2500–3000 ft, *Drège s.n.* (PRE fragments, iso!).

*Pentameris speciosa* (Lehm. ex Nees) Stapf: 515 (1897).

*Plants* caespitose, branched; *culms* 0.43–1.10 m long; *leaf sheaths* sometimes bearded at mouth, persistent, closely appressed to culm; *leaf blades* 110–290 mm long, acicular; *panicle* lanceolate, somewhat lax, 60–120 × 10–60 mm; *spikelets* 10–50, two-flowered; *glumes* 16–24 × 2–3 mm; *lemma body* 3.5–5.5 mm long; *lemma lobes* 1.3–4.0 mm long, acute-acuminate, adnate to a 7.5–12.0 mm long lateral bristle for most of their length; *awn* geniculate, 5.5–10.0 mm from base to knee, 9–16 mm from knee to tip; *palea* 6.5–11.0 mm long; *lodicules* cuneate,

glabrous; *anthers* 4.2–6.0 mm long; *fruit* broadly fusiform, 3.6 × 1.2 mm, surface colliculately sculptured; *flowering time* September to December.

Schweickerdt (1938) pointed out that both Stapf (1897) and Durand & Schinz (1895) had placed *Avena macrocalycina* in synonymy under *Danthonia macrantha*. In addition, Nees (1832) mistakenly placed *Avena macrocalycina* and its type, *Ecklon 932*, under *Pentameris macrantha*. This confusion arose as a result of the fact that there were two specimens representing different taxa distributed under the number *Ecklon 932*. The type specimen of *Avena macrocalycina*, one of the *Ecklon 932* specimens, was obtained from the Fielding-Druce herbarium, Oxford (OXF), and is designated here as the lectotype. A duplicate of this specimen is housed in the Swedish Museum (S).

This is a widely distributed species, recorded from Pakhuis Pass in the north to Cape Point in the south and eastwards to the Groendal Wilderness Reserve (Figure 11).

Vouchers: *Adamson 3980* (JF, PRE); *Ellis 2540* (PRE); *Esterhuysen 23763, 28012* (BOL, PRE); *Taylor III13* (PRE, STE).

## 6. *Pentameris oreophila* N.P. Barker, sp. nov.

Species laminis revolutis permanentibus, brevibus (<105 mm longis), falcatis, et foliorum vaginis saltem marginibus pubescentibus distinguitur.

*Pentameris* sp. 1. in Gibbs Russell *et al.*: 252. (1990).

*P. obtusifolia* sensu Ellis (1985d), Barker (1986, 1989). Note that *P. obtusifolia* (Hochst.) Schweick. is to be transferred to *Pseudopentameris*.

TYPE.—Cape, Worcester Div., Jona's Kop, common on shale band, or on peaty slopes, after fire, in different aspects but not on steep southern slopes, forming dense and, in some places, quite extensive patches, leaf tips very sharp, 5000 ft (1500 m), 19 Dec. 1971, *Esterhuysen 32681* (PRE, holo.!, BOL, iso.!).

*Plants* cushion-like or densely bushy, branched basally; *culms* erect or somewhat decumbent in older, larger tufts and then with numerous nodes, up to 530 mm long; *leaf sheaths* persistent, pubescent along margins, appressed or free from culm, especially when dead, often purple when young; *leaf blades* up to 105 mm long, permanently rolled, falcate (less so in young plants), strongly pungent; *panicle* lanceolate, somewhat lax, 30–80 × 20–40 mm; *spikelets* 8–20, two-flowered; *glumes* 14–20 × 2.1–3.0 mm; *lemma body* 3–4 mm long; *lemma lobes* 1.6–3.0(–4.0) mm long, acuminate, adnate to 7.0–10.5 mm long lateral bristle for most of their length; *awn* geniculate, 6–11 mm from base to knee, 9.5–13.0 mm from knee to tip; *palea* 5.5–8.5 mm long; *lodicules* cuneate, glabrous; *anthers* 4.0–5.5 mm long; *fruit* subglobose, 3.5–4.0 × 1.6–2.0 mm, surface colliculately sculptured; *flowering time* September to December. Figures 1E & 2B.

