

A revision of the genus *Prionanthium* (Poaceae : Arundineae)

GERRIT DAVIDSE*

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ABSTRACT

Prionanthium is revised and three species are recognized. All three species have a chromosome number of $n = 7$. The genus is unusual in having multicellular, secretory glands on the glumes and a wide range of inflorescence types. *Prionanthium* is considered to be arundinoid on the basis of its leaf anatomy, ciliate ligule, spikelet morphology and, less strongly, chromosome number. Its chromosome number, multicellular glands, two florets per spikelet, type of palea and rachilla extension relate it more closely to *Pentaschistis* than to any other extant arundinoid genus. A fully illustrated taxonomic account is presented.

UITTREKSEL

Prionanthium word hersien en drie spesies word onderskei. Al drie spesies het 'n chromosoomgetal van $n = 7$. Die genus is buitengewoon omdat dit meersellige afskeidingskliere op die glumas het en verskillende tipes bloeiwyses het. Op grond van die blaaranatomie, gesilieerde tongetjie, blompakkiemorfologie en, in 'n mindere mate, chromosoomgetal behoort *Prionanthium* tot die Arundineae. Die chromosoomgetal, meersellige kliere, twee blommetjies per blompakkie, tipe palea en ragillaverlenging dui eerder op 'n verwantskap met *Pentaschistis* as met enige ander bestaande genus in die tribus. 'n Volledige taksonomiese beskrywing word gegee.

INTRODUCTION

Prionanthium, a genus of three annual species, found only in the Cape Province, is one of the rarest grass genera of southern Africa and one of the species has been listed as endangered (Hall & Veldhuis 1985). The total number of separate populations known is 14. While collecting cytological specimens of grasses from the Cape, we were able to locate populations of all three species and this stimulated the following taxonomic revision. Ellis (in prep.) will report in detail on the leaf blade anatomy.

HISTORICAL REVIEW

The genus *Prionanthium* was first described by Desvaux (1831), who was unable to relate it to any other genus known to him. He named the only species *P. rigidum* and gave its distribution as 'India Oriental', (India and the East Indies). This was clearly an error, for the illustration that he provided clearly indicates that *P. rigidum* is the Cape species now known as *P. dentatum*. *Prionanthium* was undoubtedly based on Thunberg's collection from the Cape, the only collection known of the species until 1975, although this collection was not specifically cited by Desvaux. However, Thunberg's collection had already been described by Linnaeus the Younger (1781) as *Phalaris dentata* so that the correct name for the type species, as pointed out by Henrard (1941), is *Prionanthium dentatum* (L. f.) Henrard.

Nees (Lindley 1836) redescribed the genus as *Prionachne*, basing it on the second known species, *P. ecklonii*, and later (Nees 1841) illegitimately renamed *Prionachne* as *Chondrolaena*.

The third species, *P. pholiuroides*, was described by Stapf (1899).

For more than two centuries, the genus was associated with a mixture of genera (often recognized as subtribes (cf. Pilger 1954; Zotov 1963)) that would be termed avenoid and arundinoid in modern terms (cf. Clayton & Renvoize 1986). Following Hubbard's (1948) formal recognition of the tribe Danthonieae, Chippindall (1955) was the first to explicitly and exclusively associate *Prionanthium* with arundinoid genera in the modern sense of Clayton & Renvoize (1986). This placement has been followed by De Wet (1956), Brown (1977), Renvoize (1981, 1986), Clayton & Renvoize (1986) and Watson *et al.* (1986).

MORPHOLOGY

There are several morphological features which merit discussion beyond that provided in the formal descriptions of the taxonomic section.

Multicellular, presumably secretory, glands occur on the glumes of all three species. They are of two kinds: stalked in *P. dentatum* (Figures 1A, B; 2C) and *P. ecklonii* (Figure 1C, D) and sessile in *P. pholiuroides* (Figures 1E, F, H; 2D). The stalked glands are approximately cylindrical in shape with sloping bases. They are composed of 16 rows of cells in circumference. The apex is rounded with a shallow, basin-like depression in the centre surrounded by a low, heavily cutinized lip. The apices of the glands illustrated for *P. ecklonii* (Figure 1D) have apparently been slightly distorted through shrinkage. At the bottom of the basin-like depression is a rectangular grid formed by the raised, rigid, anticlinal adjacent cell walls of small, square cells (Figure 1H). The stalks of the glands tend to be longer toward the apex of the glume in both *P. dentatum* (Figure 1A) and *P. ecklonii* (Figure 1C).

* Missouri Botanical Garden, P.O. Box 299, St Louis, Missouri 63166, USA.

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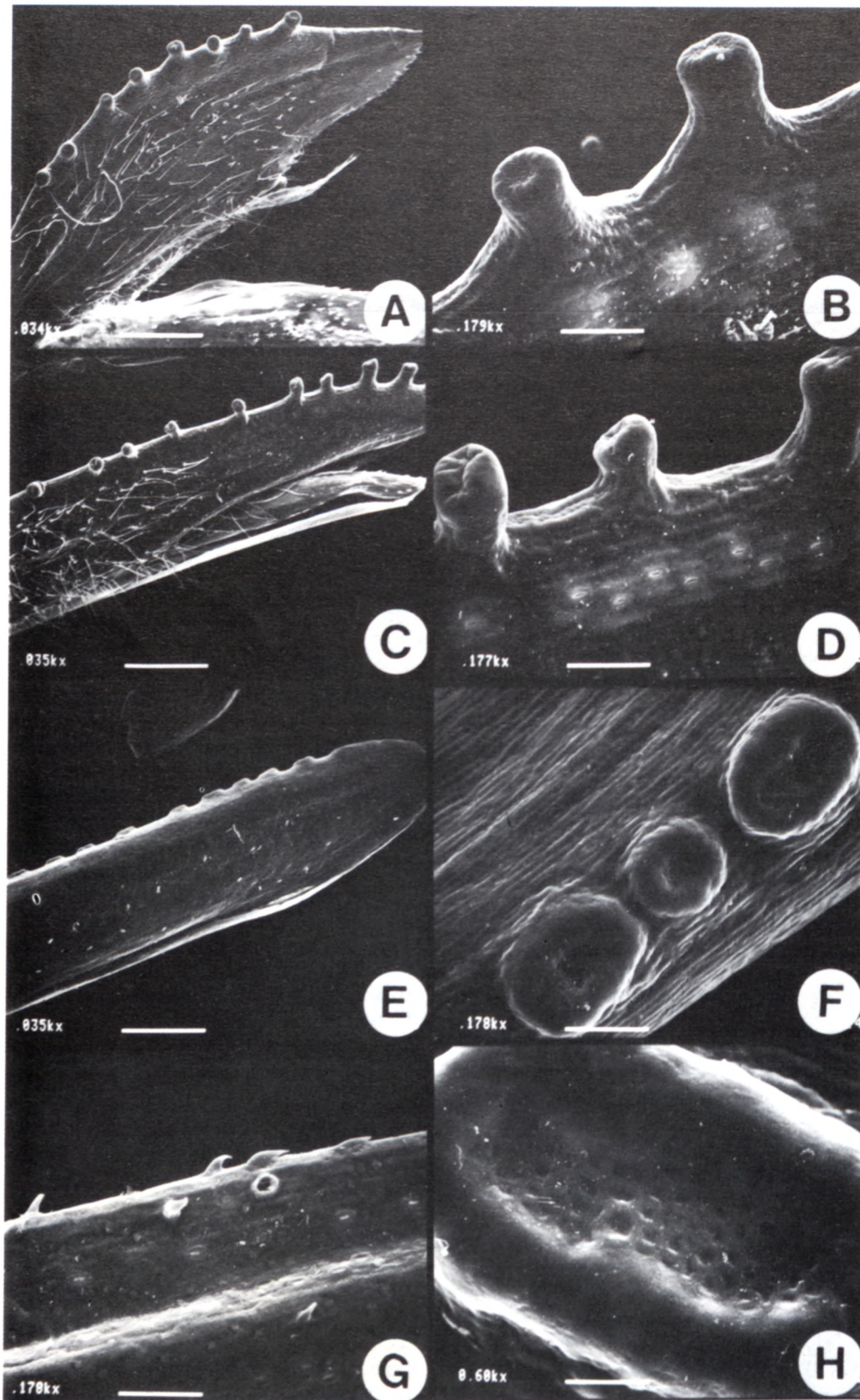


