

# Taxonomy and leaf anatomy of the genus *Ehrharta* (Poaceae) in southern Africa: the *Ramosa* group

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**Keywords:** Capensis, culm anatomy, *Ehrharta*, Fynbos, leaf anatomy, Poaceae, taxonomy

## ABSTRACT

The *Ramosa* species group in the genus *Ehrharta* is distinguished morphologically by small spikelets with sterile lemmas similar to each other, with tips rounded, truncate or mucronate, with sides glabrous, scabrous or shortly hairy, and with bases appendaged and usually bearded. The rectangular intercostal long cells with sinuous walls, the dome-shaped stomata with a raised rim surrounding the pore aperture, the absence of epicuticular wax and the microhairs without a tapering distal cell are diagnostic anatomically. The *Ramosa* group is composed of two species: *E. ramosa* (Thunb.) Swartz subsp. *ramosa*; subsp. *aphylla* (Schrad.) Gibbs Russell and *E. rehmannii* Stapf subsp. *rehmannii*; subsp. *filiformis* (Nees) Gibbs Russell; subsp. *subspicata* (Stapf) Gibbs Russell. All taxa are linked by intermediates to one or two others in the group. The closest relationship of the *Ramosa* group is to the *Calycina* species group, on the basis of both morphological and anatomical characters.

## UITTREKSEL

Die *Ramosa*-spesiegroep in die genus *Ehrharta* word morfologies onderskei deur klein blompakkies met steriele eenderse lemmas, met punte gerond, afgeknot of stekelpuntig, met kante onbehaar, skurf of kortharig, en met basisse met aanhangsels en gewoonlik bebaard. Die reghoekige tussenribbige lang selle met gekartelde wande, die koepelvormige huidmondjies met 'n verhewe rand rondom die porie-opening, die afwesigheid van epikutikulêre was en die mikrohare sonder 'n spitslopende distale sel is anatomies kenmerkend. Die *Ramosa*-groep bestaan uit twee spesies: *E. ramosa* (Thunb.) Swartz subsp. *ramosa*; subsp. *aphylla* (Schrad.) Gibbs Russell en *E. rehmannii* Stapf subsp. *rehmannii*; subsp. *filiformis* (Nees) Gibbs Russell; subsp. *subspicata* (Stapf) Gibbs Russell. Alle taksons word deur tussenvorms aan een of twee ander taksons in die groep gekoppel. Die naaste verwantskap van die *Ramosa*-groep is met die *Calycina*-spesiegroep, op grond van morfologiese sowel as anatomiese kenmerke.

## INTRODUCTION

Previous papers in this series have outlined the seven provisional species groups of *Ehrharta* in southern Africa, and have dealt with the *Setacea*, *Villosa* and *Dura* groups (Gibbs Russell & Ellis 1987, 1988; Ellis 1987a; 1987b; Gibbs Russell 1987a, 1987b). This paper examines the *Ramosa* group, which is distinguished from the other *Ehrharta* species groups by the small spikelet size (4–9 mm long), sterile lemmas similar to each other, with tips rounded, truncate or mucronate, with sides glabrous, scabrous or shortly hairy, and with bases appendaged and usually bearded (Figure 1). The rectangular intercostal long cells with sinuous walls, the dome-shaped stomata with a raised rim surrounding the pore aperture, the absence of epicuticular wax and the microhairs without a tapering distal cell are diagnostic anatomically. In contrast to the species groups covered already, in which taxa are relatively easy to define and may be distinguished by clear-cut characters, the five taxa comprising the *Ramosa* group intergrade and few consistently reliable characters adequately separate the species and subspecies. Therefore, the taxa accepted here must be considered as nodes in a continuum of intra-group variability. Despite the difficulty, it is desirable to treat the *Ramosa* group taxa formally for the following reasons: 1, most specimens fall within the node, as here defined, and only a comparative

few are intermediates; 2, the great differences between the 'ends' of the continuum, both morphological and ecological, require a means of distinguishing between, e.g., the robust bladeless subshrub of rocky places common at high altitudes (*E. ramosa* subsp. *ramosa*) and the delicate trailing herb with thin soft leaves from moist sheltered sites (*E. rehmannii* subsp. *filiformis*); 3, each of the taxa has a distinct geographical range.

The two taxa that are common in the Fynbos Biome are large plants of widespread distribution, *E. ramosa* subsp. *ramosa* and subsp. *aphylla*. They have been recognized from very early times in the study of the southern African flora (Thunberg 1794). The smaller, less common plants with more limited distribution were first treated as separate species by Stapf (1897, 1900). Previous to his classification, specimens of these taxa had been attributed to *E. ramosa* and *E. aphylla*.

As a result of the confusing pattern of variation and the inadequate early classification of the *Ramosa* group, its nomenclature has also been somewhat difficult. For each of the five taxa in the group a lectotype or neotype was designated.

## METHODS

Methods adopted for previous papers of this series were followed here (Gibbs Russell & Ellis 1987). The descriptions and keys were prepared through the DELTA computer system (Dallwitz 1984).

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MS. received: 1988.10.27.

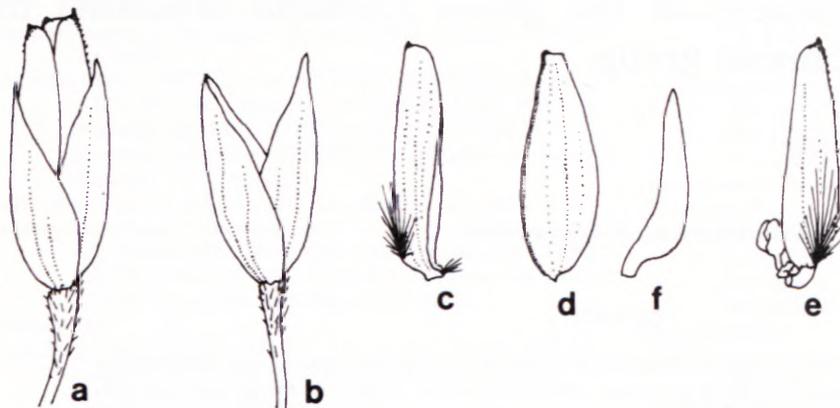


FIGURE 1.—Spikelet of *E. ramosa* subsp. *ramosa* (Esterhuysen 8343, PRE): a, whole spikelet; b, glumes; c, first sterile lemma; d, fertile lemma; e, second sterile lemma; f, palea.

#### TAXONOMY

##### Key to species in the *Ramosa* group

- Plants robust, strongly suffrutescent; leaf blades absent or reduced; sterile lemmas usually mucronate ..... *E. ramosa*  
 Plants not robust, usually herbaceous; leaf blades present, expanded; sterile lemmas usually muticous ..... *E. rehmannii*

1. *Ehrharta ramosa* (Thunb.) Swartz in Transactions of the Linnean Society 5: 49 (1802). Thunb.: 336 (1818); Thunb. ed. Schultes: 335 (1823); Schrader: 2077 (1821); Schrader in Schultes: 1370 (1830); Trinius: 25 (1839); Nees: 205 (1841); Steudel: 7 (1855); Stapf: 677 (1900); Chippindall 39 (1955); Smook & Gibbs Russell: 55 (1985). Type: Thunberg (sheet 8855), UPS, lecto. here designated — IDC microfiche 1036 in PRE!

*Melica ramosa* Thunb.: 21 (1794). *Ehrharta digyna* Thunb.: 66 (1794).

Perennial, tufted, erect or straggling, long-rhizomatous, often robust, suffrutescent. *Rhizomes* woody, branched, naked or with cataphylls. Cataphylls glabrous, thin, or thickened. *Culms* many, erect or geniculate, woody or wiry and persistent, hollow, crowded at the ends of the rhizomes, branched at base and branching above, usually with many fascicled branches, the internodes sometimes with globose orange gall-like swellings at their base. Young shoots intravaginal. *Leaves* not basally aggregated. Culm leaves with sheaths not overlapping, blades absent or reduced, sheaths held away from the culm. Basal sheaths loose, deciduous, or persistent, papery, or membranous, grey, not bearing blades. Ligule a membrane fringed with hairs, about 1 mm long.

*Inflorescence* a raceme or a panicle, open or contracted, of several to many appressed, spreading or nodding spikelets, closely subtended or enveloped below by uppermost leaf sheath or exerted from it, main axis sinuous around appressed spikelets. *Spikelets* pedicellate, distinctly compressed laterally, (5,5–)6–7,5(–9) mm long, about 2–3 mm across. Pedicels usually with short stiff hairs. Glumes keeled, subequal, slightly shorter than rest of spikelet to considerably longer than rest of spikelet, yellowish or green, somewhat spreading or appressed to lemmas at maturity. Lower glume 5–7-nerved, acute. Upper glume 3–5-nerved, acute. *Florets* with lemmas decidedly firmer than the glumes, keeled. Sterile lemmas similar in shape and texture, laterally compressed, sides flat. Lower sterile lemma about  $\frac{3}{4}$  length of upper sterile lemma to about equalling length of upper sterile lemma, with keel and margin parallel; base not stipitate, with

auriculate appendages, bearded; sides glabrous or sometimes scabrous, often short-hairy on the margins, dull, with 2–3 fairly distinct to faint longitudinal ribs and rarely with up to 12 faint transverse corrugations; tip truncate or slightly oblique, usually mucronate, but sometimes aristate or sometimes muticous. Upper sterile lemma similar to lower sterile lemma, but often with transverse corrugations, substipitate, longer than lower sterile lemma. *Fertile floret* with lemma differing from sterile lemmas, strongly laterally compressed and sides unornamented, not exceeding upper sterile lemma or sometimes slightly longer than both sterile lemmas, 7–9-nerved, sides glabrous or scabrous on nerves; tip truncate, midnerve sometimes submucronate. Palea thinner than lemma,  $\frac{3}{4}$  or more as long as lemma. Lodicules 2, fleshy at base, and membranous above, ciliate at margins, or glabrous. Stamens 6. Anthers 2,5–4 mm long, yellow. Ovary glabrous. Stigmas white. Caryopsis not seen (spikelets shed early).

Both subspecies of *E. ramosa* inhabit Mountain Fynbos, growing in xerophytic to mesophytic open habitats.

This species differs from *E. rehmannii* in its robust, consistently suffrutescent habit, bladeless or nearly bladeless leaves, and sterile lemmas with usually submucronate to shortly aristate tips. Although the break between the five taxa in the *Ramosa* group is greatest between the two species as based on the above characters, the separation is not complete, for a number of intermediates are known. The specimens are discussed in more detail under particular subspecies.

Although the majority of *E. ramosa* specimens can be identified to subspecies, there are a number which show intermediate states for the characters that separate the taxa: the size of the plant can vary with age, and in any case may not be apparent on a poor herbarium specimen; the openness of the inflorescence can vary with developmental stage, with young inflorescences of subsp. *aphylla* showing erect spikelets; glume length is variable in subsp. *ramosa*, being either slightly longer or shorter than the sterile lemmas. The difficulty of separating the subspecies has led to their treatment in synonymy as early as Trinius (1839), or as infraspecific taxa (Gluckmann ex Adamson 1942). The two taxa are treated here as subspecies because each has a distinct geographical range. Intermediate specimens are discussed under subsp. *aphylla*.

There are three sheets of *E. ramosa* in Thunberg's herbarium. Sheet 8855 was chosen as the lectotype because it is the most complete, showing typical culm size and branching, leaf sheaths and several inflorescences.

#### Key to subspecies

- Plants very robust, culms to 5 mm across; glumes usually slightly shorter than sterile lemmas; inflorescence usually contracted, pedicels erect to ascending; leaves bladeless ..... la. *E. ramosa* subsp. *ramosa*
- Plants robust, culms to 2,5 mm across; glumes slightly to considerably longer than sterile lemmas; inflorescence usually open, pedicels spreading to reflexed; leaves rarely with small blades ..... lb. *E. ramosa* subsp. *aphylla*

#### la. *Ehrharta ramosa* (Thunb.) Swartz subsp. *ramosa*

*Culms* markedly robust, woody, 300–1 000 mm long, to 5 mm across, erect, or geniculate. Culm leaves with blades absent, at most the blades occasionally represented by an apiculate inrolled tip to the sheath. *Inflorescence* a contracted raceme 30–140 mm long with appressed spikelets. *Spikelets* pedicellate, the pedicels held erect. Glumes 4,5–8 mm long, usually slightly shorter than rest of spikelet or sometimes slightly longer than rest of spikelet. Lower sterile lemma about  $\frac{3}{4}$  length of upper sterile lemma to about equalling length of upper sterile lemma; tip strongly truncate, usually purple-tinged for about  $\frac{1}{4}$  of lemma length. Fertile floret not exceeding upper sterile lemma (shorter or subequal).

Subsp. *ramosa* is distinguished from subsp. *aphylla* by its more robust habit and very thick culms, its narrow inflorescence with erect appressed spikelets, glumes that are often shorter than the lemmas, and the markedly truncate sterile lemmas with purple-tinged ends. It is characteristic of Mountain Fynbos although it extends into Grassy Fynbos and occurs at low altitudes in the eastern part of its range. Its distribution is shown in Figure 2. Subsp. *ramosa* has the widest range of the five taxa in the *Ramosa* species group, although subsp. *aphylla* extends slightly further to the north and *E. rehmannii* subsp. *rehmannii* extends slightly further to the east. It is unusual in *Ehrharta* for a taxon to have both a western and an eastern distribution and yet be absent from the Cape Peninsula-Caledon area. Subsp. *ramosa* grows in sandy or stony Table Mountain Sandstone (TMS) or lateritic soils, often in rocky places, at altitudes of 90 to 2 200 m; and is common at high altitudes. Flowering occurs from October to January.

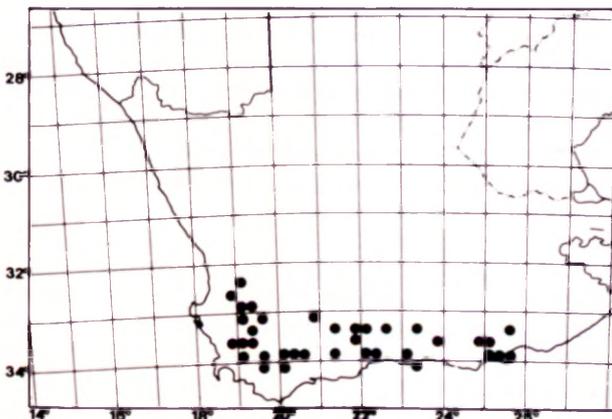


FIGURE 2. —Distribution of *E. ramosa* subsp. *ramosa*.

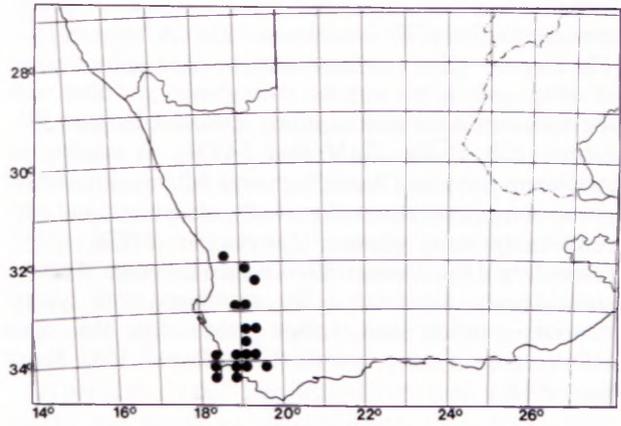


FIGURE 3. —Distribution of *E. ramosa* subsp. *aphylla*.