The species can be distinguished by its permanently rolled, short (<105 mm long), falcate leaf blades and the leaf sheaths which are pubescent at least along the margins.

The specific epithet *oreophila*, or 'mountain-loving', is chosen because this species is only found at high altitudes in the Hottentots Holland, Riviersondereinde and Hex



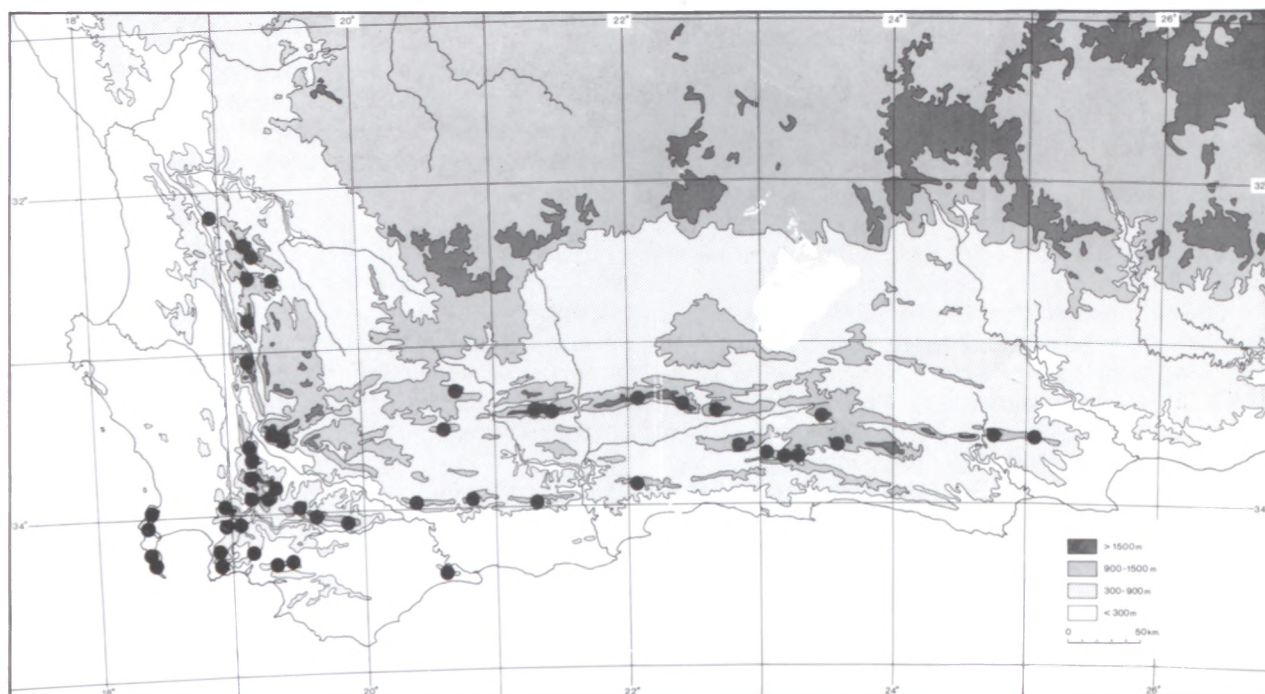


FIGURE II.—Distribution of *P. macrocalycina*.

River Mountain ranges (Figure 5). Where found, the species is abundant, especially in years immediately after fire. Its high altitude habitat receives snow in the winter months, and the cushion-like growth form (Figure 2) may be an adaptation to this.

Vouchers: Ellis 4686 (PRE); Esterhuysen 19788 (BOL, PRE); Forsyth 191 (JF, PRE); Phillips 2109 (SAM); Wasserfall 562 (BOL, NEJ).

**7. *Pentameris distichophylla* (Lehm.) Nees** in *Linnaea* 7: 314. (1832); Kunth: 317 (1833). Type: Habitat in Promontorio Bonae Spei, collector unknown (S, lecto!., PRE, fragment).

*Danthonia distichophylla* Lehm.: 41 (1831); Nees: 305 (1841).

*Pentameris dregeana* Stapf: 515 (1897); N.P. Barker in Gibbs Russell *et al.*: 252 (1990).

