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Leaf anatomy of the genus *Ehrharta* (Poaceae) in southern Africa: the Villosa group

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Keywords: *Ehrharta, E. thunbergii, E. villosa,* leaf anatomy, Poaceae, stomatal flanges, systematics

ABSTRACT

The leaf blade anatomy of *Ehrharta villosa* Schult. f. var. *villosa*, var. *maxima* Stapf and *E. thunbergii* Gibbs Russell is described and illustrated. These three taxa, constituting the Villosa species group, share a diagnostic leaf anatomy distinguished by the absence of a distinct midrib, adaxial semi-radiate mesophyll with the abaxial chlorenchyma palisade-like in arrangement, rectangular long cells and the stomatal apertures which are overlapped by four cuticular flanges projecting from the two adjacent interstomatal cells. These combined attributes characterize this species group, and the stomatal flanges are unique to this group in the genus *Ehrharta* Thunb. Microhairs are absent in *E. villosa* but are present in *E. thunbergii* which also possesses abaxial prickles and plentiful, rounded silica bodies not associated with cork cells as in *E. villosa*. These two taxa can, therefore, be separated anatomically. Nevertheless, they share many features and are undoubtedly closely related and their classification in the same species group is substantiated by the anatomical evidence presented in this paper.

UITTREKSEL

Die blaarskyfanatomie van *Ehrharta villosa* Schult. f. var. *villosa* en var. *maxima* Stapf en *E. thunbergii* Gibbs Russell word beskryf en geïllustreer. Hierdie drie taksons, wat die Villosa-spesiegroep verteenwoordig, vertoon 'n diagnostiese blaaranatomie, gekenmerk deur die afwesigheid van 'n duidelike hoofaar, semi-radiale adaksiale mesofil met die abaksiale chlorenchiem palisade-agtig gerangskik, reghoekige langselle en die huidmondjie-openinge wat oorvleuel word deur vier kutikulêre krae wat vanaf die twee aangrensende selle strek. Dié kombinasie van kenmerke onderskei hierdie spesiegroep, en die huidmondjie-krae is uniek by hierdie groep in die genus *Ehrharta* Thunb. Mikrohare is afwesig by *E. villosa* maar aanwesig by *E. thunbergii* wat ook abaksiale stekelhare en volop ronde silikaliggaampies, wat nie met kurkselle geassosieer is soos by *E. villosa* nie, besit. Hierdie twee taksons kan dus anatomies onderskei word maar het nietemin baie kenmerke gemeen en is ongetwyfeld nouverwant aan mekaar en hul klassifikasie in dieselfde spesiegroep word ondersteun deur anatomiese gegewens wat hier aangebied word.

INTRODUCTION

The species of the Villosa group of the genus *Ehrharta* Thunb. are distinguished morphologically by their large spikelets with profusely hairy, conspicuously bearded and mucronate sterile lemmas (Gibbs Russell & Ellis 1987). The leaf blades are reduced and rolled and the culms are suffrutescent, sometimes with swollen or tuberous bases. Creeping, underground rhizomes occur in all taxa.

Taxa included in this group are *Ehrharta villosa* Schult. f. var. *villosa* and var. *maxima* Stapf, and *E. thunbergii* Gibbs Russell (= *E. gigantea* Thunb.). Chippindall (1955) considered *E. villosa* var. *villosa* and *E. thunbergii* to be conspecific, whereas Smook & Gibbs Russell (1985) synonomize *E. villosa* var. *maxima* and *E. thunbergii*. In the present treatment *E. thunbergii* is considered as a separate species following Gibbs Russell (1987) and consequently, three taxa are assigned to the Villosa species group.

The leaf blade anatomy of taxa belonging to this species group has received very little attention from previous workers. Metcalfe (1960) gives a full description of *E. villosa* var. *maxima* and Engelbrecht (1956) also describes the leaf anatomy of *E. villosa* based on a representative sample of 18 specimens, 8 identified as *E. villosa* and 10 as *E. thunbergii* (= *E. gigantea*) but considered as a single species.

This paper describes and illustrates the leaf blade anatomy of the taxa of the Villosa group and discusses the affinities of these taxa and of the species group by reference to this anatomical evidence. By implication the anatomical data is compared and contrasted with the morphological data as it is reflected in the classification of the group (Gibbs Russell 1987). The herbarium voucher specimens used in this anatomical study were included in the sample on which the above taxonomic conclusions were based. The methodology is described in Gibbs Russell & Ellis (1987) and the format of the paper follows that of the first paper in the series (Ellis 1987a).