FIGURE 1.—Multicellular, secretory glands of *Prionanthium*. A–B, *Prionanthium dentatum*, Davidse 33394, on keel of glume: A, inner view of glume with stalked glands along the keel, $\times 20$; B, stalked glands, $\times 100$. C–D, *P. ecklonii*, Davidse 34018: C, inner view of glume with stalked glands along the keel, $\times 20$; D, stalked glands, $\times 100$. E–H, *P. pholiuroides*: E–F, H, sessile glands on keel of glume, Davidse 33983; E, inner view of glume, $\times 20$; F, sessile glands, $\times 100$; G, Davidse 34053, glandless glume, keel with only prickles, $\times 100$; H, close-up of sessile gland from Figure 1F, $\times 360$.



FIGURE 2.—Morphology of *Prionanthium* species. A, habit of *P. ecklonii*, Davidse 34018. B–D, inner view of glumes: B, *P. ecklonii*, Davidse 34018; C, *P. dentatum*, Davidse 33394; D, *P. pholiuroides*, Duthie s.n.

The sessile glands of *P. pholiuroides* are basically elliptical in outline to nearly circular in the smaller ones (Figure 1F, H). The cutinized lip arises directly from the surface of the glume and is more massive than in *P. dentatum* and *P. ecklonii*. The central depression of the gland has the same type of grid as the other two species (Figure 1F, H).

The glands occur primarily along the midnerve of both glumes, but they are completely absent in some plants of three populations of *P. pholiuroides* (Struisbaai, Davidse 34048, 34053 (Figure 1G); Stellenbosch Flats, Duthie 1767; Gordons Bay, Parker 3745). In one other population (Duthie s.n. in PRE-39169) of this species, they may occur on some of the lateral nerves in addition to the midnerve (Figure 2D).

Multicellular, secretory glands are rare in the Poaceae as a whole, but they occur in about half of the species of *Pentaschistis*, an arundinoid genus centred primarily in South Africa. In the glandular *Pentaschistis* species, multicellular, secretory glands occur on the leaves and inflorescence branches as well as on the glumes. Furthermore, in addition to stalked and sessile, multicellular glands, sunken glands also occur, for example in the leaf blade of *P. angustifolia* (Nees) Stapf and *P. setifolia* (Thunb.) McClean (R.P. Ellis pers. comm.).

For comparison, glands of two species of *Pentaschistis* were examined in detail. In *P. airoides* (Nees) Stapf, the glands on the inflorescence branches are fundamentally similar to those of *Prionanthium pholiuroides* in being sessile with a prominent, heavily cutinized lip, surrounding a central depression with a reticulate grid (Figure 3A). In the marginal, sessile leaf glands of *P. aspera*, the internal structure of the depression is more elaborate. The longitudinal cell walls of the grid in the central depression have developed to a size approximately half as large as the lip, and so form prominent ribs (Figure 3B). Evidently, *Pentaschistis* has a more diverse array of glands, although at least one kind is fundamentally similar to those of *Prionanthium*.

Multicellular glands also occur in many species of *Eragrostis* where they are always sessile, in the *Clavelligera* group of *Panicum*, where they are prominently stalked, and in *Sporobolus heterolepis* (A. Gray) A. Gray, where they are raised bands on the pedicels (Bessey 1884). In some *Eragrostis* species the basic structure is quite similar to that of *Prionanthium* (Nicora 1941), whereas those of *Panicum* are quite different with long, slender stalks supporting a spherical cluster of parenchyma cells and have been termed multicellular glandular macrohairs (Kabuye & Wood 1969).

The function of the glands in *Prionanthium* is not known. In some freshly collected specimens of *P. pholiuroides* the glands were glistening with a thin layer of moisture which I assume to indicate active secretion. In very glandular species of *Pentaschistis*, such as *P. aspera* (Thunb.) Stapf, *P. angulata* (Nees) Adamson, *P. angustifolia* (Nees) Stapf and others, the plants may be sticky and/or produce an unpleasant smell. The volatile substance that is produced is not known. I did not detect any kind of odour in any species of *Prionanthium*. In *Pentaschistis*, at least in those species that produce it

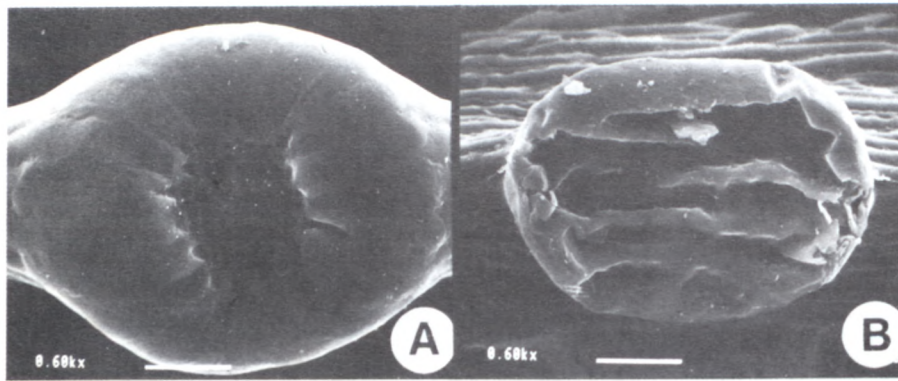


FIGURE 3.—Multicellular, secretory glands of *Pentaschistis*. A, *Pentaschistis airoides*, Davidse 34006, sessile gland on pedicel, $\times 310$; B, *Pentaschistis aspera*, Ellis 5439, sessile gland on leaf margin, $\times 310$.

copiously, the volatile substance may be an anti-herbivore mechanism. It is possible that in *Prionanthium* the glands produce a sticky substance that would allow mature spikelets with caryopses to be dispersed through adhesion to animals. I could not investigate this matter because all populations that I observed in the field were too young.