*Plants* caespitose, becoming cushion-like with age, branched basally; *culms* 0.4–1.2 m long; *leaf sheaths* pubescent to woolly, especially near mouth, appressed to culm, persistent; *leaf blades* 80–190(–300) mm long, pubescent, rolled, folded or flat; *panicle* lanceolate, somewhat lax, 50–110 × 15–60 mm; *spikelets* 12–65, two-flowered; *glumes* 12–15 × 1–2 mm, occasionally sparsely pubescent; *lemma body* 2.3–3.5 mm long; *lemma lobes* 1.0–2.6 mm long, acute, adnate to a 5.0–10.5 mm long lateral bristle for most of their length; *awn* geniculate, 4–7 mm from base to knee, 6–12 mm from knee to tip; *palea* 4–6 mm long; *lodicules* cuneate, glabrous or shortly ciliolate, rarely with arm-like extensions; *anthers* 3.0–4.5 mm long; *fruit* cuneate, 2.0 × 0.9 mm, surface rugosely sculptured; *flowering time* September to December. Figures 1 & 2.

Stapf (1897) created the epithet *dregeana* for the partial concept of the taxon which Nees (1841) called *Danthonia distichophylla*. Stapf did not agree with Nees on the

inclusion of Lehmann's description of *Danthonia distichophylla*, and in a footnote states that Lehmann's description probably refers to a *Pentastichis*. It thus appears that Stapf did not see the type of Lehmann's *Danthonia distichophylla*.

Lehmann's description (1831) states that he has seen the specimen in a dried state (v.s. = *vide siccam*). According to Nordenstam (1980), Lehmann's herbarium comprised many specimens collected by Ecklon & Zeyher. The collections of Lehmann now reside in the Swedish Museum of Natural History (S), from which the type of *Danthonia distichophylla* was obtained. The label of this specimen had been annotated (possibly by Nordenstam) to the effect that it is written in Lehmann's hand. Further confirmation of this was obtained by matching the script with that of published examples of Lehmann's handwriting (Burdet 1976; Nordenstam 1980). As there are no other labels on the specimen, the original collector of this specimen is unknown, but as Lehmann never visited southern Africa, it is possible that the specimen is an Ecklon & Zeyher collection.

Despite Stapf's comment, the Lehmann specimen is a good match to the specimens of *P. dregeana* cited by Stapf (1897). The name *P. dregeana* is therefore illegitimate as it is antedated by Lehmann's *P. distichophylla*. This taxon is therefore correctly named *Pentameris distichophylla* (Lehm.) Nees. As there is no conclusive evidence that the Lehmann specimen from S is the holotype, it is designated as the lectotype.

This species is one of the most widely distributed in the genus, ranging from the northern Cedarberg to Paarl and eastwards to the Tsitsikamma Mountains (Figure 13).

Vouchers: Esterhuysen 22352, 27321 (BOL, PRE); Hafstrom & Acocks 45 (PRE); Gillett 3835 (STE); Taylor 11590 (PRE, STE).



8. *Pentameris swartbergensis* N.P. Barker, sp. nov., *P. distichophyllae* similis sed foliorum vaginis glabris differt.

TYPE.—Cape, Toverkop, Swartberg nr Ladismith, broad ledges at base of high cliffs on S side of peak, appears to be locally dominant below cave, 6500 ft. (1 875 m), 17 Dec. 1956, Esterhuysen 26755 (PRE, holo.!; BOL, iso.!).

Plants caespitose or somewhat decumbent, basally branched; culms up to 560 mm long; leaf sheaths glabrous, appressed to culm; leaf blades up to 230 mm long, folded or rolled, sparsely pubescent near base; panicle lanceolate, 80–90 × 20–35 mm, somewhat lax; spikelets 22–56, two-flowered; glumes 11.5–13.0 × 1.5–1.6 mm; lemma body 2.8–3.0 mm long; lemma lobes, acuminate,

1.4–1.5 mm long, adnate to 2.5–3.5 mm long lateral bristle for about half their length; awn geniculate, 3 mm from base to knee, 5.5–7.0 mm from knee to tip; palea 4.5–5.0 mm long; lodicules cuneate, ciliate at apex; fruit broadly fusiform, 2.0–2.4 × 1.0 mm, surface colliculately sculptured; flowering time September to December. Figure 14.