#### lb. *Ehrharta ramosa* (Thunb.) Swartz subsp. *aphylla* (Schrad.) Gibbs Russell, stat. nov.

*Ehrharta aphylla* Schrad. in Göttingische gelehrte Anzeigen 1821: 2077 (1821); Schrad. in Schultes: 1369 (1830); Nees: 207 (1841); Steud.: 7 (1855); Stapf: 678 (1900). *Ehrharta ramosa* Thunb. var. *aphylla* (Schrad.) Gluckmann ex Adamson: 273 (1942); Chippindall: 39 (1955). Type: *Hesse*, apparently lost; neotype here designated: *Ecklon 914* (specimen in K with suffrutescent culms and bladeless leaves!).

*E. ramosa* Thunb. var. *aphylla* (Schrad.) Gluckmann ex Adamson: 273 (1942).

*E. aphylla* Schrad. var. *fasciculata* Stapf: 679 (1900). Type: tops of mountains, Baviaans Kloof, *Burchell 7725* (K, holo.!; photo and fragment in PRE!).

*Culms* not robust to robust, woody or wiry, 300–800 mm long, to 2,5 mm across, geniculate or decumbent at base. Culm leaves with blades usually absent, but occasionally present on upper leaves. *Leaf blades* when present lanceolate; to 1 mm across, to 30 mm long, rolled, erect, herbaceous, glabrous, gradually tapering at the tip. *Inflorescence* a raceme or a panicle with 1 or 2 branches, usually open or sometimes contracted, 20–90 mm long, with spikelets spreading to nodding. *Spikelets* pedicellate, the pedicels spreading to reflexed. Glumes 4,5–9 mm long, usually slightly or considerably longer than rest of spikelet but sometimes slightly shorter. Lower sterile lemma slightly shorter than upper sterile lemma, rarely purple-tinged and then only at the tips, with up to 12 corrugations; tip oblique or truncate. Upper sterile lemma usually with marked transverse corrugations. Fertile floret sometimes exceeding upper sterile lemma.

Subsp. *aphylla* differs from subsp. *ramosa* in its generally smaller size, open inflorescence with spreading to reflexed spikelets, long glumes and sterile lemmas with truncate to oblique tips that are uncommonly purple-tinged only at the tips. Its distribution is shown in Figure 3. Subsp. *aphylla* occurs only up the western mountains, and is absent from the eastern part of the range of the *Ramosa* group. It grows in Mountain Fynbos on sandy TMS-derived soil between rocks, often in dry microhabitats, and is reported 1–4 years after fire, from altitudes of 230–1 500 m. Flowering occurs from (July) September to January.

A number of specimens are intermediate between subsp. *aphylla* and subsp. *ramosa*. The specimens that occur in the area of sympatry of the subspecies fall into two groups: those with the long glumes of subsp. *aphylla* and the

contracted inflorescence and erect spikelets of subsp. *ramosa* (Du Toit 1747; Esterhuysen 3930; Liebenberg 4331; The Forester 8226) and those with the open inflorescence of subsp. *aphylla* but with the short glumes and often with the dark sterile lemmas of subsp. *ramosa* (Andreae 705; Loxton 221; Stokoe (SAM No.) 54502). A number of specimens from the Clanwilliam area fall into this second group of intermediates, and are leafy, often erect, and with remarkably short glumes (Esterhuysen 14978, 32217; Liebenberg 4308; Stokoe 7809). Within the range of subsp. *ramosa* only, there are a few specimens with typical *ramosa* spikelets and robust culms but the open inflorescence of subsp. *aphylla* (Gibbs Russell 5683, Kensit Jan. 1914).

Although the leaves of subsp. *aphylla* are usually bladeless or with very reduced blades, a few specimens show well developed blades (Du Toit 1425; Ellis 648, 4673; Gibbs Russell 5668, 5672; Hanekom 1294; Richardson 62). This may be natural or phenological variability within the taxon, or these specimens may represent a link across the species line to *E. rehmannii* subsp. *rehmannii*, although the two taxa are allopatric. Such a population at Kirstenbosch was collected in 1918 (Page s.n.) and 1955 (Salter 8665). Gluckmann in 1938 annotated the Page specimen: 'I have examined clusters of this growing in Kirstenbosch and found long-leafed forms intermingled with leafless forms'.

A second possible link across the species line is represented by specimens from the Ceres area (Esterhuysen 28110, 28396; Stokoe 2652). They have typical *aphylla* spikelets, but the plants tend to be slender and leafy with only about 5–10 spikelets per inflorescence, characteristics of *E. rehmannii* subsp. *filiformis*, which does not occur so far to the north.

The Hesse specimen on which Schrader based the name *aphylla* has not been found in GOET, LE, B or P, the herbaria where it was most likely to have been preserved. Pending its lucky discovery elsewhere, a lectotype or neotype must be selected. In his treatment of *Ehrharta* in Schultes (1830), Schrader cited an additional specimen, Ecklon 914. Nees (1832) also cited Ecklon 914 as the type of *E. aphylla* var. *filiformis*. The descriptions of the two taxa differ, Schrader's referring to a suffrutescent plant with no leaf blades, while Nees describes a specimen with soft flat leaves and a much reduced inflorescence. Stapf (1900) states that there are two specimens marked Ecklon 914 at Kew, one representing subsp. *aphylla* and one representing *E. rehmannii* var. *filiformis*. I have seen these specimens, annotated by Stapf, and propose that they serve as neotypes for these taxa. They cannot be lectotypes because there is no indication that either was seen by Schrader or Nees. It would be futile to attempt to find unequivocal lectotypes for the following reasons: 1, specimens labelled Ecklon 914 represent more than one taxon; 2, Ecklon collected a number of *Ramosa* group specimens from different places in the Kleinrivier area and his duplicates are numerous and widely distributed, many without collection numbers; 3, the whereabouts of the personal herbaria of Schrader and Nees is not known; 4, no *Ehrharta* specimens of historical importance exist any longer at B, which is the most likely location of Nees's and Schrader's lost herbaria.

2. *Ehrharta rehmannii* Stapf in Kew Bulletin: 288 (1897); Stapf: 677 (1900); Chippindall: 39 (1955). Type: Outeniqua Mountains, Montagu Pass, *Rehmann* 74 (K, lecto!, here designated; photo and fragment in PRE!).

Perennial, tufted, erect or straggling, long-stoloniferous, delicate or neither distinctly delicate nor robust, not suffrutescent but culms sometimes woody below even in small plants. *Rhizomes* branched, naked or with cataphylls. *Culms* several to numerous, erect to prostrate, woody below or wiry or herbaceous, crowded at ends of rhizome, branched at base and branching above, solid or hollow, the internodes rarely with gibbous gall-like swellings at their base. Young shoots intravaginal. *Leaves* not basally aggregated. Culm leaves with sheaths not overlapping, blades well developed. Leaves auriculate, the auricles with spreading glassy hairs, produced from top of sheath and base of blade. Basal sheaths loose, persistent, papery or membranous, grey, yellowish or whitish, bearing blades or not bearing blades. Ligule a membrane fringed with hairs, 0.3–2 mm long. Leaf blades deciduous or persistent on basal sheaths, persistent on culm sheaths, expanded, linear or lanceolate, erect or spreading, soft or herbaceous, glabrous, scabrous or hairy, with marginal vein not thickened or barely thickened, tip gradually tapering.

*Inflorescence* a raceme or a panicle, reduced or not reduced, open or contracted, not overtopping leaves to considerably overtopping leaves, of 1 to many appressed, spreading or nodding spikelets, closely subtended or enveloped below by uppermost leaf sheath or exerted from uppermost leaf sheath, secund or not secund. *Spikelets* pedicellate, distinctly compressed laterally, 4.0–8.5 mm long. Pedicels usually with short stiff hairs. Glumes keeled, subequal, slightly shorter to slightly longer than rest of spikelet, yellowish or green, gaping widely at maturity or appressed to lemmas at maturity. Lower glume 3–7-nerved; acute to apiculate. Upper glume 1–5-nerved, acute to apiculate. *Florets* with lemmas decidedly firmer than the glumes, keeled. Sterile lemmas similar in shape and texture, laterally compressed, sides flat. Lower sterile lemma about equalling or somewhat shorter than upper sterile lemma, with keel and margin parallel; base not stipitate, with auriculate appendages, bearded or not bearded; sides glabrous, scabrous or with short hairs, dull, smooth and unornamented or with 0–3 fairly distinct to faint longitudinal ribs or with 0–6 faint transverse corrugations; tip truncate or rounded, usually muticous. Upper sterile lemma similar to lower sterile lemma but with distinct corrugations in the upper half, substipitate, longer than lower sterile lemma. *Fertile floret* with lemma differing from sterile lemmas, strongly laterally compressed and sides unornamented, not exceeding upper sterile lemma, 5–7-nerved; tip truncate. Palea thinner than lemma,  $\frac{3}{4}$  or more as long as lemma. Lodicules 2, fleshy at base, or membranous above, ciliate at margins or glabrous. Stamens 6. Anthers 2.2–2.6 mm long. Caryopsis not seen (spikelets shed early).

This species usually grows in wetter habitats than *E. ramosa*, and often at lower altitudes. It differs from *E. ramosa* in its herbaceous to wiry culms, leaves with well developed blades and muticous sterile lemmas. There are three subspecies, which intergrade through a number of intermediates. These specimens are discussed below under the appropriate subspecies.

Although the two species differ in the characters mentioned above, the separation is not absolute, and a number of specimens show intermediate character conditions between *E. ramosa* subsp. *aphylla* and both *E. rehmannii* subsp. *rehmannii* and subsp. *filiformis*. These are discussed in more detail under *E. ramosa* subsp. *aphylla* above.

Stapf (1900) is responsible for the recognition of the herbaceous leafy element in the *Ramosa* species group, and the three subspecies treated here were all described (subsp. *rehmannii* and *subspicata*) or separated from the woody taxa (subsp. *filiformis*) by him. However, it is evident that his concepts of the divisions within the leafy taxa changed during the course of his work. In his original description of *E. rehmannii*, Stapf (1897) quotes seven syntypes. Three of these are also quoted as syntypes of *E. subspicata* (Stapf 1900), showing that his original concept of *E. rehmannii* included both taxa.

The studies reported here, based on far more specimens and a wider geographical representation than were available to Stapf, confirm his opinion that there are three herbaceous leafy taxa in the *Ramosa* species group. However, the boundaries between the taxa in this treatment differ from those of Stapf's as indicated by the specimens he cited. In particular, several of the narrow-leaved specimens with glabrous sterile lemmas he cited as *E. rehmannii* (including the contentious *Ecklon 914*) belong in subsp. *filiformis* rather than subsp. *rehmannii*. Several of the specimens with branched inflorescences and herbaceous glumes that Stapf cited as *E. subspicata* belong in subsp. *rehmannii*. The lectotypes and neotype were chosen from among the several specimens cited by Stapf to reflect the present concepts of each taxon.

#### Key to subspecies

- 1a Inflorescence contracted, pedicels and spikelets erect; glumes subcoriaceous ..... 2c. *E. rehmannii* subsp. *subspicata*  
 1b Inflorescence open, pedicels spreading to reflexed and spikelets spreading to nodding; glumes membranous:  
 2a Inflorescence of fewer than 20(–25) spikelets, leaf blades narrower than 4 mm; sterile lemmas glabrous on sides ..... 2b. *E. rehmannii* subsp. *filiformis*  
 2b Inflorescence of more than 20 spikelets; leaf blades to 6 mm across; sterile lemmas usually hairy on sides or tips and/or strongly scabrous on keels ..... 2a. *E. rehmannii* subsp. *rehmannii*

#### 2a. *Ehrharta rehmannii* Stapf subsp. *rehmannii*

Tufted, erect; neither distinctly delicate nor robust. *Culms* several to many, 300–1 000 mm long, to 2,5 mm across, usually hard, (but to 5 mm across in rare specimens with spongy culms), wiry or herbaceous, branches from upper nodes single or few. *Leaf blades* linear, to 6 mm across, 60–300 mm long, usually spreading but sometimes erect, herbaceous, scabrous on margins and keel. *Inflorescence* a raceme or a verticillate panicle (the lowest whorls sometimes with a few branches), not reduced, open, 45–120 mm long, considerably overtopping leaves, of more than 20 spreading or nodding spikelets, exerted from uppermost leaf sheath, secund. *Spikelets* (5–)6–8 mm long about 2 mm across laterally above the glumes. Pedicels spreading to reflexed. Glumes membranous, 5,5–8 mm long, gaping widely at maturity. Lower sterile lemma usually scabrous or with short hairs on ribs, keel,

tips or margins, rarely glabrous, with 3 fairly distinct longitudinal ribs and sometimes with up to 6 faint transverse corrugations, tip rounded.

Subsp. *rehmannii* is distinguished from the other two subspecies by the long broad leaves, the open paniculate inflorescence with more numerous spreading to reflexed spikelets, and the sterile lemmas with scabrous to shortly hairy keel, ribs and tip. Its distribution is shown in Figure 4. This subspecies grows on streambanks and in rocky places on mountain slopes and sometimes under trees, 400–660 m, flowering from August to December.

A particularly tall, long-leaved form with thick but soft culms and numerous short spikelets (5,5–6 mm long) occurs in forests and on rocky ground at George and Knysna (*Compton 23076*; *Fourcade 5529*; *Ofsowitz 29*; *Palmer s.n.*).

A putative link between leafy specimens of *E. ramosa* subsp. *aphylla* and this subspecies has been mentioned under that taxon. A further link may be the hairiness of the sterile lemmas in subsp. *rehmannii*, which could be an elaboration of their strongly scabrous condition common in *E. ramosa* subsp. *aphylla*. The sterile lemma hairs of subsp. *rehmannii* are short and appressed and restricted to the nerves, margins and tips, thus differing considerably from the longer spreading hairs on the sides of the sterile lemmas in the *E. calycina* complex.

2b. *Ehrharta rehmannii* Stapf subsp. *filiformis* (Stapf) Gibbs Russell, stat. nov. Type: *Ecklon 914* (in part) neotype here designated (specimen in K with thin culms and small leaf blades!).

*Ehrharta rehmannii* Stapf var. *filiformis* Stapf: 677 (1900). Chippindall: 39 (1955); Smook & Gibbs Russell: 55 (1985).

*Ehrharta aphylla* Schrad. var. *filiformis* Nees: 334 (1832). Nees: 207 (1841). Kleinriviersberge zwischen Zäunen, *Ecklon*.

*Ehrharta filiformis* Mez: 292 (1921). Type: Kagebiet, Kleinrivier, *Ecklon & Zeyher 85B*.