Inflorescences in *Prionanthium* display a distinct reduction series. The inflorescence of *P. dentatum* is the most unspecialized. It is a condensed panicle that is superficially spike-like. The short panicle branches are tightly appressed to the axis of the panicle. In *P. ecklonii* most of the inflorescence branches are reduced to pedicels only and they occur in pairs, one short-pedicelled (nearly sessile) the other longer-pedicelled. Only at the base of vigorous inflorescences is one order of elongated inflorescence branches developed, and the spikelets are paired on these branches, except for the apex, as they are on the main rachis of the inflorescence. Towards the apex of the inflorescence the paired arrangement is lost and the spikelets are solitary. In *P. pholiuroides* the solitary arrangement of the spikelets is maintained throughout the inflorescence. In very depauperate specimens of this species the inflorescence may be reduced to a few, or exceptionally, to a single spikelet.

Except for the non-disarticulating rachis, the structure of a *P. ecklonii* inflorescence superficially resembles a typical andropogonoid raceme, in that the spikelets are paired and borne unilaterally. As in most Andropogoneae the glumes have a much firmer texture than the lemmas and there are two functional florets. The inflorescence of *P. pholiuroides* is clearly even further reduced.

The existence of this transitional series of inflorescence types in a small genus is remarkable and clearly demonstrates how racemose inflorescence types in the Poaceae can readily arise through a series of progressive reductions from the paniculate condition. That this has happened repeatedly in the Poaceae is evident from the fact that of the 40 tribes recognized in the family by Clayton & Renvoize (1986), 24 have a racemose type of inflorescence in at least one of their constituent species.

The lodicules of *Prionanthium* are fleshy, cuneate, shallowly one or three-lobed, lack microhairs or cilia at the apex (Figure 4A–D), and generally have two vascular bundles. They clearly fall within the variation range encountered in the Arundineae (Tomlinson 1985; Clayton & Renvoize 1986). In *P. dentatum* (Figure 4A) the lodicules have a more prominent lateral lobe than those in *P. pholiuroides* (Figure 4B) and *P. ecklonii* (Figure

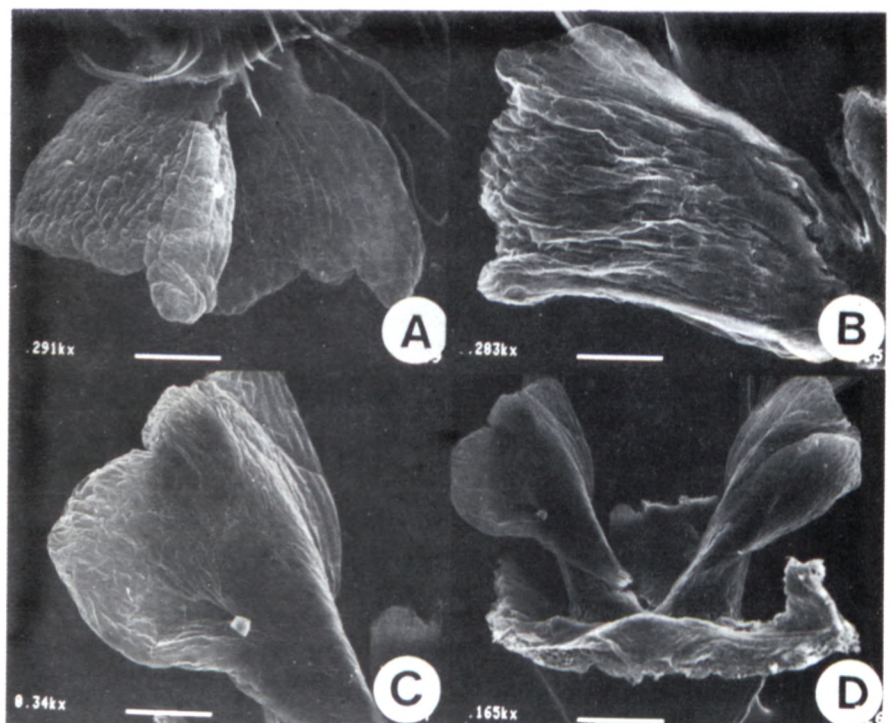


FIGURE 4.—Lodicules of *Prionanthium* species. A, *P. dentatum*, Davidse 33394, inner and outer view of a pair of lodicules with cut-off, hairy lemma at the base, $\times 150$; B, *P. pholiuroides*, Spies 3678, inner view of old, slightly distorted lodicule, $\times 150$. C–D, *P. ecklonii*, Davidse 34018: C, inner view of lodicule, $\times 175$; D, pair of lodicules at the base of the palea with lemma and ovary cut off, $\times 85$.

4C, D), and, in comparison to these two species, their point of attachment is further away from the palea, i.e., they are positioned more toward the dorsal side of the lemma. The lodicules of the latter two species are very similar.

The fruit of *Prionanthium* has never been described. That of *P. dentatum* still remains unknown but in both *P. pholiuroides* (Figure 5A, B) and *P. ecklonii* (Figure 5C, D) it is a caryopsis with the pericarp fused to the seed coat. It is narrowly lanceolate in outline, slightly convex on the embryo side and grooved on the hilum side. The hilum is linear. In *P. pholiuroides* the hilum groove is nearly as long as the caryopsis and is uniformly deep (Figure 5B). In *P. ecklonii* the hilum groove is $\frac{1}{2}$ — $\frac{4}{5}$ as long as the caryopsis and is deep in the lower half of the caryopsis but rather shallow in the upper half (Figure 5D). The embryo is $\frac{1}{4}$ — $\frac{3}{10}$ as long as the caryopsis. The caryopsis is held loosely between the lemma and palea. In all respects the caryopsis morphology is typical of arundinoids.

The manner in which the spikelet disarticulates at caryopsis maturity is, however, not entirely typical of arundinoids. As is the norm in the subfamily, disarticulation takes place between the florets, and the glumes are long-persistent. However, the florets containing the caryopsis are not shed immediately but each of the two florets of a spikelet is held between the incurved margins of the subtending glume. Although the process of disarticulation has not been observed beyond this point in the field, inferences from mature plants of *P. ecklonii* and *P. pholiuroides* which contained a high percentage of mature caryopses in their spikelets, suggest that the following events are probable: the florets containing the caryopses remain enclosed within the glumes for a long time after the caryopses have matured and after the plants have died. Presumably the glumes break off simply due to mechanical wear as the plants disintegrate

during the dry season. Mature inflorescences, with most spikelets bearing caryopses, which were soaked in water did not show any noticeable hygroscopic activity of the glumes or florets under laboratory conditions. Furthermore, it is likely that the upper floret breaks off first since the upper glume is very prominently hinged and breaks off more easily than the lower one. This process seems consistent with the tougher, chartaceous nature of the glumes compared with the delicate, hyaline florets, and this suggests that the function of protecting the caryopsis has been taken over from the lemmas and paleas by the glumes.

CYTOLOGY

No chromosome counts have ever been reported for any species of the genus. Young inflorescences were collected in Carnoy's fixative in the field. Anthers were squashed in aceto-carmin to which a small amount of iron-acetate was added. Photomicrographs of chromosome complements were made with a Reichardt Univiar microscope.