This species may be confused with *P. distichophylla*, but differs in such features as the nature of the colliculate surface of the caryopsis (which is rugose in *P. distichophylla*), the leaf sheaths (glabrous in *P. swartbergensis*, pubescent to woolly in *P. distichophylla*) and the lateral lemma bristles, which are substantially shorter in *P. swartbergensis*.

This taxon is known from only two localities in the Klein Swartberg, and is probably endemic to this mountain range

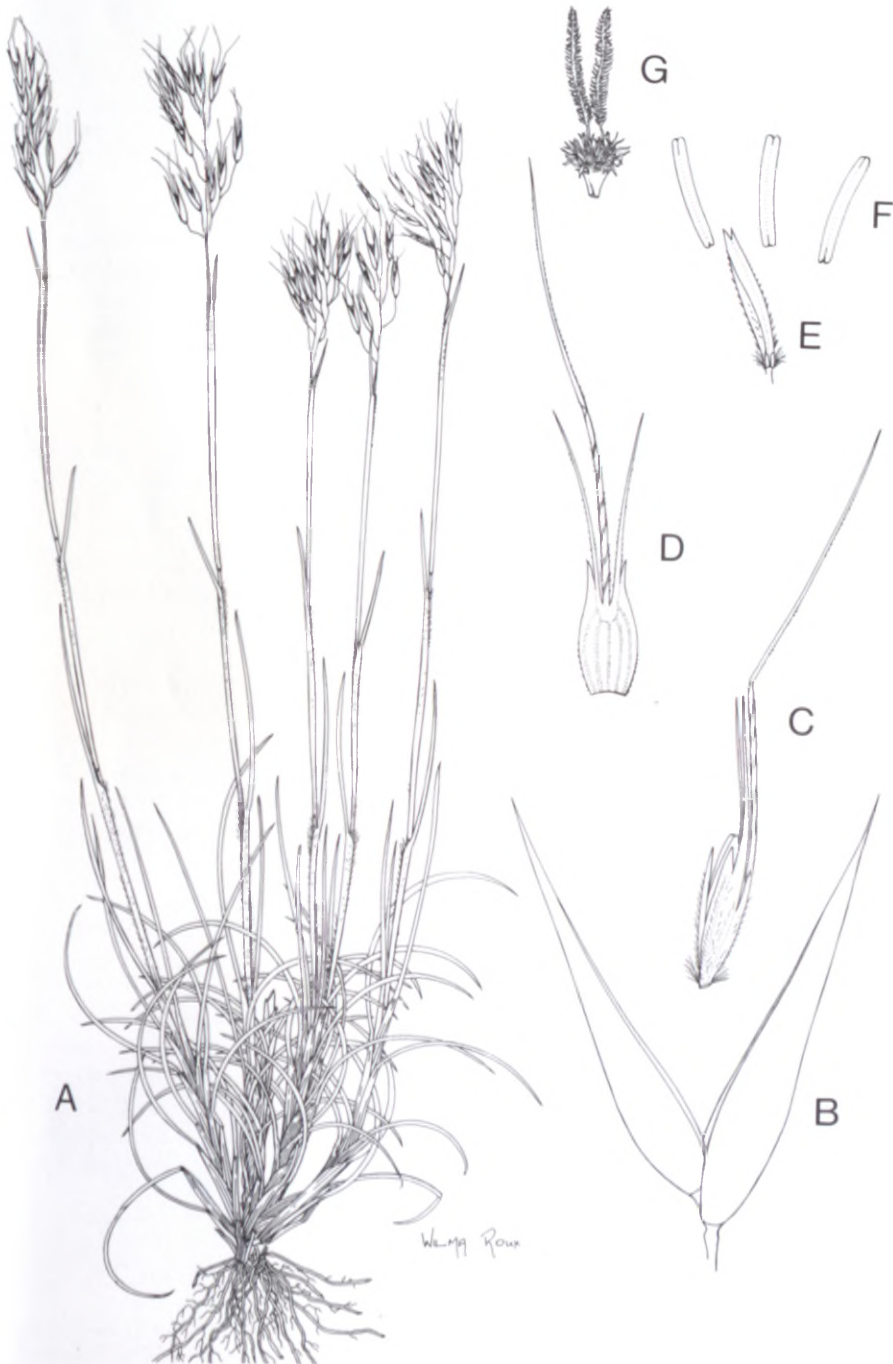


FIGURE 12.—*Pentameris oreophila* N.P. Barker. A, habit: erect culms and prickly, cushion-like basal leaf growth; note also pubescent leaf sheaths loosely appressed to stems, falcate, permanently rolled leaf blades with pungent apices. B–G, parts