LEAF ANATOMY OF THE SPECIES OF THE VILLOSA GROUP

E. villosa *Schult. f.*

Transverse section

The leaf blade is loosely inrolled (Figures 1.1, 2.1, 2.3, 3.1, 3.3) without a distinguishable keel, the median vascular bundle being structurally identical to the lateral first order bundles (Figures 1.1, 2.3, 3.3). Successive first order bundles are separated by 2–3 third order bundles except laterally where only a single smaller bundle is located between successive first order bundles.

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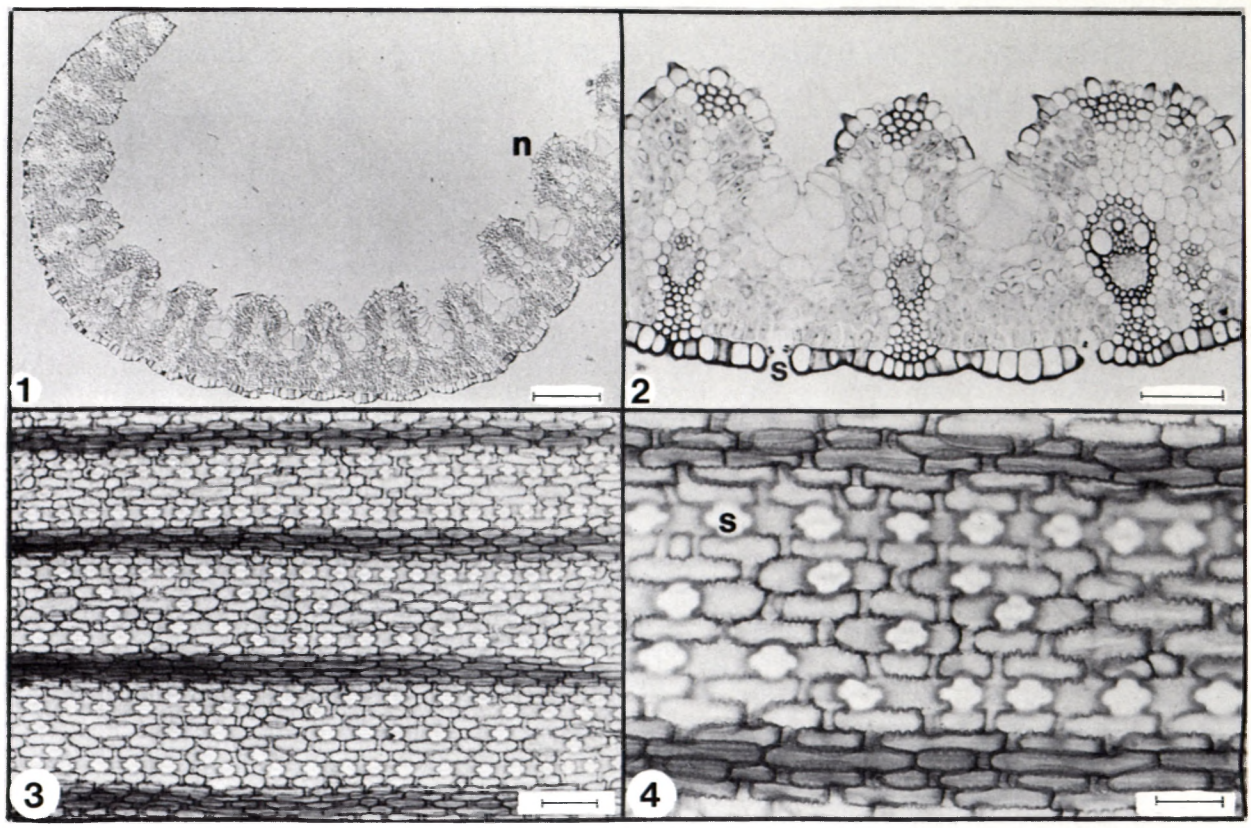

FIGURE 1. — Leaf anatomy of *Ehrharta villosa* var. *maxima, Ellis 601*: 1–2, leaf in transverse section: 1, vascular bundle arrangement and absence of keel (n), scale bar = 20 μm; 2, anatomical detail with sunken abaxial stomata (s) and mesophyll with adaxially located chlorenchyma cells radiately arranged and abaxial cells palisade-like, scale bar = 10 μm. 3–4, abaxial epidermis: 3, epidermal zonation with costal (darkly staining) and intercostal zones, scale bar = 10 μm; 4, short intercostal long cells and flanged interstomatal cells with flanges projecting over the sunken stomata (s), scale bar = 5 μm.