All species had $n = 7$ with regular bivalent pairing and no meiotic irregularities (Table 1; Figure 6A–D). The only chromosomal irregularity was the occurrence of a small B-chromosome in one sample (*Davidse 34048*) of *P. pholiuroides* (Figure 6E, F). Besides its small size, it stained slightly lighter and behaved differently from the normal bivalents (Figure 6E, F), three characteristics that define B-chromosomes (Jones & Rees 1982). The B-chromosome did not line up on the metaphase I plate (Figure 6F), but since no micronuclei were observed in the tetrads at the end of the second division it appears that the B-chromosome is randomly incorporated into any one of the tetrad nuclei. Due to a paucity of fixed material in the right stage of meiosis, it was not possible to study the behaviour of the B-chromosomes at the two meiotic anaphases nor in pollen meiosis. Although B-

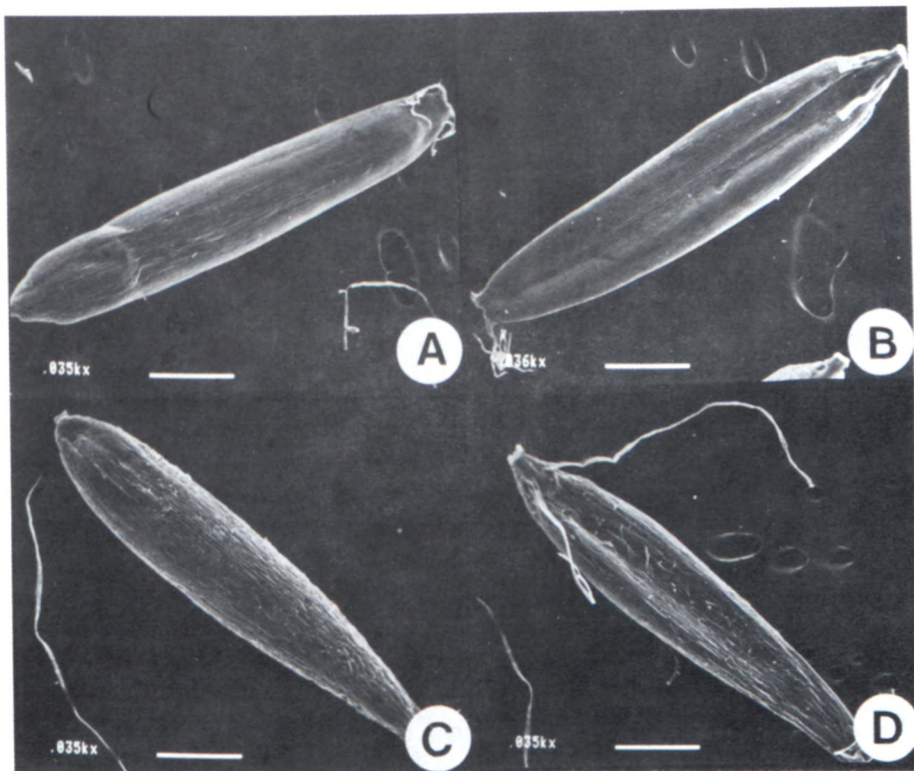


FIGURE 5.—Caryopses of *Prionanthium* species. A–B, *P. pholiuroides*, Ellis 5482A: A, embryo side; B, hilum side. C–D, *P. ecklonii*, Ellis 5503A: C, embryo side; D, hilum side. All $\times 17$.

TABLE 1.—Chromosome numbers of *Prionanthium* species

Species	Chromosome no.	Locality and voucher
<i>P. dentatum</i> (L. f.) Henrard	n = 7	CAPE.—3319 (Calvinia): 16 km S of Nieuwoudtville (–AC), <i>Davidse 33394</i> .
<i>P. ecklonii</i> (Nees) Stapf	n = 7	CAPE.—3218 (Clanwilliam): 45 km N of Citrusdal (–BD), <i>Davidse 34018</i> , <i>Spies 3693</i> .
<i>P. pholiuroides</i> Stapf	n = 7	CAPE.—3318 (Cape Town): 17 km W of Malmesbury (–BC), <i>Davidse 33983</i> , <i>Spies 3678</i> .
	n = 7 + 1B	CAPE.—3420 (Bredasdorp): 6 km N of Struisbaai (–CA), <i>Davidse 34048</i> .

chromosomes are generally considered to be genetically inert, they often affect fertility, especially when present in high numbers (Jones & Rees 1982). Nevertheless, their occurrence in the population with the most variable

spikelet morphology is noteworthy. Although this variation is probably due to simple segregation and recombination, the possibility of a B-chromosome effect cannot be entirely ruled out without further research.