of spikelet and florets: B, glumes; C, whole basal floret; D, lemma (opened, flattened and viewed from inside of floret) showing venation, lemma bristles, lemma lobes (adnate to bristles for most of their length) and geniculate awn; E, palea; F, anthers with no filaments; G, ovary with apical hairs and stigmas. A, × 0.3; B–F, × 3.7; G, × 11.



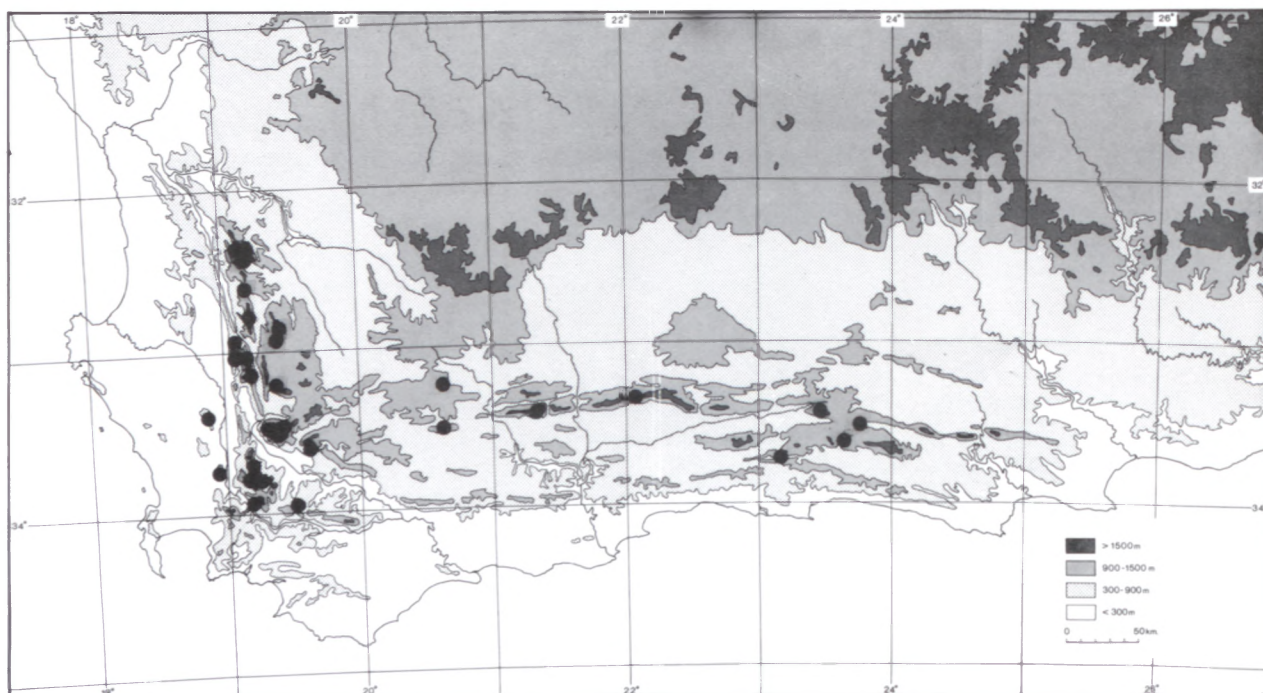


FIGURE 13.—Distribution of *P. distichophylla* (Lehm.) Nees.

(Figure 5). It grows at the foot of cliffs or rock walls in deep shade.

Vouchers: Esterhuysen 18510, 26750, 26751 (BOL, PRE); Linder 5490 (BOL).

9. *Pentameris glacialis* N.P. Barker, sp. nov., a *P. distichophylla* spiculis paucis (< 15), foliis brevibus filiformibus et habitu decumbenti molli distinguitur.