Rounded adaxial ribs are associated with all the vascular bundles (Figures 1.2, 2.2, 2.4, 3.2, 3.4), those of the first order bundles being slightly larger. Shallow, but rather narrow, furrows are present between all the ribs.

The mesophyll tissue is unusual in that it is semiradiate in arrangement, particularly the adaxially situated cells located in the ribs (Figures 1.2, 2.2, 2.4), but the arrangement of the abaxial layers of chlorenchyma cells is palisade-like (Figure 2.2, 2.4) and may be conspicuous due to denser chloroplast concentrations (Figure 3.4). The chlorenchyma cells are relatively large, somewhat variable in shape but tightly packed so that no large intercellular air spaces are visible in transection (Figures 2.2, 2.4). The chloroplasts are evenly but densely distributed throughout all the chlorenchyma cells.

Abaxial epidermis

Costal and intercostal zones are clearly differentiated (Figure 1.3, 2.5) due to differential staining, although the epidermal cells of these two zones do not necessarily differ greatly in structure (Figure 2.6). The costal zones lack stomata and consist of narrower cells (Figure 1.4). The intercostal long cells are rather short, and rectangular with slightly undulating walls. The cells of the central files of each zone may tend to be longer and wider than the lateral cells (Figure 2.5). These larger cells are sometimes also evident in the leaf sections (Figure 1.2, 2.4).

Stomata are common in 3–5 files in each intercostal zone (Figure 1.3, 2.5).They are clearly sunken well below the level of the rest of the epidermis with the guard and subsidiary cells being overlapped by four distinct cuticular flanges extending over the stomatal aperture from the adjacent interstomatal long cells (Figures 1.2, 2.2, 2.4). In surface view a distinct cross-shaped aperture is formed by these flanges, below which the stomatal apparatus is located (Figure 1.4, 2.6). SEM studies reveal that the flanges are papilla-like (Figures 4.1–4.4).

Costal silica bodies are not well differentiated and are usually small, rounded and intimately associated with an enfolding cork cell (Figure 1.4, 2.6). In less typical specimens, however, the silica bodies may be much more evident and numerous (Figures 6.1, 6.3). Prickles are absent but prickles are present on the adaxial costal zones which are equivalent to the ribs as seen in transverse section (Figures 1.2, 2.4, 3.2). No microhairs were seen either with the light or the scanning electron microscope (Figures 1.4, 2.6, 4.1–4.4).

Specimens examined

E. villosa var. *villosa*

CAPE.—3218 (Clanwilliam): Lamberts Bay (–AB), *Ellis 4640* (atypical tending toward *E. thunbergii*). 3318 (Cape Town): Darling Dist., Yzerfontein (–AC), *Ellis 1686*. 3420 (Bredasdorp): Bredasdorp Dist., De Hoop Nature Reserve (–AD), *Ellis 1284, 4665*. 3421 (Riversdale): Mossel Bay Dist., Albertinia (–BA). *Ellis 1651* (atypical tending toward *E. thunbergii*).