Tufted, erect or straggling, delicate or neither distinctly delicate nor robust, often growing in dense masses. *Culms* many to numerous, 120–800 mm long, 0,3–0,5 mm across, erect to decumbent or prostrate in smaller forms, usually herbaceous or sometimes woody toward base of culm, branching at upper nodes varies from seldom-branched with single branches to fascicled with many branches. *Leaves* borne all along the culms to just

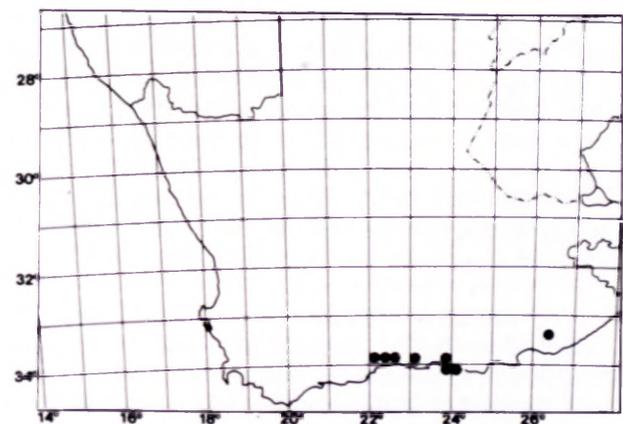


FIGURE 4. —Distribution of *E. rehmannii* subsp. *rehmannii*.

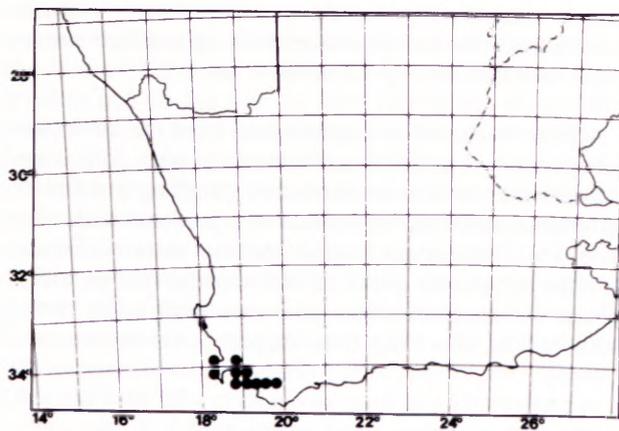


FIGURE 5.—Distribution of *E. rehmannii* subsp. *filiformis*.

below the inflorescence. Leaf blades linear, usually small, thin and soft, to 4 mm across but most leaves very fine, 15–100 mm long, spreading, sparsely glabrous. *Inflorescence* a reduced open raceme, 10–100 mm long, not or only a little overtopping leaves, of 1–15(–24) spreading to nodding spikelets, exerted from uppermost leaf sheath. *Spikelets* 4–6,5(–8) mm long. Pedicels spreading to reflexed. Glumes membranous, 4–6,5 mm long, gaping widely at maturity. Lower sterile lemma glabrous on sides, with 2–3 fairly distinct to faint longitudinal ribs and rarely with up to 6 faint transverse corrugations, tip rounded, mucous. Lemma of fertile floret rarely with very faint corrugations.

Subsp. *filiformis* is distinguished from the other two subspecies by the often delicate habit, the small, soft, thin leaf blades and the inflorescence with few spikelets borne on spreading to reflexed pedicels. Its distribution is shown in Figure 5. It grows on sandy (TMS) and humic soils, at streamsides, in moist places, and in the shade of rocks, from altitudes of 25–2 000 m, flowering from October to February. It is most commonly collected after fire.

A few specimens occur that are intermediate between subsp. *filiformis* and both other subspecies. *Gibbs Russell 5674* is a typical subsp. *filiformis* and was collected within its range, but the sterile lemma margins are hairy, a characteristic of subsp. *rehmannii*. The intermediates to subsp. *subspicata* are discussed under that subspecies.

As discussed above under *E. ramosa* subsp. *aphylla*, this taxon must be typified by a specimen of *Ecklon 914* with thin culms, soft leaves and few spikelets. There is no evidence that the Kew specimen of this description was seen by Nees, so it is designated as a neotype rather than a lectotype. A fragment of a since-destroyed specimen from Berlin, allegedly annotated by Nees, exists in PRE but it lacks a complete spikelet so therefore its identity cannot be unequivocally determined. Mez (1921) quoted Nees's (1841 not 1832) epithet as the basionym when raising the taxon to species rank, but he cited a different specimen from those cited by Nees in either publication.

2c. *Ehrharta rehmannii* Stapf subsp. *subspicata* (Stapf) *Gibbs Russell*, comb. et stat. nov. Type: stream from Retreat to Muizenberg, *Wolley Dod 3519* (K, lecto!., here designated; BOL, photo and fragment in PRE!).

*Ehrharta subspicata* Stapf: 676 (1900), Chippindall: 39 (1955).

Tufted erect, neither distinctly delicate nor robust. *Culms* several, 300–600 mm long, to 2 mm across, erect or decumbent at base, herbaceous, branching above, the branches few and single. *Leaf blades* linear or lanceolate, 4–8,5 mm across and 30–120(–170) mm long, flat or rolled from both margins, erect, herbaceous, glabrous or margins scabrous. *Inflorescence* a narrow contracted raceme, 25–70 mm long, somewhat overtopping leaves, of 12–36 erect, appressed spikelets, usually closely subtended or enveloped below by uppermost leaf sheath. *Spikelets* 6–8,5 mm long. Pedicels erect. Glumes subcoriaceous, nerves obscure; lower glume 6–8,5 mm long; upper glume 5,5–8 mm long. Lower sterile lemma glabrous on sides, smooth and unornamented or with transverse corrugations; 0–3 ribs; 0–4 corrugations, faint; tip truncate or rounded, rarely submucronate.

Subsp. *subspicata* is distinguished from the other two subspecies by the broad erect leaves and narrow inflorescences of erect spikelets with subcoriaceous glumes. Its distribution is shown in Figure 6. It grows in sandy or gravelly soil in moist places such as streamsides and seepage areas, near sea level, flowering from October to December.

Several specimens from limestone areas near the coast appear to be intermediates between subsp. *filiformis* and subsp. *subspicata* (*Acocks 24130*; *Ellis 1295, 4660*; *Gibbs Russell 5644, 5646*). They have the somewhat delicate branched culms that are woody below and the small spikelets of subsp. *filiformis* but the narrow inflorescence and erect spikelets with subcoriaceous glumes of subsp. *subspicata*. Their distribution is not in the area of sympatry of the two subspecies, but lies to the east of the range of subsp. *filiformis* and in the middle of the range of subsp. *subspicata* (Figure 6). The limestone area where these specimens were collected is noted for its distinctive local flora (*Bond & Goldblatt 1984*). However, because of the general difficulty of delimiting taxa in the *Ramosa* group and the paucity of specimens, no formal taxonomic ranking is applied at this time to the entity represented by these specimens.

A single specimen, *Von Breitenbach 60*, appears to be intermediate between subsp. *subspicata* and subsp. *rehmannii*. It has the erect leaves and narrow inflorescence with erect spikelets of subsp. *subspicata* but the membranous glumes and scabrous-keeled sterile lemmas of subsp. *rehmannii*.

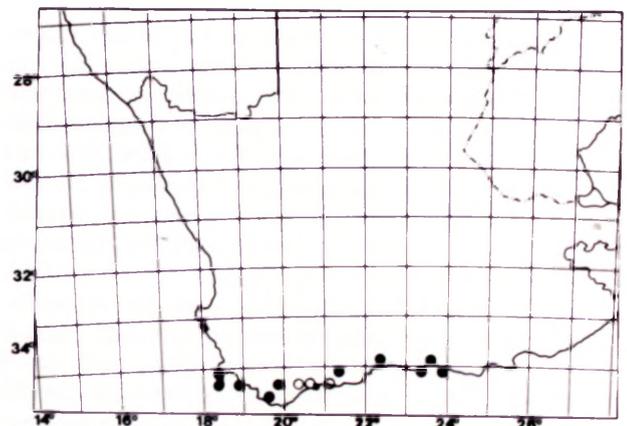


FIGURE 6.—Distribution of *E. rehmannii* subsp. *subspicata*. The 'limestone' intermediates to subsp. *filiformis* are shown by open dots.

## LEAF BLADE ANATOMY

The leaf blade anatomy of the species of the *Ramosa* group is distinctive and distinguishes this group from the other seven species groups in *Ehrharta* (Gibbs Russell & Ellis 1987). However, the leaf anatomy of the five taxa constituting the *Ramosa* group exhibits no clear structural disjunctions between the taxa themselves. A large proportion of the specimens studied have anatomy intermediate between adjacent taxa and it appears from this voucher sample as if the taxa recognized only on morphology reflect trends of specialization in this species group. This is confirmed by the fact that a number of herbarium specimens are intermediate between the taxa as defined and a continuous and reticulate variation pattern is also evident in external morphological characters, in accord with the anatomical evidence.

The identifications of the anatomical voucher specimens naturally also reflect this variation pattern with a disproportionately large number of intermediates. This situation is further exacerbated by taxa with a suffrutescent habit, usually with caducous leaves which hamper leaf anatomical studies. In these taxa only atypical morphological specimens possessing leaf blades were suitable for examination. The anatomical sample was, therefore, not fully representative of all the taxa, particularly as far as anatomical vouchers closely matching type specimens is concerned.

For these reasons it is obvious that detailed anatomical descriptions and diagnoses of individual taxa are impractical, particularly as the taxa are barely separable morphologically, being recognized as two species with five subspecies. It has, therefore, been decided to give a full anatomical description for the *Ramosa* group as a whole followed by brief comments on the anatomical trends in each of the constituent taxa.

*Transverse section*

The leaf blade is always loosely inrolled from both margins (Figures 8A; 9A; 11A, C; 13A; 14A, C; 15A, D) and there is no evidence of infolding. The margins themselves range from rounded and blunt to tapering to the pointed projection of Figure 15E. The midrib is consistently a median vascular bundle only, without associated parenchyma development (Figures 8A; 9A, D; 11A, C, E; 13A; 14A, C, E; 15A, D). Successive first order bundles are separated by 2–5 smaller bundles but this pattern or arrangement differs in different specimens of the same taxon or even on opposite halves of the same blade, as in Figure 15A where either two or four third order bundles are located between the midrib and the first lateral first order bundle on either side.

Ribs and furrows may be absent (Figures 11E, F; 13A, B; 14A–F; 15A, B) or slight ribs may be present over the bundles (Figures 8B; 9B, E; 11A–D; 15E). Both conditions appear to occur in all taxa. The mesophyll generally accommodates a well developed, centrally located bulliform cell group, the central cell of which may be large and shield-shaped (Figures 11D, F; 13B; 14F). The chlorenchyma is of the compact type with small to medium, isodiametric or angular cells (Figures 9B, E; 11B, D, F; 13B; 14B, D, F; 15B). These cells are as large as

or slightly larger than the parenchyma sheath cells with the chloroplasts often peripherally located. The cell walls are not straight but there is a definite tendency in all taxa for some of the walls to have slight indentations, particularly in the abaxially situated cells (Figures 9B, E; 11D, F; 13B). These resemble small invaginations of the walls but do not appear to be homologous with arm cells. They require further study but present technical difficulties as perfect fixation is needed for their elucidation.

The chlorenchyma tissue sometimes displays a somewhat radiate arrangement in thicker leaves with 4–6 chlorenchyma cell layers (Figures 9B, E; 11D, F; 13B). This pattern is not evident in thinner leaves of 2–3 cell layers (Figures 14B, D, F; 15B). The thicker leaves tend to have elongated, angular chlorenchyma cells whereas in thinner leaves they are more equidimensional.

*Abaxial epidermis*

Costal and intercostal zones are always clearly differentiated (Figures 8C, E; 12A, C; 13C; 14G; 15C, F). The intercostal long cells are elongate-rectangular with the anticlinal walls sinuous but not appearing inflated (Figures 8D, F; 9C; 12B, D; 13D). There is a tendency towards a fusiform, hexagonal shape in a few specimens (Figure 14H) but this species group can be characterized by the rectangular shape of the long cells and their very sinuous walls (Figures 10A, C; 16A, C, E, F).

Successive long cells in a file are separated from one another by single short cells, short cell pairs, hooks, micro-hairs or stomata, and very seldom adjoin one another. This arrangement along a given file alternates with that of adjacent long cell files resulting in a distinct brickwork pattern which is particularly conspicuous with the SEM (Figure 16C, E). Cell size and shape is uniform across the width of each intercostal zone.

Two files of stomata usually occur in each interstomatal zone, the stomata in a file being separated by single interstomatal long cells. The stomata are clearly dome-shaped and their structure is consistent throughout the group (Figures 8D; 12B, D; 13D; 14H). With the SEM the stomata are seen to possess a distinct, raised rim surrounding the pore aperture and they are not associated with wax deposits (Figures 10B, D; 16D, F). Epicuticular wax is also not typical of this group but may be present as very fine platelets (Figure 10D).

Costal silica bodies are variable in shape, being of the irregular dumbbell-shaped type (Figures 8D, F; 12B, D; 13D). Costal zones are narrow, seldom exceeding three cells in width.

Prickle hairs occur in all taxa but vary in form and frequency of occurrence. They vary continuously between those with very short barbs (Figures 8F; 9C; 13D; 15F) to types with elongate barbs which resemble macrohairs (Figures 8D; 12C; 15C). These latter types are unicellular and do not have specialized epidermal cells associated with their bases and, therefore, are not macrohairs by definition. Both types may be either costal or intercostal although the costal prickles on any given specimen are larger than the intercostal hooks.