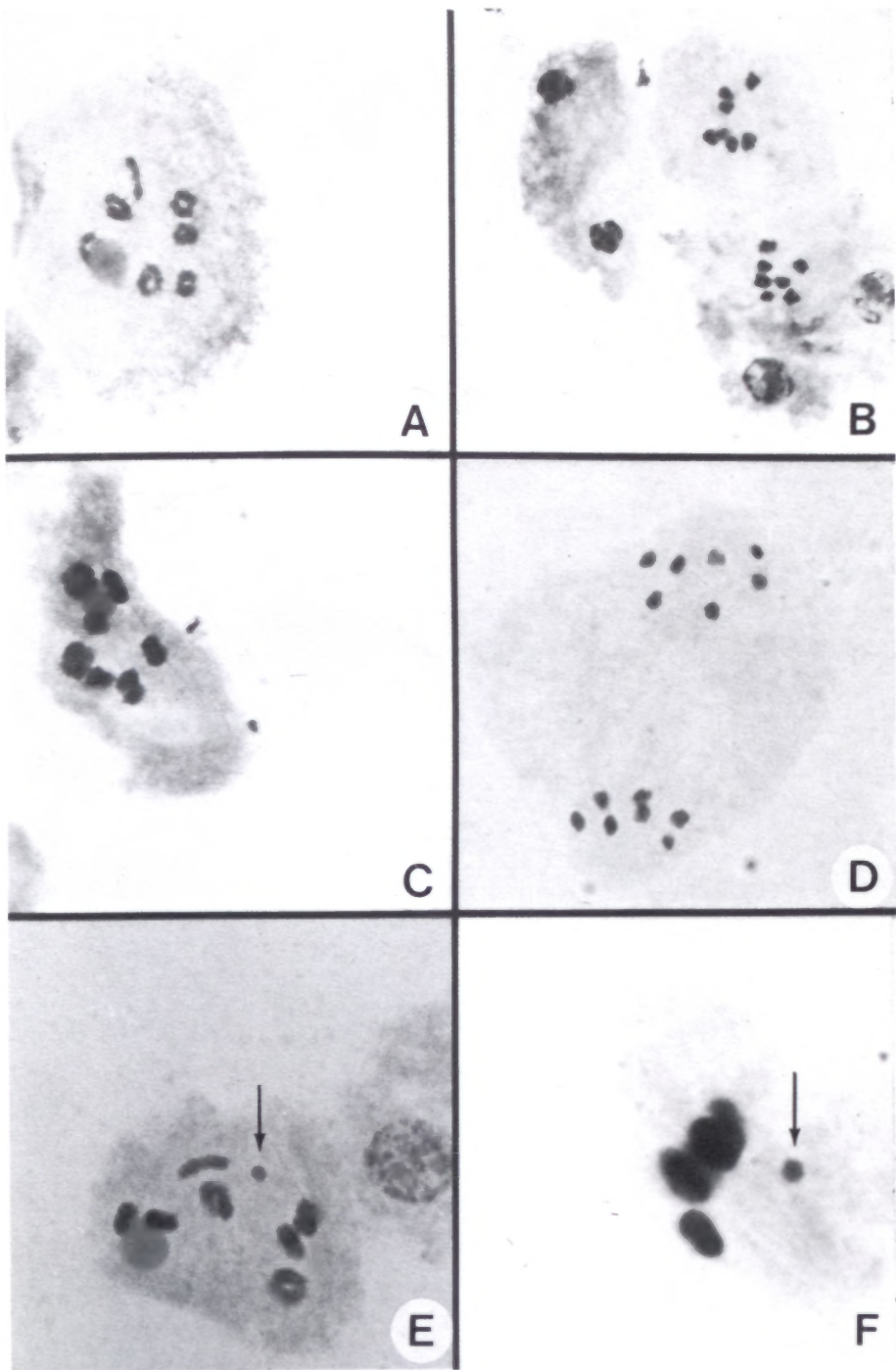


FIGURE 6. — Meiotic chromosomes of *Prionanthium* species. A–B, *P. dentatum*, *Davidse 33394*, n = 7: A, diakinesis; B, metaphase II. C, *P. ecklonii*, *Davidse 34018*, diakinesis, n = 7. D–F, *P. pholiuroides*: D, *Davidse 33983*, anaphase I, n = 7; E–F, *Davidse 34048*; E, diakinesis, n = 7 + 1B; F, metaphase I, B-chromosome excluded from the metaphase plate. Arrows point to B-chromosome.

GENERIC RELATIONSHIPS

Although Chippindall (1955) expressed reservations about the classification of *Prionanthium* in the Danthonieae (= Arundineae, cf. Clayton & Renvoize 1986), it has not been challenged since that time (De Wet 1956; Renvoize 1981; Watson *et al.* 1986; Clayton & Renvoize 1986). I agree with this assessment based on data from leaf anatomy, gross morphology and chromosome number.

Leaf anatomy has previously been studied by De Wet (1956) and Renvoize (1981, 1986) in *P. pholiuroides* and Watson *et al.* (1986) in an unspecified species. (Although De Wet (1956) noted that he had studied *P. ecklonii* anatomically, the specimen that he cites as a voucher apparently is one of the Duthie collections made in the Stellenbosch Flats and actually represents *P. pholiuroides*. His reference to 'type' is inexplicable if interpreted as 'type collection' since none of the *Prionanthium* type collections originated in the Stellenbosch area. Perhaps he meant to indicate the kind or 'type of *P. ecklonii* originating in Stellenbosch', which, as I have just indicated, represents *P. pholiuroides*.) A detailed study of leaf blade anatomy will be presented by Ellis (in prep.).

From the published results it is clear that *Prionanthium* is typically arundinoid in its anatomy. It has a non-Kranz leaf anatomy that typifies most arundinoid genera, including double bundle sheaths, non-radiate mesophyll with a maximum lateral cell count greater than four, adaxial ribs, bulliform cell groups not associated with colourless cells, finger-like microhairs with tapering distal cells, domed subsidiary cells and sinuous long cells in the abaxial epidermis, and dumbbell-shaped to nodular silica bodies. Two unusual features for the subfamily were noted by Renvoize (1986): 1, the chlorenchyma extends between the outer bundle sheath and upper sclerenchyma girders or between upper and lower sclerenchyma girders, a feature also noted by Watson *et al.* (1986); 2, the upper and/or lower epidermal cells are large and thin-walled. Although unequivocally arundinoid, the anatomical evidence available to date is not sufficient for a detailed comparison with other possibly related genera.

All *Prionanthium* species have a ciliate ligule, a characteristic that is shared with all other arundinoid genera recognized by Clayton & Renvoize (1986).

The relationship of *Prionanthium* to other arundinoid genera has only been explicitly discussed by Clayton & Renvoize (1986: 165), who consider it to be one of the primitive arundinoid genera, along with *Tribolium*, *Urochlaena*, *Elytrophorus*, *Spartochloa*, *Notochloe*, *Zenkeria*, *Piptophyllum*, and *Styppeiochloa*. They based this assessment on the short glumes and multinerved lemmas with entire tips of these genera. Furthermore, they (Clayton & Renvoize 1986: 171) noted that '*P. dentatum* hints at a distant relationship with *Tribolium*', without indicating on which character(s) they made this judgement. Presumably they suggested this relationship because *P. dentatum* has the most fully developed panicle of the three species and its proportionally short and broad spikelets superficially resemble those of the *Lasiachloa* alliance of *Tribolium*.

Four spikelet characters point to a relationship between *Prionanthium* and *Pentaschistis*: the occurrence of well differentiated multicellular glands, two florets per spikelet, a small rachilla extension above the upper floret, and similar paleas. Since multicellular glands are rare in the family, I consider this character especially important in relating *Prionanthium* to *Pentaschistis*.

Although *Prionanthium* and *Pentaschistis* share a number of features, their relationship is not a close one, as many differences in spikelet characteristics demonstrate. Of the three characters explicitly mentioned by Clayton & Renvoize (1986) as typical of the primitive Arundineae, *Prionanthium* does not differ strongly from *Pentaschistis* in two: 1, short glumes (in both genera the glumes are as long as the spikelet and are as long as or longer than the uppermost floret); 2, awnless lemmas (all species of *Prionanthium*, 10 out of ± 65 species of *Pentaschistis*); 3, multinerved lemmas (3–5-nerved in *Prionanthium* and 5–11-nerved in *Pentaschistis*).

The primary basic chromosome number of the Arundinoideae has been considered to be $x = 12$ (Clayton & Renvoize 1986). However, it is more likely that this is a secondary base number derived by polyploidy, since a number of arundinoid genera are now known with $n = 6$: *Tribolium* (Davidse *et al.* in preparation, not $x = 7$ as incorrectly reported by De Wet 1960), *Merxmuellera* and *Karroochloa* (as *Danthonia*, De Wet 1954, 1960; Du Plessis & Spies 1988; Spies & Du Plessis 1988), *Chinochloa* (as *Danthonia*, Singh & Godward 1963), *Schismus* (numerous reports, the latest Faruqi & Quraish 1979; Du Plessis & Spies 1988 and Spies & Du Plessis 1988) and *Pseudopentameris* (Spies & Du Plessis pers. comm.). Stebbins (1956) and Hunziker & Stebbins (1987) also consider $x = 6$ to be the basic chromosome number of the Arundinoideae. Less common base numbers in the subfamily are $x = 7$ and 13 in *Pentaschistis* (Tateoka 1965; Hedberg & Hedberg 1977). *Prionanthium* with $n = 7$ has a number that is unusual for arundinoids but one that is matched at the diploid level, $n = 7$, in part of the genus *Pentaschistis* (De Wet 1954, 1960; Du Plessis & Spies 1988; Spies & Du Plessis 1988). There is also a resemblance between the two genera in the size of the chromosomes, among the largest chromosomes in the subfamily.