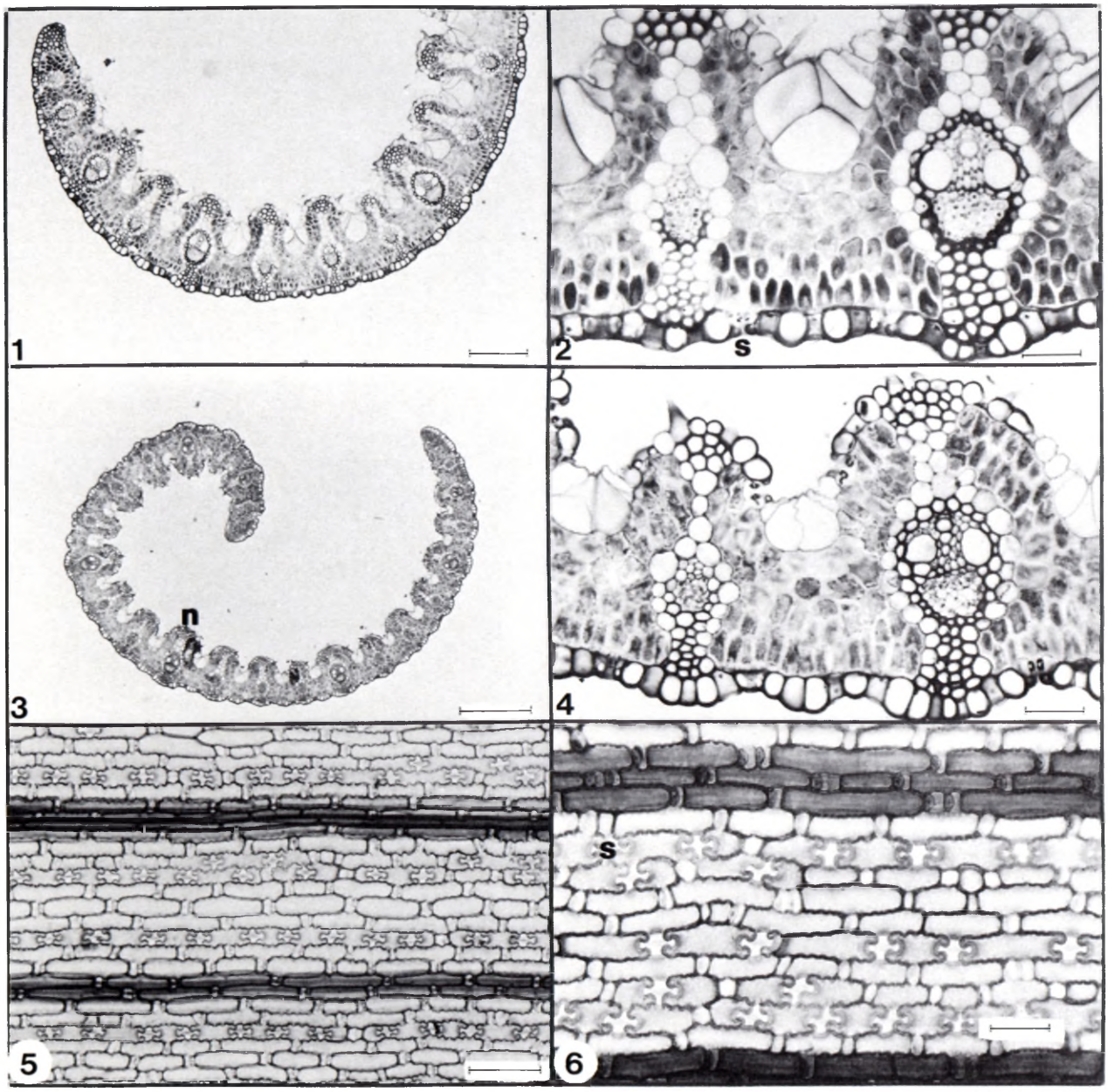

FIGURE 2. — Leaf anatomy of *Ehrharta villosa* var. *villosa* specimens resembling var. *maxima* in structure. 1–2, *Ellis 1686,* leaf blade transection: 1, loosely inrolled blade without a keel, scale bar = 20 μm; 2, detail of the chlorenchyma showing dense abaxial palisade-like cells; note sunken stomata (s) with overlapping flanges, scale bar = 5 μm. 3–4, *Ellis 1284,* transection: 3, inrolled leaf, median vascular bundle (n) only, scale bar = 20 μm; 4, anatomical detail showing sunken guard cells and radiate arrangement of the chlorenchyma, scale bar = 5 μm. 5, *Ellis 1284,* abaxial epidermis with costal zones and intercostal zones with stomatal files, scale bar = 10 μm. 6, *Ellis 1686,* abaxial epidermis with detail of stomatal flanges (s) and costal zones, scale bar = 5 μm.