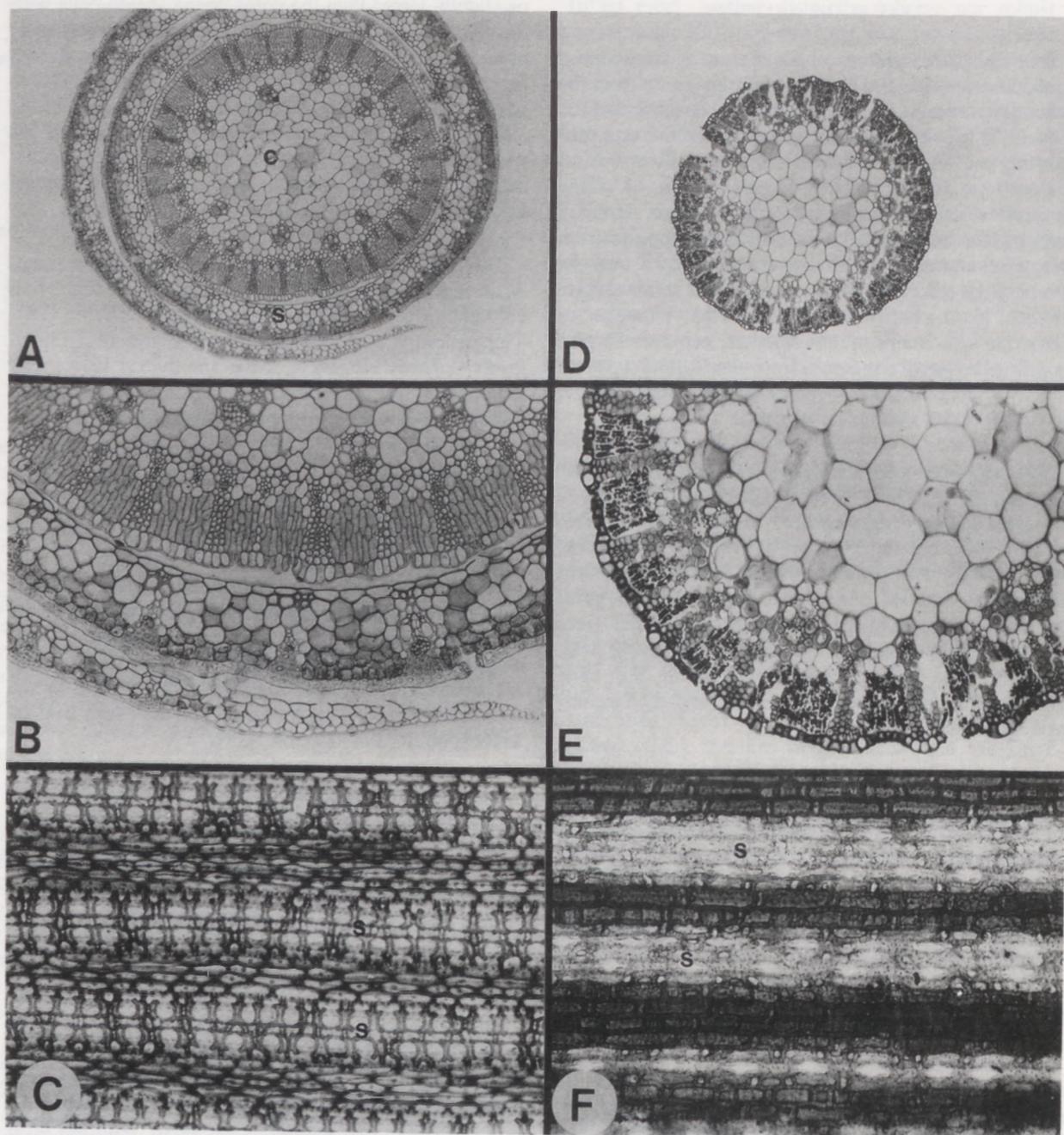


FIGURE 7.—Culm anatomy of *Ehrharta ramosa*. A–C, *E. ramosa* subsp. *ramosa*, transverse section: A, culm (c) and surrounding leaf sheath (s),  $\times 100$ ; B, detail of culm and leaf sheath vasculature and mesophyll tissue,  $\times 250$ ; C, culm epidermis showing stomatal files (s) in the intercostal zones between successive sclerenchyma girders,  $\times 250$ . A, B, *Ellis 634*; C, *Ellis 5525*. D–F, *E. ramosa* subsp. *aphylla*, *Ellis 4634*, transverse section: D, culm outline,  $\times 100$ ; E, detail of mesophyll, vasculature and pith,  $\times 250$ ; F, epidermal structure illustrating alternating costal and intercostal zones, the latter with the stomatal files (s),  $\times 400$ .

Microhairs are common and with the aid of the SEM are seen to be of a characteristic type (Figures 10B, D; 16B, D, F, H). The basal and distal cells are almost equal in length. The distal cell is deciduous and has a blunt apex which does not taper but the hair has a consistent width throughout its length. This type of microhair occurs in all taxa of this species group but nowhere else in *Ehrharta*.

This leaf anatomy is diagnostic for the *Ramosa* species group and serves to distinguish it from the other species groups in the genus. A definite anatomical trend is evident within the group, from specimens with relatively thick leaf blades, in which the chlorenchyma cells are rather elongated with cell wall indentations and displaying a somewhat radiate arrangement, to very thin leaves. These

have isodiametric chlorenchyma cells without wall indentations or radiate-type arrangement. This continuum is paralleled by a trend for the margins to become more tapering and for the epidermal prickles to become smaller and fewer in number. However, these anatomical trends do not appear to be reflected in the classification of this species group and are assumed to be of no taxonomic relevance.

#### *E. ramosa*

Leaf blades in this species are absent or minute and, if present, are short-lived and caducous. As a result very few specimens possess leaf blade material and, consequently, are unsuitable for comparative anatomical study

of the leaf blade. All specimens with typical morphology were devoid of leaf blades and only culms were available for study. The results are briefly described below and illustrated in Figure 7.

The culm may be encircled by a leaf sheath which has overlapping margins (Figure 7A), a very thick cuticle, stomata, vascular bundles and chlorenchyma only in the outer cell layers (Figure 7B). Often the bladeless sheaths are also dehiscent and absent (Figure 7D).

The culm outline is circular (Figure 7A, D) with a simple epidermis. The stomata are adjacent to the chlorenchyma zones with the subsidiary cells being flush with the epidermal cells (Figure 7B). No prickles or other epidermal appendages are present.

A discontinuous ring of chlorenchyma is present beneath the epidermis. Each chlorenchyma zone consists of 5–8 radially arranged columns of tabular cells, 2–3 cells deep (Figure 7B, E). These zones are separated by the sclerenchyma girders of the peripheral vascular bundles and are bounded internally by a continuous ring of sclerenchyma and collenchyma in which the peripheral vascular bundles are embedded (Figure 7B, E). This sclerenchymatous ring encloses the central parenchymatous pith which may or may not contain vascular bundles near the periphery (Figure 7A, D).

The vascular bundles in the culms of *E. ramosa* subsp. *ramosa* are arranged in two rings, a ring situated in the pith tissue and a ring embedded in the sclerenchymatous ring (Figure 7A). In subsp. *aphylla* there is only a single ring associated with the sclerenchyma (Figure 7D). This

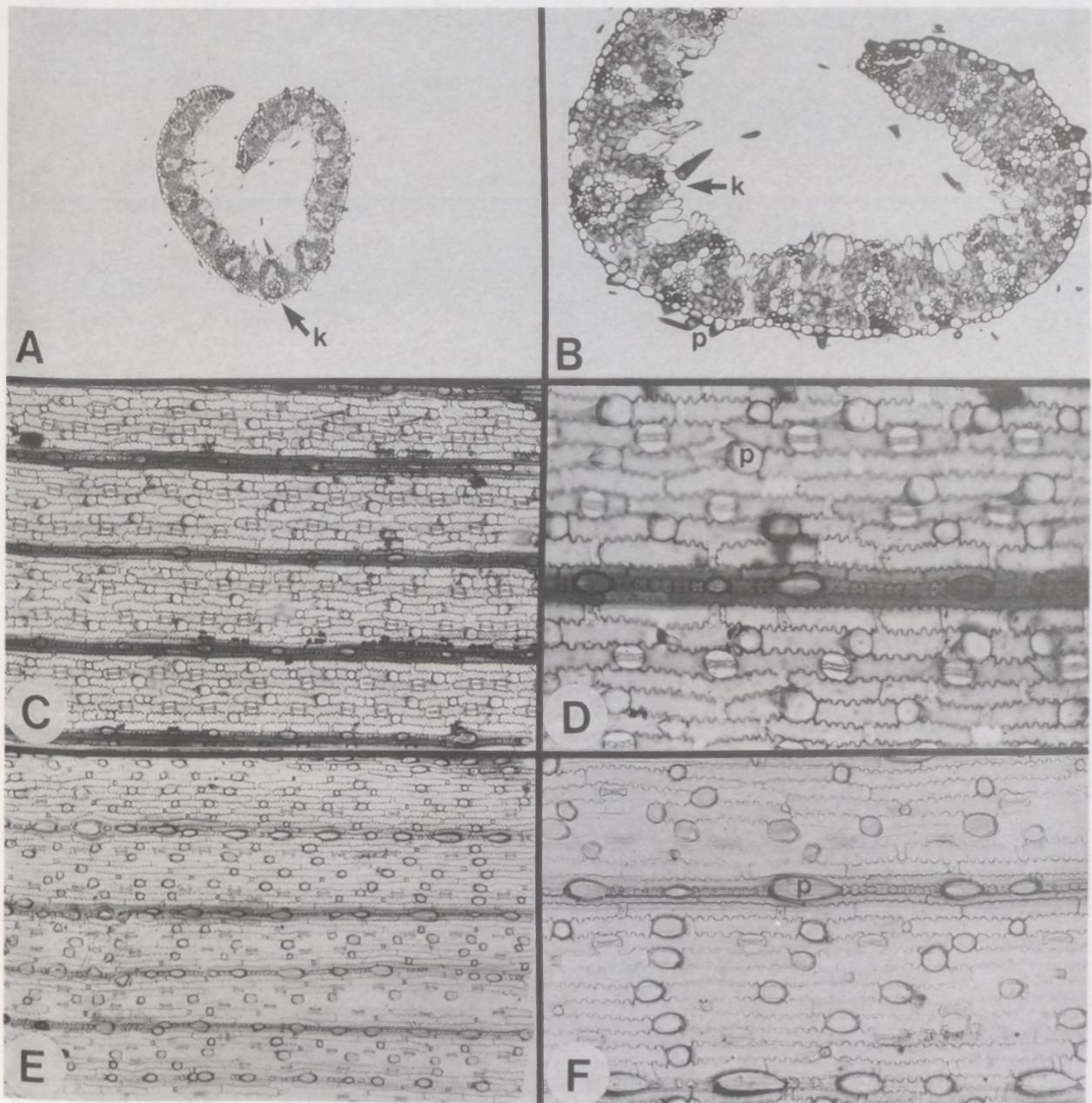


FIGURE 8.—Leaf blade anatomy of *Ehrharta ramosa* subsp. *ramosa*. A, B, transectional anatomy: A, inrolled outline of leaf blade with undifferentiated keel (k),  $\times 100$ ; B, anatomical detail with many prickles (p) in both epidermides,  $\times 250$ . C–F, abaxial epidermis: C, cell arrangement,  $\times 160$ ; D, detail of costal and intercostal prickle hairs (p), intercostal long cells and stomata,  $\times 400$ ; E, cell arrangement and numerous prickle hair bases,  $\times 160$ ; F, detail of costal and intercostal prickles (p), long cells, silica bodies and stomata,  $\times 400$ . A–D, *Ellis 4694*; E, F, *Ellis 1632*.

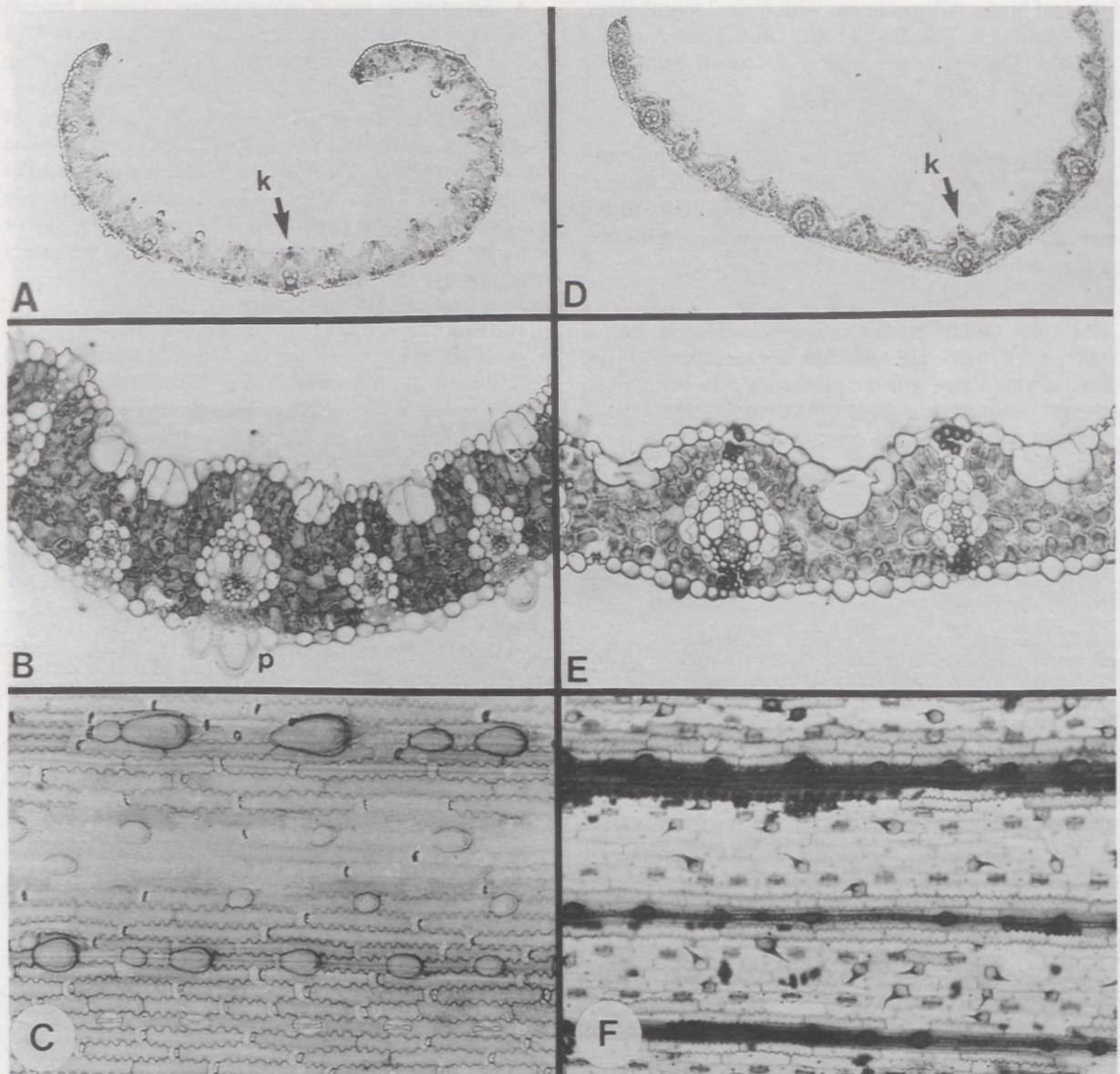


FIGURE 9.—Leaf blade anatomy of *Ehrharta ramosa* subsp. *aphylla*. A, B, leaf transverse section: A, loosely inrolled leaf outline and absence of keel (k),  $\times 100$ ; B, chlorenchyma and vascular bundle detail; note slight invaginations of chlorenchyma cell walls and prominent abaxial prickle hair base (p),  $\times 400$ ; C, abaxial epidermis showing rectangular, sinuous long cells and large costal prickle hairs,  $\times 400$ . D, E, leaf in transverse section: D, outline with median vascular bundle only (k),  $\times 100$ ; E, chlorenchyma detail,  $\times 400$ . F, abaxial epidermis showing costal prickles and intercostal hooks,  $\times 250$ . A–C, *Ellis 2235*; D–F, *Ellis 4673*.

is a reflection of the difference in size and robustness of these subspecies. The vascular bundles have a clearly developed mestome sheath but the parenchyma sheath is not clear and appears to be replaced by the parenchyma or sclerenchyma ground tissue (Figure 7B, E). This was also noted by De Wet (1960).