CONSERVATION STATUS

All three species of *Prionanthium* have been included in the *South African red data book* (Hall & Veldhuis 1985). The status of both *P. ecklonii* and *P. dentatum* (as *P. rigidum*) is listed as uncertain, whereas *P. pholiuroides* is listed as endangered. From the fieldwork and herbarium research that I conducted, it is apparent that *P. pholiuroides* is the most widely distributed of the three species (Figure 7). The population of *P. pholiuroides* reported on by Hall & Veldhuis (1985) was revisited on 21 September, 12 October and 16 November 1987 and still existed as a population of thousands of individuals. However, the local distribution was very spotty and clumped. Similar sites only a few kilometers away lacked any sign of *P. pholiuroides*. It had also managed to establish itself in a small area of disturbance along the roadside. The main population grows in a heavily over-grazed depression invaded by introduced species of *Acacia*.

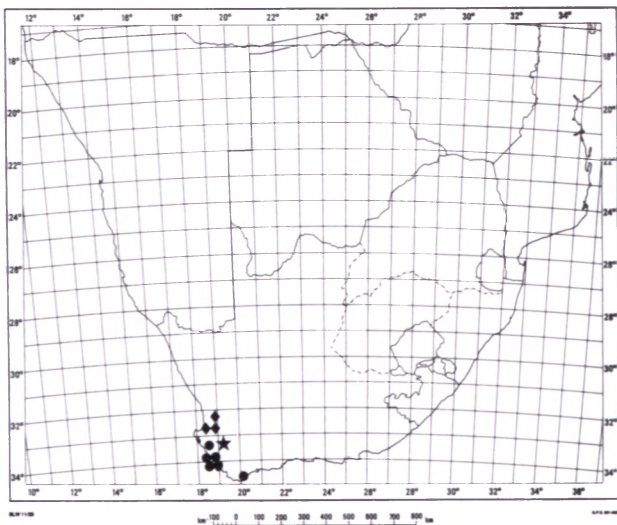


FIGURE 7.—Distribution of *Prionanthium dentatum*, ★; *P. ecklonii*, ◆; *P. pholiuroides*, ●.

We discovered a modest range extension for this species (Davidse 34048, 34053). Its total distributional range, although very disjunct, is approximately 250 km, and not 60 km as noted by Hall & Veldhuis (1985). At this new site, the species grew on a limestone outcrop, especially in small sandy soil pockets on the eroded limestone. This indicates that its habitat requirements may not be quite as specialized as believed by Hall & Veldhuis (1985). It seems quite probable that the species has been largely eliminated from localities such as the Stellenbosch Flats, which have been extensively urbanized. It was common there from the 1920s to at least the 1940s, judging by the Duthie and Rehm collections, and although I believe it likely that some plants may still exist in the flats between Gordon's Bay, Cape Town and Stellenbosch, these are likely to be so few and isolated that the species must for practical purposes be considered extinct in this area. Thus, although the species is on the whole rare, it may not be in immediate danger of extinction.

By contrast, *P. dentatum* and *P. ecklonii* appear to have a much more limited distribution and on this basis must be considered to be endangered.

Not surprisingly for annual species, samples of *P. pholiuroides* (Ellis 5482A) and *P. ecklonii* (Ellis 5503A) collected in November 1987 showed good caryopsis production. In both species, at random, five spikelets from five different plants were examined for caryopsis production in both the upper and lower florets. In *P. pholiuroides* the lower florets had 92% caryopsis production and the upper 88%. In *P. ecklonii* 96% of the lower florets and 92% of the upper florets produced caryopses.

All three species appear to be able to exist in areas of moderate disturbance such as that encountered in the typical grazed veld of the Cape. All three species also grew on roadsides which may actually undergo less disturbance than adjacent grazed veld since animals generally do not have access to roadsides. However, road construction projects could have drastic effects on these small roadside populations since the vegetation may be completely scraped off by heavy machinery at any time.

TAXONOMY

Prionanthium Desv., Opusculs sur les sciences physiques et naturelles: 65, t.4, fig. 3 (1831); Stapf: 455 (1899); Chippindall: 271 (1955); R.A. Dyer 2: 833 (1976); Watson *et al.*: microfiche 3 (1986); Clayton & Renvoize: 170 (1986). Type: *P. rigidum* Desv. = *P. dentatum* (L. f.) Henrard.

Prionachne Nees in Lindley: 447 (1836). *Chondrolaena* Nees: 133 (1841), nom. superfl. pro *Prionachne*. Type: *P. ecklonii* Nees = *Prionanthium ecklonii* (Nees) Stapf.

Annuals. Leaves linear; ligule a ciliate membrane. Inflorescence a spike-like panicle or a secund raceme or spike bearing solitary or paired, sessile or short-pedicellate spikelets. Spikelets 2-flowered with a small rachilla extension, laterally compressed, keeled; disarticulation above the glumes and between the florets. Glumes subequal, with the lower slightly longer than the upper, as long as the spikelets, slightly asymmetrical, keeled, rigidly chartaceous and 5–8-nerved in the centre, membranous to hyaline marginally, long persistent after spikelet maturity and each individually enclosing one of the florets at caryopsis maturity; bases coriaceous and hinged, the upper more prominently hinged than the lower; keels usually with prominent, multicellular glands. Florets bisexual. Lemmas hyaline, 3–5-nerved, subequal, nearly as long as or slightly shorter than the glumes, covering the palea wings but not the palea keels at spikelet maturity. Paleas nearly as long as or slightly shorter than the lemmas, 2-nerved and 2-keeled, the back and wings hyaline, narrow, the keels prominent, thickened, well developed, exposed at spikelet maturity. Lodicules 2, cuneate, fleshy, glabrous, shallowly 1- or 3-lobed. Stamens 3. Ovary glabrous; styles 2, separate; stigmas plumose, laterally exserted. Caryopsis narrowly lanceolate in outline, convex on the embryo side, shallowly grooved on the hilum side, especially toward the base; hilum linear; embryo $\pm \frac{1}{4}$ as long as the caryopsis.

Genus of three species endemic to the Cape Province.

Key to species

- 1a Florets pubescent 1. *P. dentatum*
- 1b Florets glabrous:
 - 2a Spikelets solitary; inflorescence usually unbranched; glands on glume keels sessile or slightly stalked, rarely absent 3. *P. pholiuroides*
 - 2b Spikelets paired except solitary near the apex of the inflorescence; inflorescence (except in depauperate specimens) with appressed branches at the base; glands on glume keels conspicuously stalked 2. *P. ecklonii*

1. *Prionanthium dentatum* (L. f.) Henrard in Blumea 4: 530 (1941). Type: Cape, Bockland, 1773, Thunberg s.n. (UPS, holo.—PRE, microf.; PRE, fragm!; BM!, K!, MO!).