E. villosa var. *maxima*

CAPE.—3325 (Port Elizabeth): Port Elizabeth, Swartkops Beach (–DC), *Ellis 601.*

Comments

E. villosa possesses the characteristic leaf anatomy of the Villosa group being distinguished by the absence of a keel or midrib, the palisade-like abaxial mesophyll, the flanged stomata, and the rectangular long cells. The anatomy of var. *villosa* and var. *maxima* is very similar and these two taxa appear to show close affinities, being indistinguishable on leaf blade anatomy, a fact which appears to corroborate their separation at only the varietal level.

Although the var. *maxima* anatomical sample used in this study is inadequate, the specimen examined *(Ellis 601)* conforms in all respects to the description given by Metcalfe (1960) for material from Western Australia even though his microtechnique procedures did not allow a detailed examination of the mesophyll. These two specimens reveal that the leaf anatomy of var. *maxima* conforms very closely with that of var. *villosa,* with some specimens of the latter being virtually indistinguishable from var. *maxima* in leaf anatomy (Figures 2.1–2.6).

E. villosa var. *villosa* is a rather variable taxon anatomically. Some specimens of var. *villosa* correspond very closely in leaf size and thickness to the relatively large leaves of var. *maxima,* as a compari-

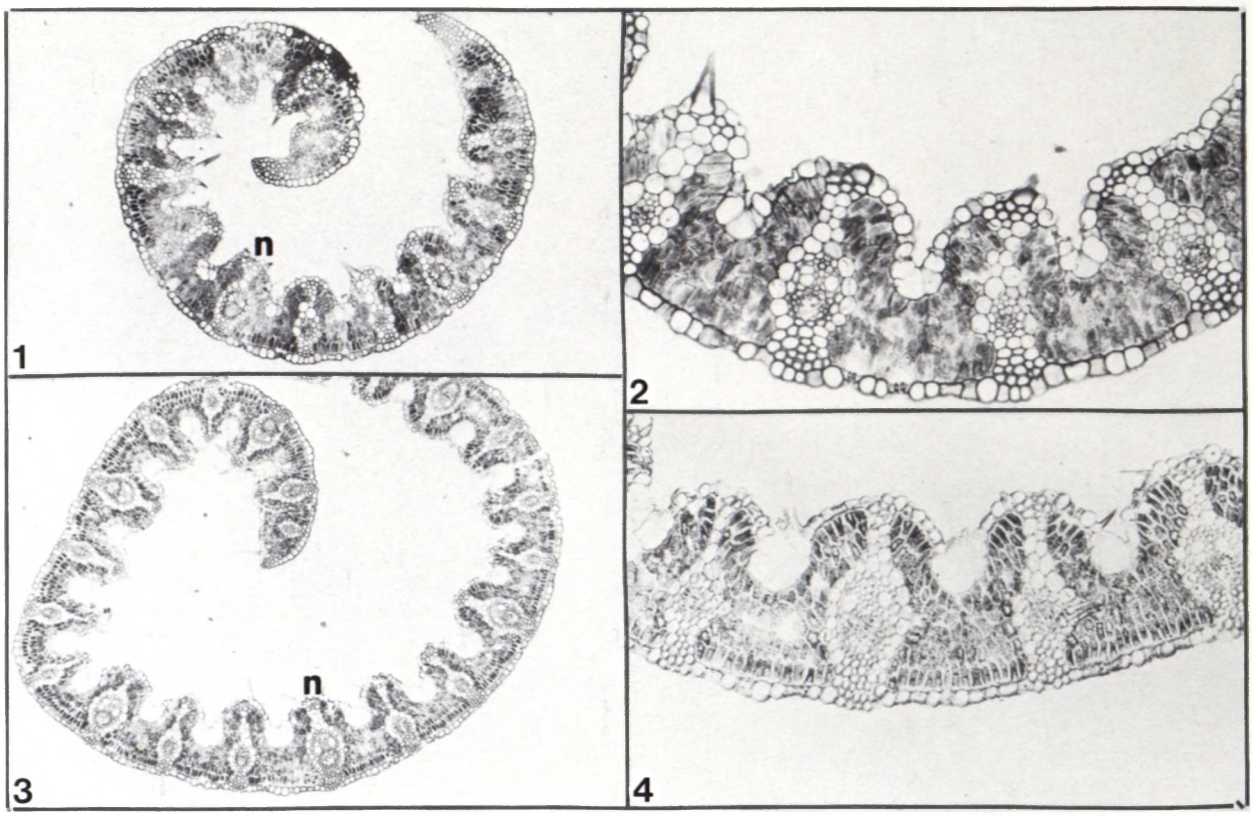

FIGURE 3. — Transectional leaf anatomy of *Ehrharta villosa* var. *villosa*. 1–2, *Ellis 4665*: 1, inrolled outline with median bundle (n) only, scale bar = 20 μm; 2, anatomical detail showing rather angular chlorenchyma cells with radiate adaxial layers and palisade-like abaxial layers, scale bar = 10 μm. 3–4, *Ellis 4640*: 3, inrolled outline without additional parenchyma in association with the median bundle (n), scale bar = 20 μm; 4, interference contrast illumination of detail of chlorenchyma cell arrangement, scale bar = 10 μm.

son of Figures 1.1, 1.2 and 2.1–4 shows. Others, however, resemble *E. thunbergii* with thinner leaves (Figures 3.3, 3.4). A similar trend is also evident in the epidermal structure, with Figures 2.5, 2.6 resembling the var. *maxima* condition, whereas Figures 6.1, 6.3 approximate closely some of the *E. thunbergii* specimens. *E. villosa* var. *villosa,* therefore, is intermediate in leaf anatomy between var. *maxima* and *E. thunbergii* and the interface between these two taxa is not very distinct.