The culm epidermis reflects this internal anatomy with alternating bands of stomatal files overlying the chlorenchyma zones, and thickened epidermal cells overlying the sclerenchyma girders (Figure 7C, F). The form of the costal cells overlying the girders appears to differ between *E. ramosa* subsp. *ramosa* (Figure 7C) and subsp. *aphylla* (Figure 7F) and this may be a taxonomically important difference between these two taxa. However, a larger study sample is needed before this can be substantiated.

#### *E. ramosa* subsp. *ramosa*

Two anatomical voucher specimens (*Ellis 1632, 4694*) have been identified as belonging to this taxon although

they both deviate from the taxon diagnosis in possessing leaf blades. They are both suffrutescent and woody but also possess leaf blades and have erect pedicels. They, therefore, resemble *E. rehmannii* subsp. *subspicata* in the latter two characters but this taxon is not generally suffrutescent. These specimens, therefore, are not typical subsp. *ramosa* specimens but were the only plants found which also possessed leaves and, consequently were suitable for this leaf anatomy study. They appear to represent very young flowering plants with recent vegetative growth, perhaps in response to physical damage. Nevertheless, they do not represent typical examples of this subspecies and the anatomical results must be evaluated accordingly.

The anatomy of subsp. *ramosa* conforms closely to that given for the *Ramosa* species group (Figure 8). The leaf in transection exhibits all the characteristic features of this species group and even slight cell wall invaginations are

visible (Figure 8B). The numerous prickle hair bases evident in the epidermis are a notable feature (Figure 8B).

The abaxial epidermis is dominated by the large number of prickle hairs present (Figure 8C–F), both in the costal and intercostal zones. These may be either typical prickles with short barbs (Figure 8F) or macrohair-like with much longer barbs (Figure 8D). The abundance of these prickle hairs appears to be a feature of this species with reduction in their size and number in several specimens of *E. rehmannii*. The silica bodies in subsp. *ramosa* are elongated dumbbell-shaped and tend to be shorter than in *E. rehmannii*. The microhairs are typical of those so diagnostic of the *Ramosa* species group (Figure 10B).

#### Specimens examined

CAPE. — 3319 (Worcester): Hex River Mts, Milner Peak (–AD), *Ellis* 5525 (culm only). 3321 (Ladismith): Langeberge, Cloete's Pass (–DC), *Ellis* 634 (culm only), *Ellis* 4694 (leaves with reduced blades). 3323 (Willowmore): Uniondale Dist., Uniondale Poort (–CA), *Ellis* 1632 (short leaf blades).

#### *E. ramosa* subsp. *aphylla*

Typical material of this taxon is also without leaf blades, as in *Ellis* 4634. The voucher material which was assigned

to this taxon once again presented problems with identification as all plants found with leaf blades were either sterile or only had very young inflorescences. Positive identification was, therefore, not possible because the position of the pedicels (whether reflexed or not) was not yet visible.

The anatomy of *Ellis* 2235 is virtually identical to that of subsp. *ramosa*, both in transection (Figure 9A, B) and the abaxial epidermis (Figure 9C). The large prickle hair bases enhance this resemblance as do the slight cell wall indentations (Figure 9B).

Another specimen, *Ellis* 4673, which is intermediate to *E. rehmannii* subsp. *rehmannii* in spikelet characters, resembles the anatomy of *E. rehmannii* subsp. *rehmannii* more closely than that of subsp. *ramosa*. This is particularly evident in the adaxial ribs and furrows in the leaf section (Figure 9E) which generally is very similar to that of *Ellis* 4697 and 4699 (Figure 11B, D), *E. rehmannii* subsp. *rehmannii*. However, the epidermal features of this specimen do not corroborate this resemblance with *E. rehmannii* but, then, neither do they suggest affinities with other *E. ramosa* specimens. Although the very small hooks are unusual, the micro-

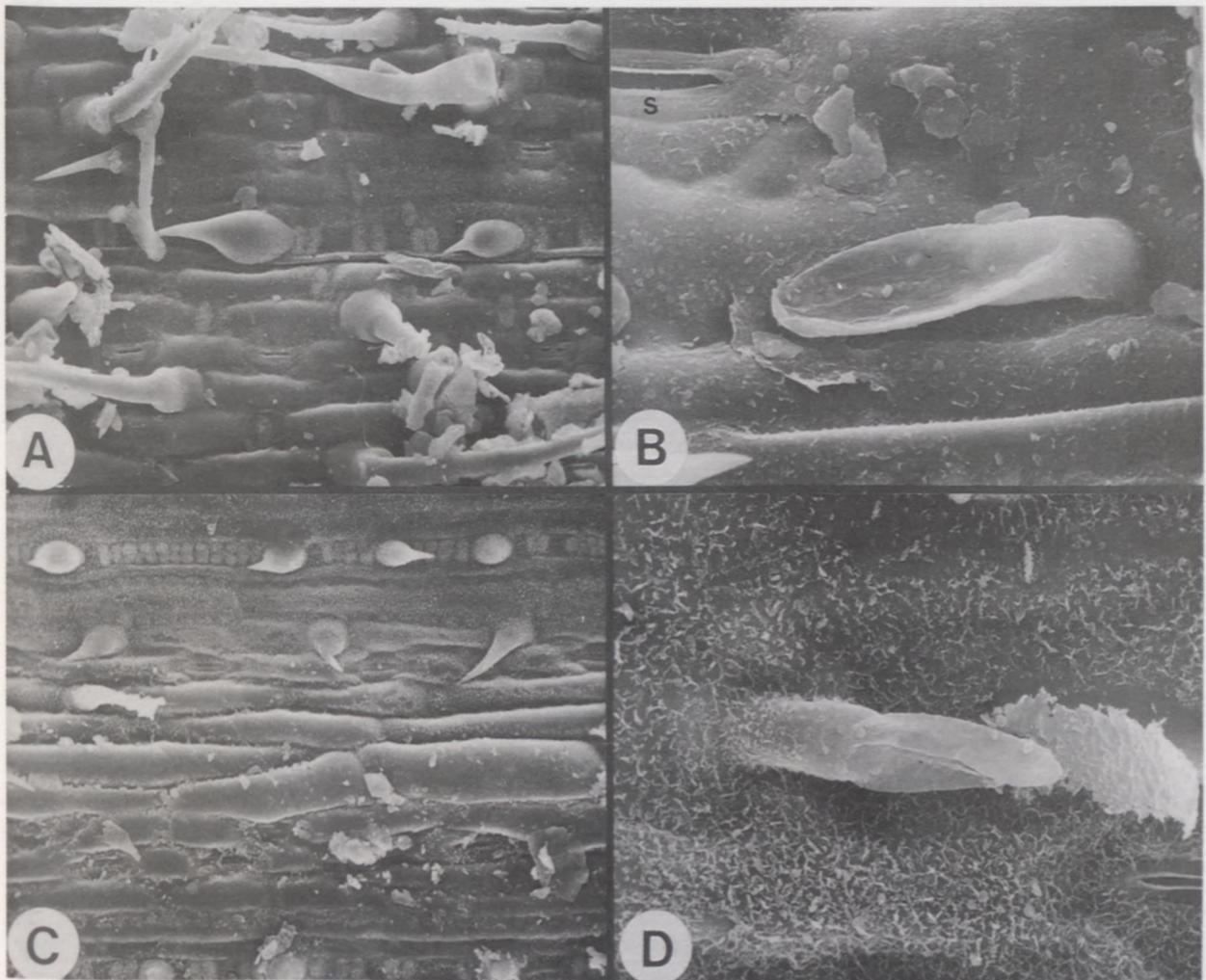


FIGURE 10.—Scanning electron micrographs of the abaxial epidermis of *Ehrharta ramosa*. A, B, *E. ramosa* subsp. *ramosa*, *Ellis* 4694: A, intercostal prickle hairs, stomata and rectangular long cells,  $\times 200$ ; B, microhair with distal cell not tapering and stoma (s) with distinct rim and without associated wax deposits,  $\times 1000$ . C, D, *E. ramosa* subsp. *aphylla*, *Ellis* 4673: C, inflated, rectangular intercostal long cells, stomata and hooks; costal zones with prickles and silica bodies,  $\times 200$ ; D, microhair with exuding distal cell and stoma with distinct rim,  $\times 1000$ .

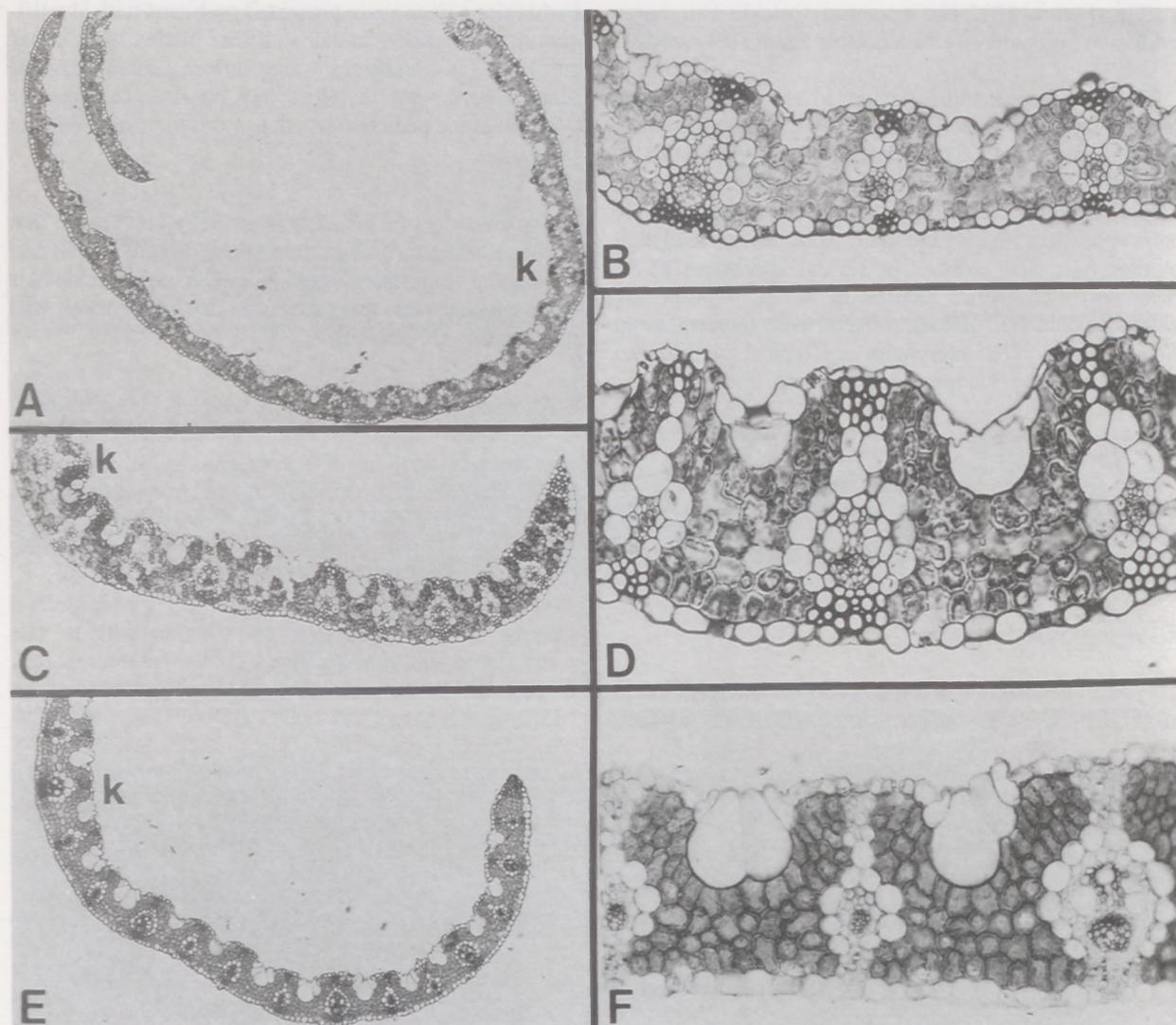


FIGURE 11.—Transsectional leaf blade anatomy of *Ehrharta rehmannii* subsp. *rehmannii*. A, B, *Ellis* 4699: A, inrolled outline without keel (k) and associated parenchyma,  $\times 100$ ; B, vascular bundle and mesophyll arrangement and chlorenchyma cell detail,  $\times 400$ . C, D, *Ellis* 4697: C, outline with undifferentiated keel (k) and tapering margin,  $\times 100$ ; D, chlorenchyma cell detail showing slight cell wall invaginations,  $\times 400$ . E, F, *Ellis* 618: E, outline showing median vascular bundle without associated parenchyma tissue (k),  $\times 100$ ; F, compact chlorenchyma cells with slight wall indentations,  $\times 400$ .

hairs and stomata (Figure 10D) are typical of those of the *Ramosa* group.

#### *Specimens examined*

CAPE.—3219 (Wuppertal): Clanwilliam Dist., Pakhuis Pass (—AA), *Ellis* 4634 (culm only). 3318 (Cape Town): Jonkershoek State Forest, Jakkalsvlei (—DD), *Ellis* 2235 (reduced blades present). 3418 (Simonstown): Hottentot Hollands Mts, Sir Lowry's Pass (—BB), *Ellis* 4673 (few, reduced blades).

#### *E. rehmannii*

Although this species is characterized by herbaceous culms and blade-bearing leaves, several anatomical voucher specimens have suffrutescent culms and reduced, caducous blades. Examples are *Ellis* 648 which is morphologically intermediate between subsp. *rehmannii* and *E. ramosa* subsp. *aphylla* and *Ellis* 1295 and 4660 which are morphologically intermediate between subsp. *filiformis* and subsp. *subspicata*. However, no anatomical intermediacy is evident in these specimens, making their interpretation difficult.

No clear anatomical discontinuities exist between any of the three subspecies of *E. rehmannii* or with *E. ramosa*. Instead there is a general trend from *E. ramosa* through *E. rehmannii* subsp. *rehmannii* to subsp. *filiformis* along which leaf thickness decreases, the margins tend to become more tapered and the prickles become smaller and fewer in number. Several exceptions to this pattern exist, so the trend may represent an ecological gradient rather than a phylogenetic lineage.

#### *E. rehmannii* subsp. *rehmannii*

All specimens have relatively thick mesophyll tissue displaying a tendency to the radiate condition (Figure 11B, D, F). The chlorenchyma cells are not isodiametric but more elongated with slight cell wall indentations. The leaf margin is more acute than in *E. ramosa* and may taper to a definite point (Figure 11C). The adaxial surface may be flat (Figure 11F) or ribbed (Figure 11B, D).

The epidermal structure is remarkably uniform throughout the sample (Figure 12A–D) with rectangular long cells being conspicuous. Only *Ellis* 4697 (Figure 12C, D) has

a few intercostal hooks, these with very long barbs. All have a few costal prickles with short barbs. The silica bodies are variable in shape but generally are shorter dumbbell-shaped than in *E. ramosa*.