TYPE.—Cape, Oudtshoorn, Waboornsberg, growing in humic gullies on south slopes, 14 Dec. 1991, N.P. Barker 995 (BOL, holo.!; B, CANB, G, GRA, J, K, NBG, NSW, NU, P, PRE, STE, all iso.!).

Plants decumbent; culms thin, flexuous, up to 550 mm long, tinged with purple; leaf sheaths glabrous or pubescent along margins, loosely appressed to culm; leaf blades filiform, short, up to 100 mm long, rolled; panicle lanceolate, to 70 × 30 mm, lax to somewhat contracted; spikelets 6–12 (–15), two-flowered; glumes 13.0–14.5 × 1.3–1.5 mm; lemma body 2.5–3.0 mm long; lemma lobes acuminate, 1.0–1.9 mm long, adnate to 3.5–4.5 mm long lateral bristle for less than half its length; awn geniculate, 3.5–5.5 mm from base to knee, 7.5–8.5 mm from knee to tip; palea 3.5–4.2 mm long; lodicules cuneate, glabrous; fruit an achene, 2.5 × 1 mm, surface colliculately sculptured; flowering time October to December.

This species, first collected in 1987 by Ellis, bears superficial resemblance to *P. macrocalycina*, but is distinguishable from that species by the slender, geniculate culms, the rolled but not acicular leaf blades, the panicles with few spikelets, as well as by the size of the floral structures, which are substantially smaller in *P. glacialis*. The species is generally found to be locally abundant, growing in narrow gullies, rock ledges and overhangs in black, humic but sandy soils. Such habitats are thought

to become particularly heavily snowed up in winter. This habitat appears to preclude *P. macrocalycina*, which is found in more stony sites, as well as *P. distichophylla*, which appears to prefer northern aspects and rock crevices. The woolly leaf bases and sheaths of *P. distichophylla* separate this species from *P. glacialis* (Figure 15).

When visited in mid-October 1991, the plants and rocks at the type locality were covered in a thick layer of ice. Such conditions may persist for three or more months of the year in the winter and spring, depending on the severity of the frontal systems associated with the winter rainfall regime of the southwestern Cape. This harsh, icy environment gave rise to the specific epithet.

A subsequent visit in mid-December 1991 provided an indication of the range of climatic extremes in which this species survives, with very hot, dry conditions prevailing. The steep-sided, rocky gullies in which this species is found were, however, cooler, being shaded for much of the day, and the humic soil was still damp. Figure 5 shows the distribution of this species.

Vouchers: N. Barker 995, 996 (BOL, GRA, J, NBG, S, STE, UWC), 997 (BOL, K, PERTH, PRE), 1019 (BOL); Ellis 5620 (PRE).

#### INCERTAE SEDIS

A single unusual specimen, undoubtedly belonging to the genus *Pentameris* (possessing an achene with apical hairs) was collected from Cockscomb Peak by Ellis in 1987. This specimen, Ellis 5605 (PRE), is morphologically similar in certain respects to *P. glacialis*, but differs in its leaf anatomy.

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FIGURE 14.—*Pentameris swartbergensis* N.P. Barker. A, habit: erect culms (folded back, based on type material) and branched basal parts. B–F, parts of spikelet and florets: B, glumes; C, whole basal floret; D, lemma (opened, flattened and viewed from inside of floret) showing venation, lemma bristles, lemma lobes (adnate to bristles for most of their length) and geniculate awn; E, palea; F, developing fruit with apical hairs, note that fruit appears to develop in a basipetal direction, uppermost region becoming swollen and associated surface sculptured, appearing at apex first. A,  $\times 0.5$ ; B–E,  $\times 4.8$ ; F,  $\times 14.6$ .