Phalaris dentata L. f.: 106 (1781); Thunberg: 19 (1794). *Phleum dentatum* (L. f.) Pers. 1: 79 (1805). *Chilochloa dentata* (L. f.) Trin.: 168 (1824), nom. nud., 1: t. 73 (1827). *Prionanthium rigidum* Desv.: 65 (1831); Stapf: 455 (1899). *Lasiachloa pectinata* Trin.: corr. & emend. t. 73 (1836), nom. illeg. superfl. pro *Phalaris dentata* L. f. *Chondrolaena dentata* (L. f.) Steud.: 355 (1840). *Prionachne dentata* (L. f.) Nees: 134 (1841), pro syn. *Chondrolaena phalaroides* Nees.

Culms 30–430 mm tall, unbranched or branched only at the base, glabrous. *Sheaths* short-pubescent; ligule 0,5–1,4 mm long, the membrane 0,05–0,2 mm long, the cilia 0,4–1,3 mm long; blades 15–105 × 0,5–3,0 mm, short-pubescent. *Inflorescence* a condensed, cylindrical spike-like panicle, 5–75 mm long, reduced to a single spikelet in depauperate individuals; rachis cylindrical, pubescent; branches tightly appressed to the rachis, shortened upward; pedicels short stumps or to 1 mm long. *Spikelets* 3,2–5,2 mm long, not obviously borne in pairs, laterally arranged; glumes 5–7-nerved, the side facing the rachis pubescent (Figures 1A, 2C), the hyaline margin broader than the chartaceous centre, the keel with prominent stalked glands, the tip shortly awn-pointed; lemmas evenly pubescent, 3-nerved, shortly awn-pointed; paleas glabrous on the margins, pubescent on the back; anthers 1,8–2,3 mm long. *Chromosome number*: $2n = 14$ (Figure 6A, B).

Only known from the Nieuwoudtville area of the western Cape at an elevation of ± 700 m in Western Mountain Karoo (Figure 7).

Vouchers: *Davidse* 33394, 33396; *Ellis* 2452, 5416, 5417.

Nees (1841) and Chase & Niles (1962), among others, considered Thunberg's (1794) *Phalaris dentata* to be new and different from the *Phalaris dentata* of Linnaeus (1781). This is incorrect because both names are based on Thunberg's collection from 'Bockland' (= Bokkeveld). This is clear from Juel's (1918) account explaining how Linnaeus published hundreds of new species based on Thunberg's Cape collections. I interpret Thunberg's usage to be based on Linnaeus's (1781) name without proper attribution and using a different and original description. For this reason, I consider all other combinations made with the epithet *dentatum* to be based on Linnaeus's (1781) initial usage of this name.

Until Ellis re-collected it in 1975, this species was only known from the type collection made by Thunberg in 1773. Thunberg's collection, however, was a large one and a number of duplicate specimens were distributed to other herbaria so that very good type material exists.

2. *Prionanthium ecklonii* (Nees) Stapf in *Flora capensis* 7: 456 (1899); Chippindall: 271 (1955). Type: 'C. b. sp.' (Cape of Good Hope). Lectotype (chosen here): ad Olifantsrivier fluviam alt. I, Clanwilliam, *Ecklon s.n.* (MO!; BM, isolecto!; PRE, fragment!; US, isolecto!).

Prionachne ecklonii Nees in Lindley: 448 (1836). *Chondrolaena phalaroides* Nees: 134 (1841), nom. illeg. superfl. pro *Prionachne ecklonii*. *Chondrolaena phalaroides* Nees var. *dentata* Nees: 134 (1841).

Culms 190–370 mm tall, usually branched, purple, glabrous. *Sheaths* puberulous or glabrous, usually ciliate. Ligule 0,3–0,6 mm long, the membrane 0,05–0,1 mm long, the cilia 0,3–0,5 mm long; blades 40–160 × 0,5–1,5 mm, glabrous or appressed pubescent. *Inflorescence* an inconspicuously secund spike-like raceme or panicle, 15–95 mm long; rachis cylindrical, glabrous to sparsely puberulent; branches 30 mm long, tightly appressed to the main rachis; pedicels unequal stumps. *Spikelets* 4,4–6,1 mm long, usually borne in pairs in the middle part of the inflorescence, solitary toward the apex of

the inflorescence and its branches, laterally arranged, the pairs borne alternately; glumes 5–8-nerved, the side facing the rachis pubescent, narrower, 1–3-nerved, the side away from the rachis usually broader and glabrous, sometimes sparsely pubescent, 3–4-nerved, the midrib with prominent, stalked multicellular glands; lemmas hyaline but herbaceous at the tip, sometimes scaberrulous on the midrib, otherwise glabrous, 3-nerved; paleas glabrous, usually bilobed at the apex, sometimes sparsely ciliate at the apex; anthers 2,9–3,9 mm long; caryopsis 2,5–3,2 mm long, the hilum $\frac{1}{2}$ – $\frac{4}{5}$ as long as the caryopsis (Figure 5D). *Chromosome number*: $2n = 14$ (Figure 6C).

Only known from the south-western Cape Province at low elevations, rare, in Coastal Renosterveld (Figure 7).

Vouchers: *Davidse* 34018; *Drège s.n.*; *Ecklon s.n.*; *Ecklon & Zeyher s.n.*; *Spies* 3693.

This species was until recently only known from three collections, two made by Ecklon and one by Drège. When Nees (in Lindley 1836) described *Prionachne ecklonii*, he did not indicate a type and only a general geographical distribution was provided. However, from his use of Ecklon's name as the epithet and the fact that all three of the collections had been available to him by 1836 (Gunn & Codd 1981), it is clear that he was basing his species on these collections. This is confirmed from a later publication (Nees 1841), dedicated to Drège, Ecklon and Zeyher, where he redescribed and renamed this species as *Chondrolaena phalaroides* with two varieties, var. *dentata* and var. *edentula*, and explicitly cited the Ecklon and Drège collections. He also referred to his 1836 treatment of *Prionachne* in the synonymy. Unfortunately he did not directly refer to *P. ecklonii* but made the new, but illegitimate, combination *Prionachne dentata*. This new synonym was based on Linnaeus's (1781) *Phalaris dentata*, which was also cited in synonymy, but was in fact misapplied. The fact that Nees explicitly states that he was publishing a substitute name for his *Prionachne* indicates that he considered *Chondrolaena phalaroides* and *Prionachne ecklonii* to be the same species. Accordingly I have chosen to lectotypify *Prionanthium ecklonii* with the Ecklon collection from the Olifantsrivier. This preserves the usage that Stapf (1899) initiated in his excellent treatment of the genus in *Flora capensis*.