The intermediate nature of var. *villosa* is also evident in its spikelet size and habitat requirements and several specimens have proved difficult to assign to either var. *villosa* or *E. thunbergii* on morphological criteria. This is particularly the case if the rhizome characters are not evident. But *E. villosa* is a species of deep, loose sand of the lowland fynbos and only occurs at higher altitudes where drift sand occurs as a result of wind or water deposition.

The clinal variation in anatomical structure in var. *villosa* appears to be a reflection of these habitat gradients. Those specimens most resembling var. *maxima* are all from coastal dune habitats (Figures 2.1–2.6) to which var. *maxima* appears to be confined. With increasing altitude and distance from the sea the var. *villosa* specimens (Figures 3.1–3.4, 6.1, 6.3) tend to merge with *E. thunbergii,* which is a species of higher altitudes, heavier soils and the mountain fynbos.

E. thunbergii *Gibbs Russell*

Transverse section

Blade loosely to rather tightly inrolled (Figures 5.3, 5.5). A slight keel may sometimes be developed, as evidenced by the presence of additional colourless parenchyma associated with the median vascular bundle (Figures 5.3, 5.5). This development is not equally evident in all specimens and several have the median bundle structurally identical to the lateral first order bundles, without additional parenchyma (Figure 5.1). One or two third order bundles occur between consecutive first order bundles.

Adaxial ribs are slight but rounded (Figure 5.2) or may be more conspicuous but then abaxial intercostal ribs alternate with the adaxial costal ribs (Figures 5.4, 5.5). Adaxial furrows are shallow and wider than in *E. villosa.*

The mesophyll is rather variable but all specimens conform to the general pattern so characteristic of this group. Examples with semi-radiate chlorenchyma with an abaxial palisade-like layer are illustrated in Figures 5.2, 7.1 and 7.3 and correspond closely to the *E. villosa* specimens illustrated in Figures 3.2 and 3.4. Other *E. thunbergii* specimens, with thinner leaves and fewer chlorenchyma cell layers differ slightly from this pattern (Figure 5.4). The chlorenchyma cells themselves remain rather large, somewhat angular and tightly packed with very small intercellular air spaces (Figures 5.2, 5.4).