*Ellis 4697* is noteworthy in that it differs in having a tapering margin (Figure 11C), has the thickest leaf with definite ribs (Figure 11D) and possesses intercostal prickles (Figure 12C). This deserves further comment as it was collected together with *Ellis 4698* and *4699* from an actively growing and spreading population recovering after a fire. The latter two specimens differ from *Ellis 4697* in having more abrupt margins, thinner blades (Figure 11A, B) and no prickles (Figure 12A). Thus, within a single population, considerable anatomical variation is evident, even in those characters which show a trend through this species group. This supports the decision not to attach any taxonomic importance to these anatomical differences.

Although anatomical differences may, therefore, not be reflected in the morphology, the reverse is also true. *Ellis 648* is morphologically intermediate between *E. rehmannii* subsp. *rehmannii* and *E. ramosa* subsp. *aphylla* but anatomically virtually identical to *Ellis 618*, subsp. *rehmannii*. Reference to Figures 11E, F; 12B and 13A–D illustrate this resemblance clearly, both specimens with distinctive thick, compact mesophyll and well developed bulliform groups, without adaxial ribs and without large prickles in the epidermis. These two specimens are more alike in leaf anatomy than they are to all the other specimens in the *Ramosa* group. It therefore appears that

there is little or no congruence between leaf anatomy and morphology in this species group, a situation which differs from that in the other groups of *Ehrharta*.

#### Specimens examined

CAPE. — 3320 (Montagu): Barrydale Dist., Tradouw's Pass (–DC), *Ellis 648* (intermediate between subsp. *rehmannii* and *E. ramosa* subsp. *aphylla*), 3322 (Oudtshoorn): Outeniqua Mts, Robinson's Pass (–CC), *Ellis 4697, 4698* and *4699*. 3323 (Willowmore): Groot River Pass between Plettenberg Bay and Storms River (–DC), *Ellis 618*.

#### *E. rehmannii* subsp. *filiformis*

This taxon is placed at one end of the continuum of anatomical variation and has the thinnest leaves, the most tapering margins and few, small prickles. The leaf blades are thin and inrolled from both margins (Figure 14A, C, E). The chlorenchyma beneath the bulliform cells is only two to four cells deep and no radiate tendency is evident (Figure 14B, D, F). The margins are also distinctly tapering (Figure 14A, C, E). The silica bodies are usually few in number and small and hook-like (Figure 14G, H). The stomata and microhairs are typical of those of the *Ramosa* species group (Figure 16H). The intercostal long cells are distinctly hexagonal in outline (Figure 14G, H), a feature not apparent in any other specimens.

This anatomy is consistent with the small, soft, thin leaf blades of this subspecies and the leaf anatomy is uniform throughout the study sample. The anatomy is also fairly

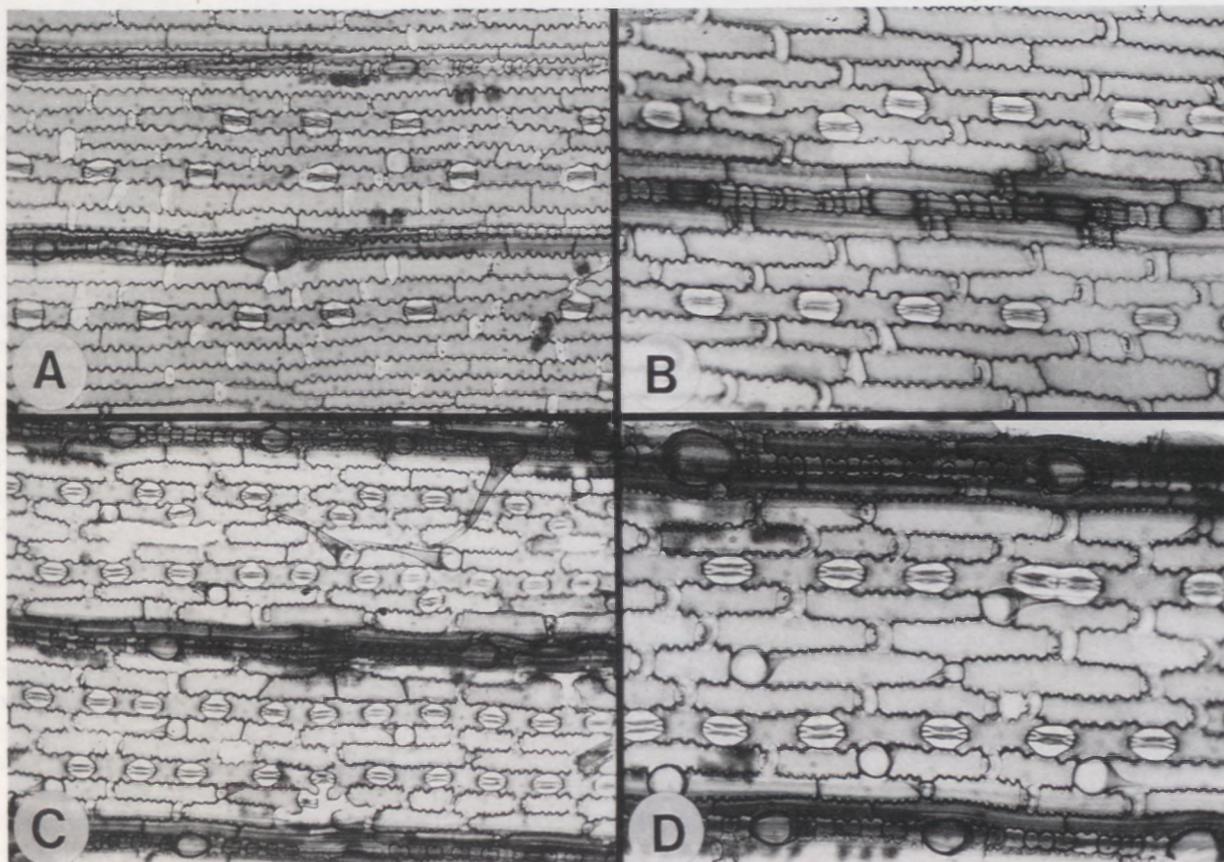


FIGURE 12. — Abaxial leaf blade epidermis of *Ehrharta rehmannii* subsp. *rehmannii*. A, *Ellis 4699*, with sinuous, rectangular intercostal long cells, stomata and costal prickles,  $\times 250$ . B, *Ellis 618*, illustrating costal and intercostal cell detail and arrangement,  $\times 400$ . C, D, *Ellis 4697*: C, showing costal and intercostal zone configuration and elongated prickle hairs,  $\times 250$ ; D, detail showing costal prickles and silica bodies and intercostal long cells, stomata and hooks,  $\times 400$ .

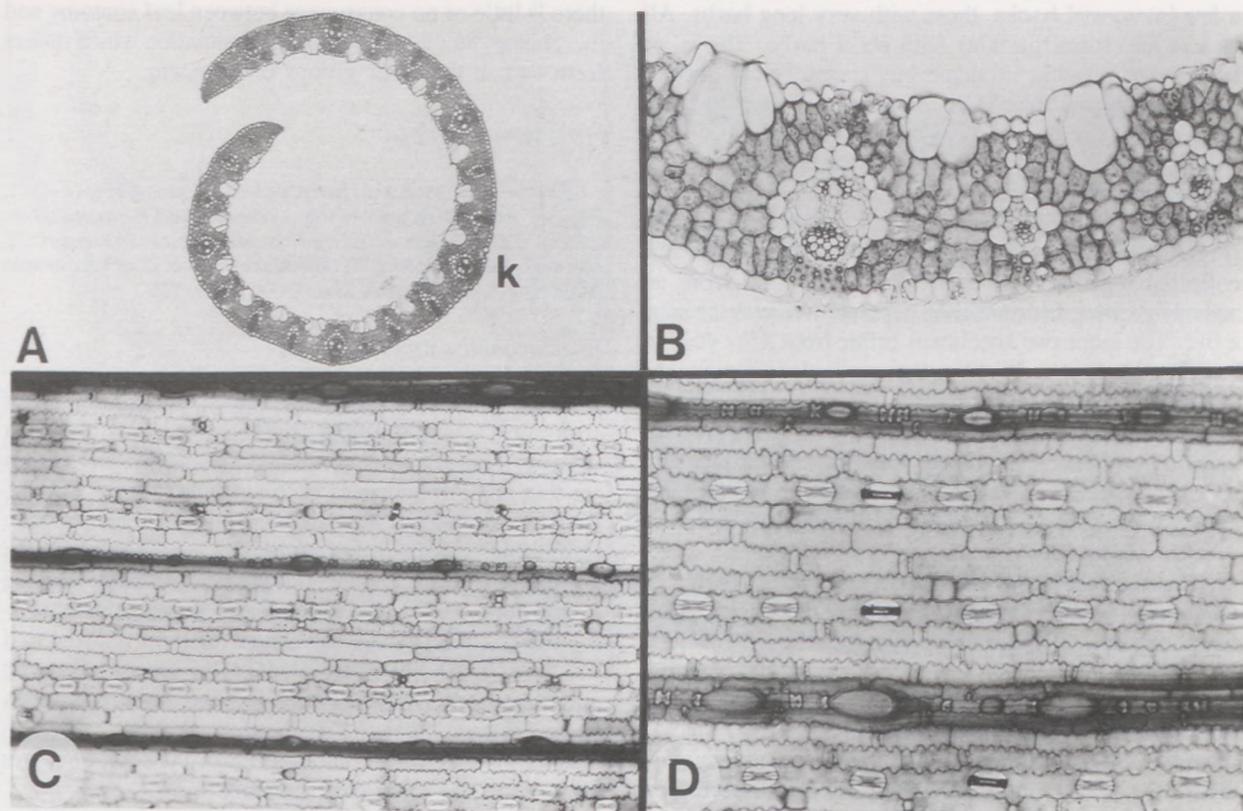


FIGURE 13. —Leaf anatomy of specimen morphologically intermediate between *Ehrharta rehmannii* subsp. *rehmannii* and *E. ramosa* subsp. *aphylla*, Ellis 648. A, B, leaf transverse sections: A, inrolled outline and median bundle without associated parenchyma tissue,  $\times 100$ ; B, detail of chlorenchyma and vascular bundles,  $\times 400$ . C, D, abaxial epidermis: C, epidermal zonation,  $\times 250$ ; D, elongated, rectangular intercostal long cells, dome-shaped stomatal subsidiaries, irregular silica bodies and costal prickles,  $\times 400$ .

distinct from that of the other taxa in the *Ramosa* species group and subsp. *filiformis* appears to represent a more clear-cut entity than do the other taxa of the group.

Once again, intermediate specimens tend to confuse these patterns, in this case specimens intermediate between subsp. *filiformis* and subsp. *subspicata* from the limestones of the De Hoop area. Ellis 1295 and 4660 both diverge considerably in both morphology and leaf anatomy from the rest of the sample representing this taxon (Figure 15A–F). The leaf blade of Ellis 1295 has a tapering margin (Figure 15A), is very thin (Figure 15B), has hexagonal long cells, elongated dumbbell-shaped silica bodies and very numerous, conspicuous macrohair-like prickles (Figure 15C). This anatomy is distinct and does not closely resemble any other *Ramosa* species group specimen. Ellis 4660 also has very distinctive anatomy, the leaf being very narrow (Figure 15D) with the tapering margins exaggerated into a pointed projection (Figure 15E). The abaxial epidermis of this specimen does not have macrohair-like prickles but has numerous normal prickles with short barbs (Figure 15F). Both these specimens differ greatly from all the others examined and also differ considerably from one another although they come from virtually the same locality.

These intermediate specimens from this specialized limestone habitat are abnormal in that they are woody and suffrutescent with very few leaves but they are small plants and their spikelets are similar in form to subsp. *subspicata* but fall within the size range of subsp. *filiformis*. They are retained in subsp. *filiformis* even though their leaf anatomy does not correspond closely to that of either subsp. *filiformis* or subsp. *subspicata*.

#### *Specimens examined*

CAPE. —3318 (Cape Town): Jonkershoek (–DD), Ellis 4676. 3418 (Simonstown): Hottentot Hollands Mts, Sir Lowry's Pass (–BB), Ellis 2288, 2289. 3419 (Caledon): Hermanus Dist., Olifantsberg (–AD), Ellis 4677. 3420 (Bredasdorp): between Malgas and Wydgelegen (–AD), Ellis 1295, 4660 (intermediate to subsp. *subspicata*).

#### *E. rehmannii* subsp. *subspicata*

No authentic material of this subspecies was freshly collected in the field for this study. Consequently, comparative studies were not possible but herbarium material (Taylor 7667) was examined in order to gain an understanding of the anatomy of this taxon. Indications are that it belongs closest to *E. ramosa* along the trend which is evident in this species group. The leaf appears to be rather thick with abrupt margins but the epidermis is without numerous well developed prickles. This must be confirmed from freshly fixed material.

#### DISCUSSION AND CONCLUSIONS

The spikelet morphology and leaf anatomy of the five taxa of the *Ramosa* group is diagnostic and defines them as a group separate from the other species groups in *Ehrharta*. No spikelet characters are unique to the *Ramosa* group alone, but all taxa in the *Ramosa* group may be distinguished by the following combination of characters: small spikelets less than 9 mm long, with the sterile lemmas similar in shape and size and about as long as the fertile lemma, and having the bases appendaged and usually bearded, the sides glabrous, scabrous or shortly hairy and the tips rounded, truncate or mucronate. In addition, all species are perennial and may be suffrutescent, leaf

blades may be absent, glumes are two-thirds as long to longer than the lemmas and the upper sterile lemma is not stipitate.

Anatomically, the *Ramosa* group taxa share the following unique characters: mesophyll cells compact with slight cell wall invaginations, stomata dome-shaped with a rim surrounding the aperture and lacking associated wax deposits, and the microhairs with the distal cells not tapering. Other characters which together differentiate the group include: leaf blades (when present) inrolled, midrib

lacking parenchyma, ribs and furrows absent or only slightly developed, costal and intercostal zones differentiated, intercostal long cells rectangular with sinuous walls, silica bodies tending to dumbbell shape; prickly hairs always present, varying from small and hook-like with short barbs to macrohair-like with elongated barbs, and epicuticular wax usually absent. Characters which are particularly consistent throughout the group are inrolled leaf blades and the midrib lacking parenchyma. Characters of ribs, chlorenchyma, silica bodies and prickly hairs tend to be more variable.