Nees (1841) did not truly understand the differences between the two species that had been collected by this time. This is apparent from the fact that he synonymized *Phalaris dentata* (= *Prionanthium dentatum*) with his new species *Chondrolaena phalaroides* (= *Prionanthium ecklonii*). When he renamed *Prionachne ecklonii* as *Chondrolaena phalaroides*, he recognized two varieties, var. *dentata* and var. *edentula*. Under var. *dentata* he listed all but one of the combinations and usages of this name, including his own illegitimate new combination, *Prionachne dentata*. He excluded Thunberg's (1794, 1813) interpretation of *Phalaris dentata* because he felt that Thunberg's description, which was substantially different from that of Linnaeus (1781), could not apply to the same species. In fact, Thunberg's descriptive statements queried by Nees, spike 'subpaniculatum' and 'glumas ovatas', do apply to *Prionanthium dentatum*, especially in contrast to the inflorescence and glume

shapes of *P. ecklonii*. Actually, Thunberg's entire glume description (glumae ovatae, concavae, glabrae, bimarginatae vel cinctae, intra marginem linea duplici aut triplici elevata, viridi, sinuato-serratae) applies very well to the two glumes considered as a single unit. Furthermore, Thunberg (1794) explicitly cites the locality of the collection (crescit in Bockland) which leaves no doubt that it was based on his own collection from the Cape, which was, as noted before, also studied by Linnaeus (1781).

Nees's var. *edentula* should be referred to *Prionanthium pholiuroides* (see the discussion following that species).

3. ***Prionanthium pholiuroides* Stapf** in Flora capensis 7: 456 (1899). Chippindall: 271 (1955). Type: Cape, Fish Hoek Valley, damp hollow, Nov. 1897, *Wolley Dod 3394* (K, holo.; BM!, BOL!, MO!, PRE!).

Chondrolaena phalaroides Nees var. *edentula* Nees: 134 (1841). Type: not located, probably destroyed at B.

Prionachne pholiuroides (Stapf) Phillips: 6, t.63 (1931).

Culms 40–250 mm tall, usually branched, purple, glabrous. *Sheaths* glabrous; ligules 0.3–0.9 mm long, the membrane 0.1–0.3 mm long, the cilia 0.2–0.7 mm long; blades 15–70 × 0.5–1.5 mm, glabrous below; scaberrulous above. *Inflorescence* a secund, 2-ranked spike, 15–60 mm long; rachis triquetrous, curved outward at spikelet insertion, glabrous to scaberrulous; pedicel reduced to a stump. *Spikelets* 3.1–7.0 mm long, the terminal one longest, usually borne singly and alternately on the rachis, the lateral side of the lower glume of each spikelet appressed to the rachis; glumes 7–8-nerved, the midrib and sometimes some or all the nerves with prominent sessile glands, rarely eglandular with prickles on the keels (Figure 1G), glabrous, except pubescent on the inner side of the lower glume, rarely also puberulent on the outer side of the lower glume or completely glabrous; lemmas hyaline but herbaceous in the middle toward the apex and slightly scabrous, otherwise glabrous, the lower 3–5-nerved, the upper 3-nerved; paleas glabrous; anthers 1.8–3.5 mm long. *Caryopsis* 2.5–3.0 mm long, the hilum nearly as long as the caryopsis (Figure 5B). *Chromosome number*: $2n = 14$ and $14 + 1B$ (Figure 6D–F).

Only known from the Cape Province, at low elevations, rare, primarily in shallow depressions that temporarily collect water (Figure 7).

Vouchers: *Anderson 8*; *Davidse 33983*; *Duthie 1767*; *Ellis 5434*; *Rehm 6054*.

When Nees (1841) described *Chondrolaena phalaroides* var. *edentula*, he described the glumes as non-dentate (i.e., lacking stalked, multicellular glands) and the spikelets as entirely alternate (i.e., spikelets borne singly on the rachis). This description applies well to *Prionanthium pholiuroides*, especially when contrasted to *P. ecklonii*. Nees also noted that he only saw a fragment of this taxon, intermixed with other specimens. Presumably this fragment was included with one of the three cited specimens, although he does not specify which one. All three were presumably destroyed since all his Poaceae

specimens were acquired by B in 1855 (Stafleu & Cowan 1981). I have not seen similar fragments or specimens among duplicates of the Ecklon and Drège collections that I have examined. Nees suspected it to represent a new species, but, presumably because of the fragmentary nature of the specimen, decided to recognize it at a lower rank.

A recently discovered population near Struisbaai (*Davidse 34048, 34053*) is quite variable in spikelet morphology. It has the smallest spikelets of all known populations, 3.1–5.2 mm versus 4.5–7.0 mm for all others. However, more importantly, individual plants within the population have spikelets with glumes that vary from completely eglandular and glabrous to those that are typically glandular and pubescent on the inner side, to glandular-glabrous, or eglandular-pubescent. Since these plants are seemingly segregating for these characters, these variations are not taxonomically recognized. The Malmesbury population represented by *Davidse 33459* is variable with regard to glabrous and pubescent spikelets. The only population, apparently now extinct, with glands on nerves other than the mid-nerve of the glumes, is the Stellenbosch Flats population sampled by Duthie from 1925 to 1928.

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SPECIMENS EXAMINED

- Adamson 3268 (3) BOL, BM, NBG; Anderson 8 (3) BOL, K, MO, PRE, STE.
- Davidse 33394 (1) BOL, MO, NBG, PRE; 33396 (1) MO, PRE; 33459 (3) BOL, MO, NBG, PRE; 33983 (3) BOL, MO, NBG, PRE; 34018 (2) BOL, MO, NBG, PRE; 34048 (3) BOL, MO, NBG, PRE; 34053 (3) BOL, MO, NBG, PRE; Drège s.n. (2) BM, K, MO, NBG, PRE; Duthie 1767 (3) BOL, PRE, STE; 1795 (3) PRE, STE; s.n. (3) PRE.
- Ecklon s.n. (2) BM, MO, NBG, PRE, US; Ecklon & Zeyher s.n. (2) PRE; Ellis 2452 (1) PRE; 2453 (1) K, PRE; 5416 (1) PRE; 5417 (1) PRE; 5433 (3) PRE; 5434 (3) PRE; 5435 (3) PRE; 5482A (3) MO; 5503A (2) MO; Esterhuysen s.n. (3) BOL.
- Parker 3745 (3) BOL, K, NBG.
- Rehm 6054 (3) BM, K, PRE; Ronaasen s.n. (3) NBG.
- Spies 3678 (3) PRE; 3693 (2) PRE.
- Thunberg s.n. (1) BM, K, MO, PRE.
- Wolley Dod 3394 (3) BM, BOL, K, MO, PRE.
- Zeyher s.n. (as Pappe s.n.) (3) BOL, NBG, PRE.

Note added in proof

Stalked, multicellular glands also occur on the back of the lower lemma in many species of *Panicum* sect. *Stolonifera* [Zuloaga, F.O. & Sendulsky, T. 1988. A revision of *Panicum* subgenus *Phanopyrum* section *Stolonifera* (Poaceae: Paniceae). *Annals of the Missouri Botanical Garden* 75: 420–455] of tropical America. Although the walls of the stalk are similar to those of *Prionanthium*, the central depression is nearly smooth and lacks the rectangular grid. It is probable that these *Panicum* glands are secretory, but this has not yet been conclusively demonstrated.