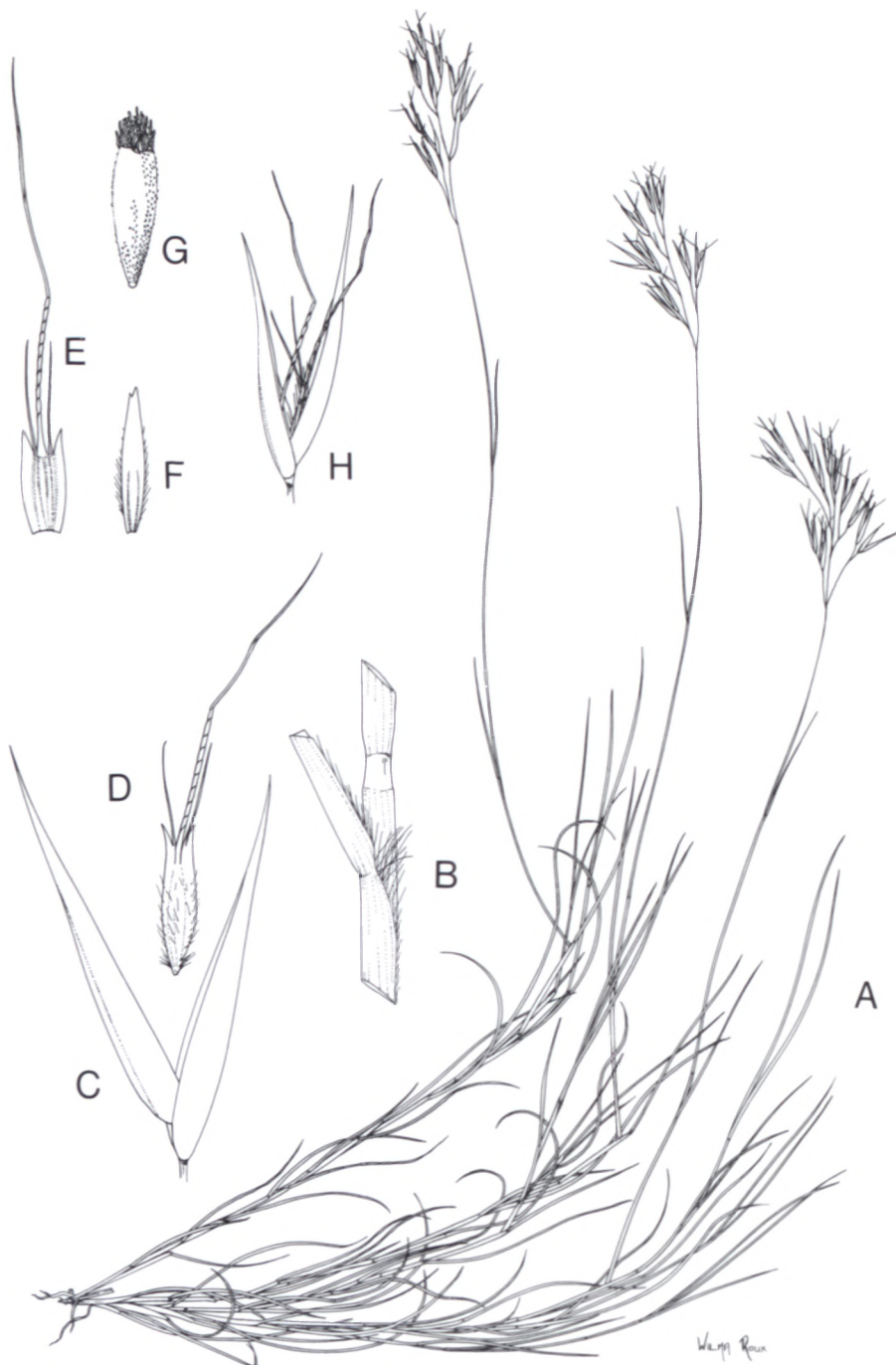


FIGURE 15.—*Pentameris glacialis* N.P. Barker. A, habit: showing thin, decumbent culms; B, indumentum of sheath, pubescent along margin, sheath mouth and leaf blade. C–H, parts of spikelet and florets: C, glumes; D, whole basal floret with mature fruit; E, lemma (opened, flattened and viewed from inside of floret) showing venation, lemma bristles, lemma lobes (adnate to bristles for about half their length) and geniculate awn; F, palea; G, fruit with apical hairs; H, spikelet. A,  $\times 0.4$ ; B–F,  $\times 3.7$ ; G,  $\times 6$ ; H,  $\times 2.4$ .

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