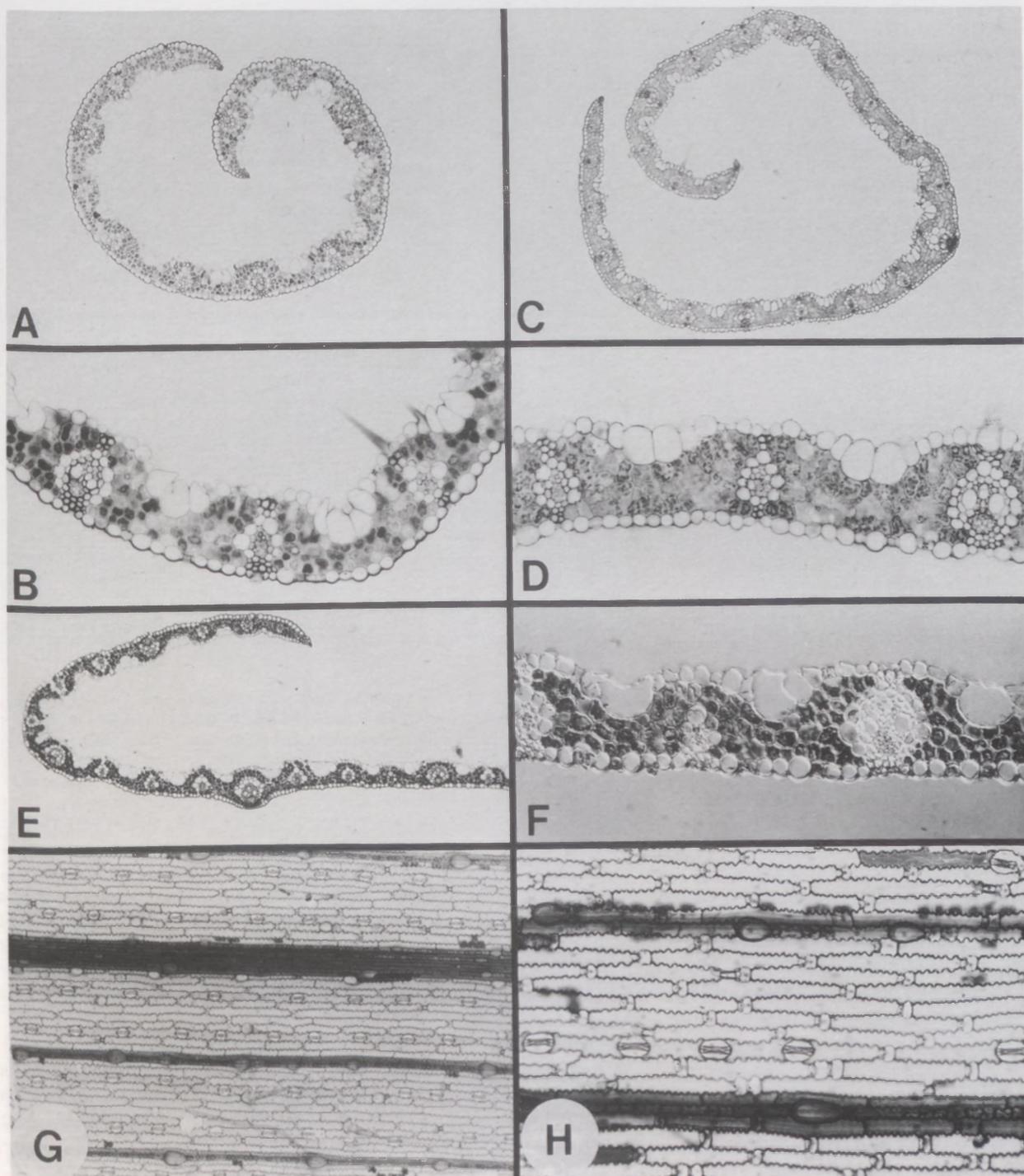


FIGURE 14. — Leaf blade anatomy of *Ehrharta rehmannii* subsp. *filiformis*. A–F, transectional anatomy: A, inrolled blade with tapering margins and median bundle only,  $\times 100$ ; B, chlorenchyma and vascular bundle structural detail and adaxial prickles,  $\times 400$ ; C, loosely inrolled outline without keel and with tapering margins,  $\times 100$ ; D, vascular bundle and mesophyll structure and arrangement,  $\times 400$ ; E, leaf blade outline showing inrolled margin and median bundle only,  $\times 100$ ; F, thin mesophyll layer but cells with slight wall indentations,  $\times 400$ , interference contrast. G–H, abaxial epidermis: G, showing epidermal zonation and prickly hairs,  $\times 160$ ; H, with fusiform long cells, stomata and costal prickles,  $\times 400$ . A, B, *Ellis* 2288; C, D, *Ellis* 2289; E, F, H, *Ellis* 4676; G, *Ellis* 4671.

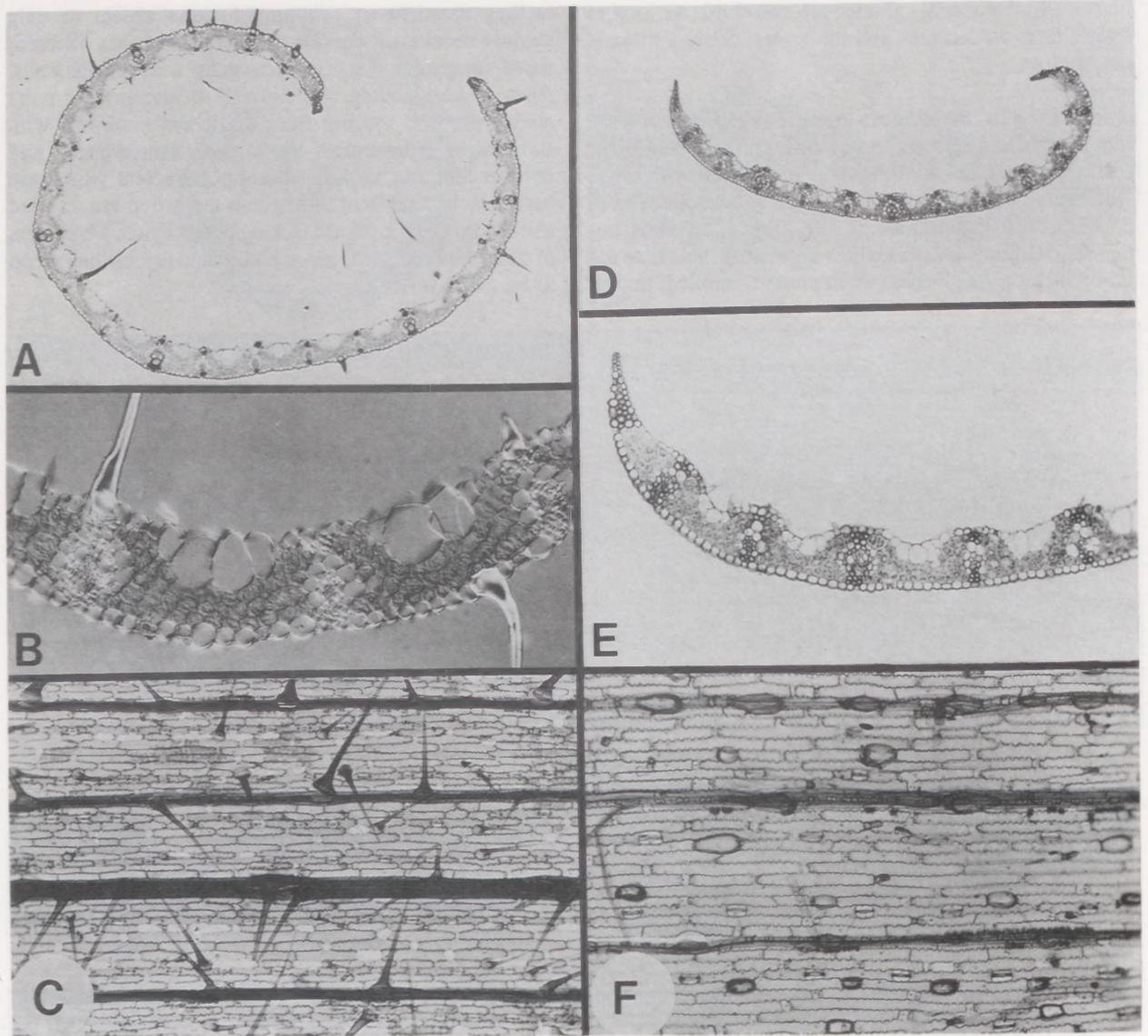


FIGURE 15.—Leaf anatomy of specimens intermediate between *Ehrharta rehmannii* subsp. *filiformis* and subsp. *subspicata*. A–C, *Ellis 1295*: A, leaf outline showing thin inrolled lamina with prominent prickles and without a keel,  $\times 100$ ; B, detail of abaxial and adaxial macro hair-like prickles and few chlorenchyma cell layers,  $\times 400$ , interference contrast; C, costal and intercostal prickles which resemble macrohairs in surface view,  $\times 160$ . D–F, *Ellis 4660*: D, outline showing narrow blade with undifferentiated keel and markedly tapering margins,  $\times 100$ ; E, detail of narrow projecting margin,  $\times 250$ ; F, abaxial epidermis showing elongated, rectangular long cells, and costal and intercostal prickles with short barbs,  $\times 250$ .

The *Ramosa* group is most closely related to the *Calycina* group for both morphological and anatomical features. Auriculate appendages at the base of the second sterile lemma occur only in these two groups. Also, the truncate or tapering mucronate sterile lemma tips of both the *E. ramosa* subspecies are similar to those of *E. calycina*, and the hairs on the sides of the sterile lemmas in most specimens of *E. rehmannii* subsp. *rehmannii* tend toward the longer hairs on the lemma sides of all members of the *Calycina* group. The anatomical relationship between the two species groups is not so marked. The long cells of the *Ramosa* group are usually rectangular, but a few specimens of *E. rehmannii* have fusiform long cells, an elongated hexagonal shape which is characteristic of the *Calycina* group.

Other characters show apparent similarities between the *Ramosa* group and other species groups, but closer examination shows that they are not closely related. Suffrutescent, bladeless species occur in both the *Ramosa*

and *Villosa* groups: *E. ramosa* is similar in habit to *E. thunbergii* and *E. villosa* in the *Villosa* species group. While this might indicate a relationship between the groups, it is also possible that the bladeless suffrutescent condition, with photosynthetic culms that persist from year to year, is an adaptation to conserve plant parts in the low nutrient soils in the Mountain Fynbos and seaside dunes where these species occur.

The indentations in the walls of the chlorenchyma cells present in many of the specimens in the *Ramosa* group may be taken to resemble the invaginations characteristic of arm cells. Engelbrecht (1956) reported arm cell-like invaginations in representatives of the *Ramosa* group (*E. ramosa*, *E. rehmannii* and *E. subspicata*) based on preparations from herbarium material. However, the present study does not confirm Engelbrecht's observations because closer examination of well preserved young leaf material shows that these structures are not inward projections of cell walls but merely the wavy outlines of these walls.

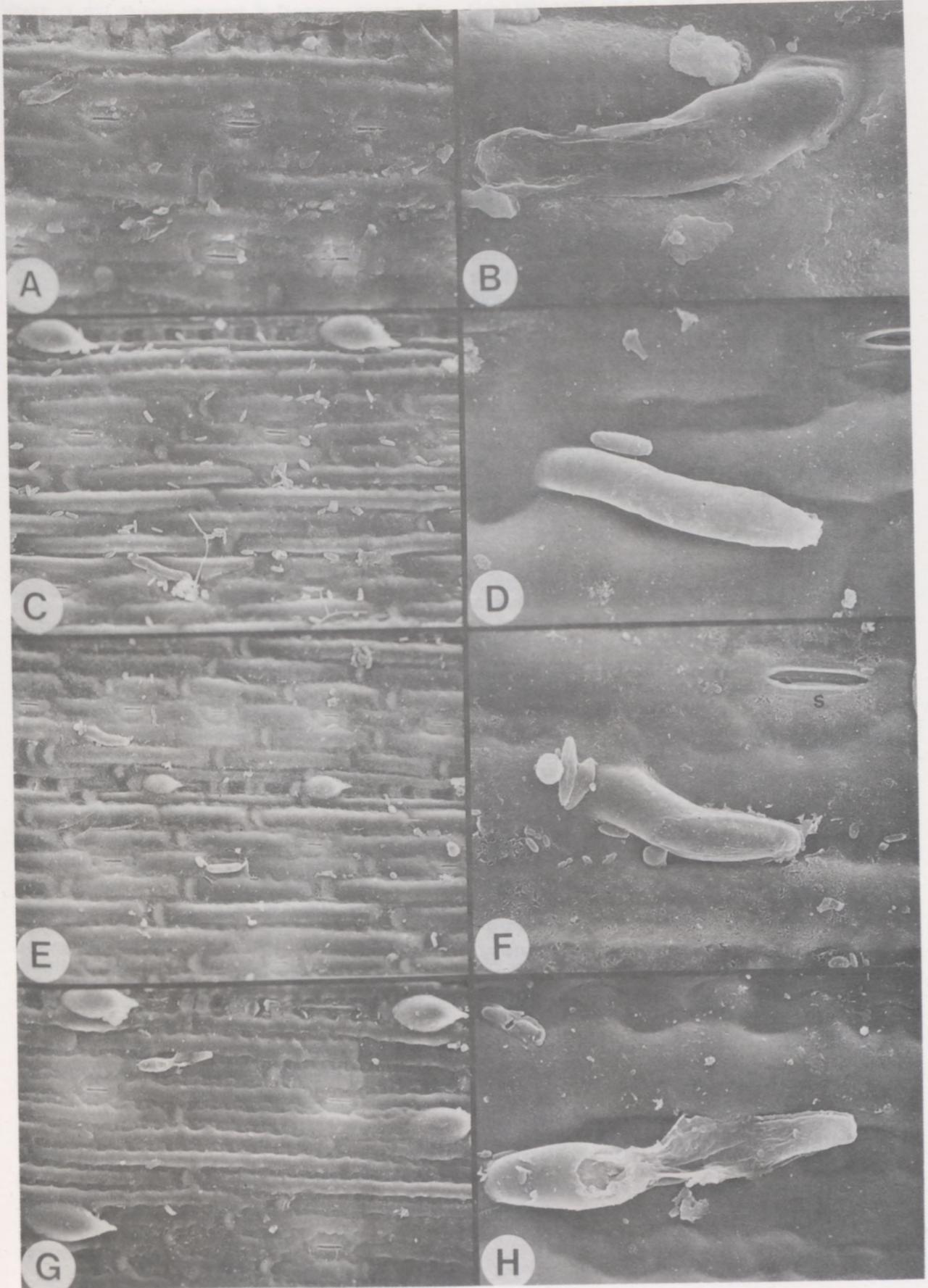


FIGURE 16. — Abaxial epidermal ultrastructure of *Ehrharta rehmannii*. A–F, *E. rehmannii* subsp. *rehmannii*: A, rectangular long cells, stomata with rims and dumbbell-shaped silica bodies,  $\times 200$ ; B, detail of bicellular microhair without tapering distal cell,  $\times 1\,000$ ; C, elongated, rectangular long cells and costal prickles,  $\times 200$ ; D, microhair with distal cell not acutely tapering,  $\times 1\,000$ ; E, rectangular long cells with brickwork type of arrangement and small costal prickles,  $\times 200$ ; F, microhair with intact distal cell and stoma with distinct rim (s),  $\times 1\,000$ . *E. rehmannii* subsp. *filiformis*: G, long cells elongate rectangular with thick, sinuous anticlinal walls, stomata with rims and prickles with short barbs,  $\times 200$ ; H, detail of microhair with collapsed but truncated distal cell and thickened, sinuous anticlinal walls of long cells,  $\times 1\,000$ . A, B, Ellis 4697; C, D, Ellis 4698; E, F, Ellis 4699; G, H, Ellis 4671.

Nevertheless, these loose folds of the walls are unique to and diagnostic for the *Ramosa* group. They do not appear to be homologous with arm cells and therefore do not indicate affinities with the *Setacea* group or with the *Bambusoideae*.

Individual specimens from the far north-western distribution limit of the *Ramosa* Group also show inter-group relationships. A population from Van Rhyn's Pass in the Bokkeveld Mountains shows the spikelet shape and hairiness of *E. calycina*, but the plants are suffrutescent, growing in bushy clumps similar to *E. rehmannii* (Ellis 1147, 4625, Gibbs Russell 5588). The anatomy of these specimens resembles that of the *Ramosa* group, with inrolled blades, absence of a midrib and ribs, compact mesophyll and numerous prickles. However, the stomata are not of the *Ramosa* type and the silica bodies are not dumbbell-shaped. The microhairs appear to be intermediate, being narrower than the *Ramosa* type but not tapering to a point as in the *Calycina* group. Long cell shape is variable, with some specimens having rectangular *Ramosa*-type cells and others showing fusiform *Calycina*-type cells. Specimens of this population appear to establish a clear morphological and anatomical link between these two species groups and possibly represent a hybrid between them.

A single specimen (Ellis 5511) from Sneekop Peak in the Cedarberg area probably represents a new species. It has the open inflorescence, long glumes and appendaged mucronate glabrous sterile lemmas of *E. ramosa* subsp. *aphylla*, but its culms are herbaceous and the base of the plant is extraordinarily leafy, with long erect blades similar in number and position to those of *E. dura*, but with leaf anatomy similar to *E. capensis*. Its correct species group is therefore presently unknown.

Apart from this single specimen, the *Ramosa* group shows affinities only with the *Calycina* group, otherwise occupying an isolated position within the genus. The anatomy of the group is distinct, with several unique features.

The imprecision of defining the taxa in the *Ramosa* group is in contrast to other species groups (e.g. *Villosa*, *Dura*, *Capensis*) where the species and infraspecific taxa are more easily delineated. There are two sources of doubt in identifying specimens in the *Ramosa* group: first, many

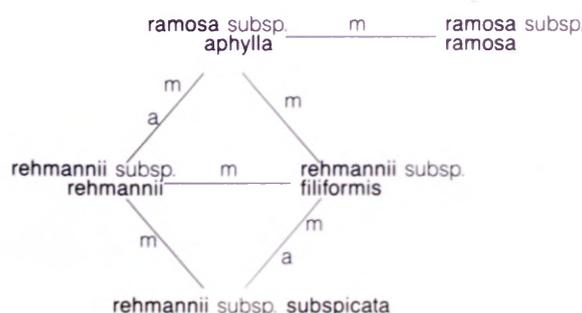


FIGURE 17.—The occurrence of intermediates between subspecies in the *Ramosa* group is shown by a line between taxa. The symbol 'm' indicates morphological intermediates and the symbol 'a' indicates anatomical intermediates.

intermediates for both morphological or anatomical characters have been recorded (Figure 17); second, some of the most useful characters for separating taxa depend on character states that may vary during the life cycle of an individual. It is particularly difficult to distinguish an open inflorescence from a contracted one early in the flowering season, and it appears from field observations that plants which become suffrutescent and bladeless when mature may be herbaceous and conspicuously leafy when young. Long-term phenological studies related to fire frequency are necessary to understand the true relationship between the infraspecific taxa in the *Ramosa* group.

#### ACKNOWLEDGEMENTS

The following herbaria are thanked for the now long-standing loans of *Ehrharta* specimens: BOL, J, JF, NBG & SAM, STE. Specimens from K, P and LE were examined at Kew. We thank the Keeper, Mr G. Lucas, and Deputy Keeper, Dr W.D. Clayton, for visitor's facilities and especially for the generous gift of many colour photographs of specimens; the Director of B for visitor's facilities; A. Romanowski for photography, S. Perold for scanning electron microscopy, G. Condy for the spikelet drawing and H. Ebertson, A. Botha and W. Roux for technical assistance.

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## SPECIMENS EXAMINED

- Acocks* 19908 (1a) K, PRE; 21178 (2c) PRE; 22484 (2b) K, PRE; 24130 (2b/2c) K, PRE; *Acocks & Hafstrom* 13.II.1938 (1b) PRE. *Adamson* 597 (1b) PRE; 675 (2b) PRE; 1250 (1b) BOL; 1253 (2b) BOL; 2427 (2b) BOL; 2696 (2c) BOL; 2734 (1b) BOL; 3701 (2c) BOL, PRE; 3969 (1b) JF. *Andreea* 30 (1b) PRE; 705 (1a/1b) PRE; 1298 (1a) PRE. *Archibald* 3480 (1a) BOL, PRE.
- Balkema* 48 (1b) STE. *Barnard* (1a) SAM (No. 28386). *F. Bolus* Nov. 1913 (1b) PRE; Oct. 1913 (2b) NBG; Jan. 1913 (2b) PRE; Nov. 1913 (2b) K, PRE; Dec. 1913 (2b) PRE; Dec. 1915 (2b) BOL; Jan. 1915 (2b) BOL, K. *H. Bolus* 4733 (1b) BOL; 14670 (1b) K; 14740 (2) K. *Bond* 1613 (2a) PRE; s.n. (2a) NBG. *Boshoff* P302 (1a) STE. *Boucher* 1456 (2b) JF, STE; 1661 (1b) JF, PRE, STE; 1724 (1b) PRE, STE; 2380 (1b) PRE, STE; 2646 (2b) STE; 4202 (1a) PRE, STE. *Burchell* 543 (1b) K, PRE; 4648 (1a) K; 5974 (2) K; 6712 (2) K, PRE (fragment). 7011 (1a) K; 7312 (1a) K; 7725 (1b) K, PRE (photo and fragment). *Burt Davy* 15121 (1a) K.
- Carmichael* s.n. (1b) PRE. *Cleghorn* 2020 (2c) PRE; 2491 (2c) K, PRE; 2498 (2) K; 3103 (2c) PRE, STE; 3143 (2b) K, PRE, STE; 3164 (1b) STE, PRE. *Compton* 8245 (2b) NBG; 12870 (1a) BOL, NBG; 16962 (2b) NBG; 18595 (1b) NBG; 20228 (1b) NBG; 23076 (2a) K, NBG. *Crook* 1021 (1b) K, BOL, NBG, PRE; 1035 (2b) BOL, K, NBG, PRE.
- Dahlstrand* 2970 (1a) J, PRE, STE. *Durand* 299 (1a) JF. *Drège* (1a) SAM (No. 19639); *Du Toit's Kloof* (1a) K; *Giftberg* (1b) K; *Paarl Mts* (1b) K; *Table Mtn* (1b) K; s.n. (1a) P. *Du Toit* 1345 (1b) PRE, STE; 1425 (1b/2a) PRE, STE; 1747 (1a/2a) STE.
- Ecklon* 914 (in part) (1b) K; 914 (in part) (2b) K; s.n. (1a) P. *Ecklon & Zeyher* s.n. (1a) B. *Ellis* 618 (2a) PRE; 634 (1a) PRE; 648 (1b/2a) PRE; 1295 (2b/2c) PRE; 1632 (1a) PRE; 2235 (1b) PRE; 2288 (2b) PRE; 2289 (2b) PRE; 4634 (1b) PRE; 4660 (2b/2c) PRE; 4671 (2b) PRE; 4673 (1b) PRE; 4676 (2b) PRE; 4694 (1a) PRE; 4697 (2a) PRE; 4698 (2a) PRE; 4699 (2a) PRE; 5511 (?) PRE; 5525 (1a) PRE. *Esterhuysen* 580 (2b) PRE; 632 (1b) NBG; 3930 (1a/1b) BOL; 6690 (1a) K, BOL, PRE; 6751 (2a) BOL, K, NBG, PRE; 8343 (1a) K, BOL, NBG, PRE; 8605 (1b) BOL; 9840 (1a) BOL; 10607 (2a) BOL, PRE; 10815 (1a) PRE; 11317 (1a) PRE. 11785 (1b) PRE; 11786 (2b) PRE; 11787 (2b) BOL; 12348 (1b) BOL, PRE; 13505 (1b) BOL, PRE; 13581 (2a) BOL, NBG, PRE; 14978 (1a/1b) NBG; 27314 (2a) BOL, PRE; 27426 (1a) PRE; 28011 (1a) BOL, PRE; 28110 (1b/2b) BOL, PRE; 28396 (1b/2b) BOL, NBG, PRE; 28651 (2b) BOL, PRE; 32217 (1a/1b) BOL; 32499 (1b) BOL; 33393 (2b) BOL, PRE; 33720 (2c) BOL, K, PRE; 34075 (2c) BOL; 34468 (2c) BOL; 35541 (2b) BOL, K; 35856 (1a) BOL.
- Fairale* 284 (2c) PRE; 286 (1b) PRE; 297 (2c) PRE. *Forsyth* 354 (1b) JF. *Fourcade* 921 (2a) BOL; 1589 (2a) BOL; 2478 (1a) BOL, PRE; 2815 (2a) BOL, K, PRE, STE; 4259 (1a) K, STE; 5529 (2a) STE; 6496 (1a) BOL, STE; s.n. STE. *Fries, Norlindh & Weimarck* 611 (1a) PRE.
- Galpin* 149 (1a) STE; 165 (1a) K, PRE, STE. *Geldenhuyss* 286 (2a) PRE. *Gericke* 18.8.1950 (2c) PRE; s.n. (2a) PRE. *Gibbs Russell* 5602 (1b) PRE; 5633 (1a) PRE; 5644 (2b/2c) PRE; 5646 (2b/2c) PRE; 5651 (2b) PRE; 5654 (2b) PRE; 5657 (1b) PRE; 5659 (2b) PRE; 5660 (1b) PRE; 5662 (1b) PRE; 5664 (2b) PRE; 5668 (1b/2a) PRE; 5672 (1b/2a) PRE; 5674 (1a/1b) PRE; 5679 (1a) PRE; 5683 (1a/2a) PRE; 5687 (1a) PRE; 5688 (1a) PRE; 5695 (2a) PRE; 5697 (2a) PRE; 5698 (1a) PRE; 5699 (1a) PRE. *Gluckman* 11.10.38 (1b) J. *Grobler* 31.10.62 (2b) K, STE.
- Hanekom* 1294 (1b/2a) K, PRE; 2045 (1a) PRE. *Harvey* 318 (2) K; 329 (2b) K; 335 (2b) K. *Haynes* H460 (1b) JF, K, PRE, STE; 596 (2b) JF, PRE; 597 (1b) JF, PRE. *Henderson* 1278 (1b) NBG. *Howes* 202 (1b) K.
- Jacot Guillarmod* 8478 (2a) K, PRE.
- Kensit* Nov. 1913 (1b) K; Jan. 1914 (1a/2a) BOL, PRE; Jan. 1914 (2a) BOL; s.n. (1b) J. *Kerfoot & Haynes* 8 (1b) JF. *Kruger* 340 (1b) JF, PRE.
- Laughton* s.n. (2a) BOL (No. 22542); *Levy's* 9816 (2b) BOL; s.n. (1b) BOL. *Liebenberg* 3805 (2a) K; 3808 (2a) K; 4011 (2a) PRE; 4064 (1b) PRE, STE; 4308 (1a/1b) PRE; 4331 (1a/1b) K, STE; 5589 (1b) PRE, STE. 8358 (2a) PRE. *Loubser* 3219 (2b) STE. *Loxton* 221 (1a/1b) PRE.
- MacGillivray* 392 (1b) K. *MacOwan* 1692 (1b) K, SAM. *McCallum Webster* N59a (1b) K. *Marloth* 3051 (1a) PRE, STE; 3062 (1b) PRE; 3065 (1b) PRE, STE; 3074 (1a) PRE. *Meebold* 13862 (1b) PRE; 13864 (1b) PRE. *Moss* 7641 (1b) J. *Muir* 3802 (1a) PRE. *Mund & Maire* (1a) K, PRE (photo).
- Ofsowitz* 29 (2a) PRE.
- Page* Feb. 1918 (1b/2a) BOL. *Palmer* s.n. (2a) K, PRE. *Parker* 4035 (2b) K, NBG, PRE; 4681 (1b) BOL, K, NBG, PRE; 4931 (2c) BOL, K, NBG, SAM. *Pearson* 3222 (1b) K, J; 3533 (1b) K; 5133 (1a) BOL, K. *Phillips* 49 (1a) NBG; 1382 (1b) SAM; 1686 (1a) SAM; s.n. NBG. *Pocock* S123 (1a) PRE. *Prior* Sept. 1846 (1b) K, SAM; Apr. 1903 (2a) K.
- Rehm* 267 (1b) B, K; s.n. (2b) B. *Rehmann* 74 (1a) K, PRE (photo and fragment). *Richardson* 63 (1b/2a) JF. *Ronassen* Dec. 1943 (1b) NBG. *Rycroft* 14.12.1945 (2b) JF.
- Salter* 9648 (2b) BOL; 9665 (1b/2a) BOL, PRE. *Sandwith* 51 (1b) K; 128 (1b) K, PRE. *Scharf* 1050 (1a) K, PRE; 1594 (1a) PRE; 1705 (1a) PRE. *Schlechter* 7285 (2b) BOL, P, PRE; 9180 (1b) BOL, K, P, PRE; 9417 (2b) BOL, K, P, PRE; 9873 (1a) K, BOL, PRE. *Smook* 3697 (1b) PRE; 4083 (2a) K, PRE. *Stokoe* 2652 (1b/2b) BOL, SAM (No. 49380, No. 67676); 7809 (1a/1b) BOL; 7811 (2b) BOL, SAM (No. 67673, 67674); 8639 (1b) K; SAM No. 54502 (1a/1b) SAM. *Story* 2389 (1a) PRE.
- Taylor* 3636 (2b) PRE, STE; 4235 (1a) PRE, STE; 4502 (2b) PRE, STE; 4590 (2b) STE, PRE; 5223 (1b) K, PRE, STE; 7667 (2c) PRE. *The Forester* 8266 (1a/1b) PRE. *Thompson* 2253 (1a) PRE, STE.
- Van Daalen* 137 (2a) PRE. *Van der Merwe* 26-02 (1b) STE; 936 (1b) PRE, STE; 1794 (1b) STE; 2106 (1b) STE. *Van Rensburg* 11 (1b) STE; 212 (1b) PRE, STE; 214 (2b) K, PRE, STE. *Van Wyk, Fellingham & O'Callaghan* 432 (1a) STE. *Von Breitenbach* 60 (2a/2c) PRE.
- Wells* 3236 (1a) PRE. *Williams* 3152 (2b) K, PRE. *Wolley Dod* 2385 (2b) K; 3118 (2b) BOL; 3121 (2b) BOL; 3477 (2b) BOL, K, PRE; 3519 (2c) BOL, K, PRE (photo and fragment). *Wright* s.n. (1b) K.
- Zeyher* 85 (1b) BOL; 293 (1a) BOL, NBG, PRE, SAM, STE. 4510 (1a) BOL; 4511 (1a) PRE; 4571 (1b) SAM; Oct. 1830 (1a) PRE; s.n. (1a) BOL, P; (1b) SAM (No. 40069). *Zinn* Feb. 1940 (1b) SAM.

Note that specimens from B, K, LE and P are not included on the distribution maps.