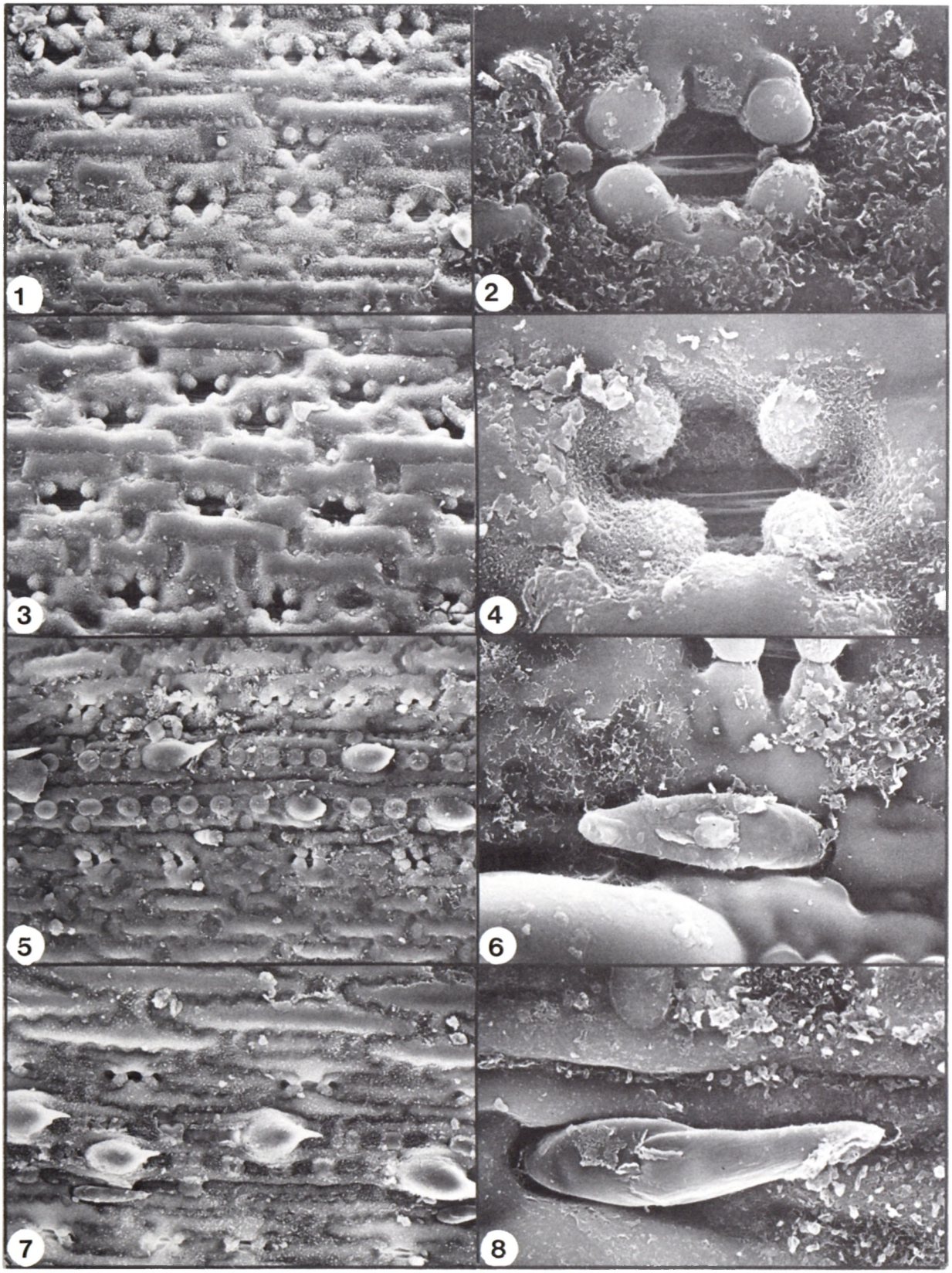

FIGURE 4. — Abaxial epidermal ultrastructure of representatives of the Villosa group. 1–4 *Ehrharta villosa* var. *villosa*. 1–2, *Ellis 4640*: 1, thickened epidermal cells, no microhairs and flanged stomata, × 200; 2, detail of the four papilla-like flanges overarching the stomatal apparatus with the guard cells visible below this aperture, × 1000. 3–4, *Ellis 4665*: 3, thick cuticle, sunken stomata and microhairs absent, × 200; 4, guard cells beneath the overarching papillate flanges, × 1000. 5–8, *Ehrharta thunbergii*. 5–6, *Ellis 4648*: 5, distinct costal zone with raised, round silica bodies and prickles; intercostal zone with microhairs and files of flanged stomata, × 200; 6, detail of microhair with tapering distal cell and flanges obscuring adjacent stoma, × 1000. 7–8, *Ellis 4626* illustrating anatomical variation in *E. thunbergii*: 7, costal prickles, intercostal microhairs and flanged stomata, but note the diamond-shaped intercostal long cells, × 200; 8, microhair with tapering distal cell, × 1000.

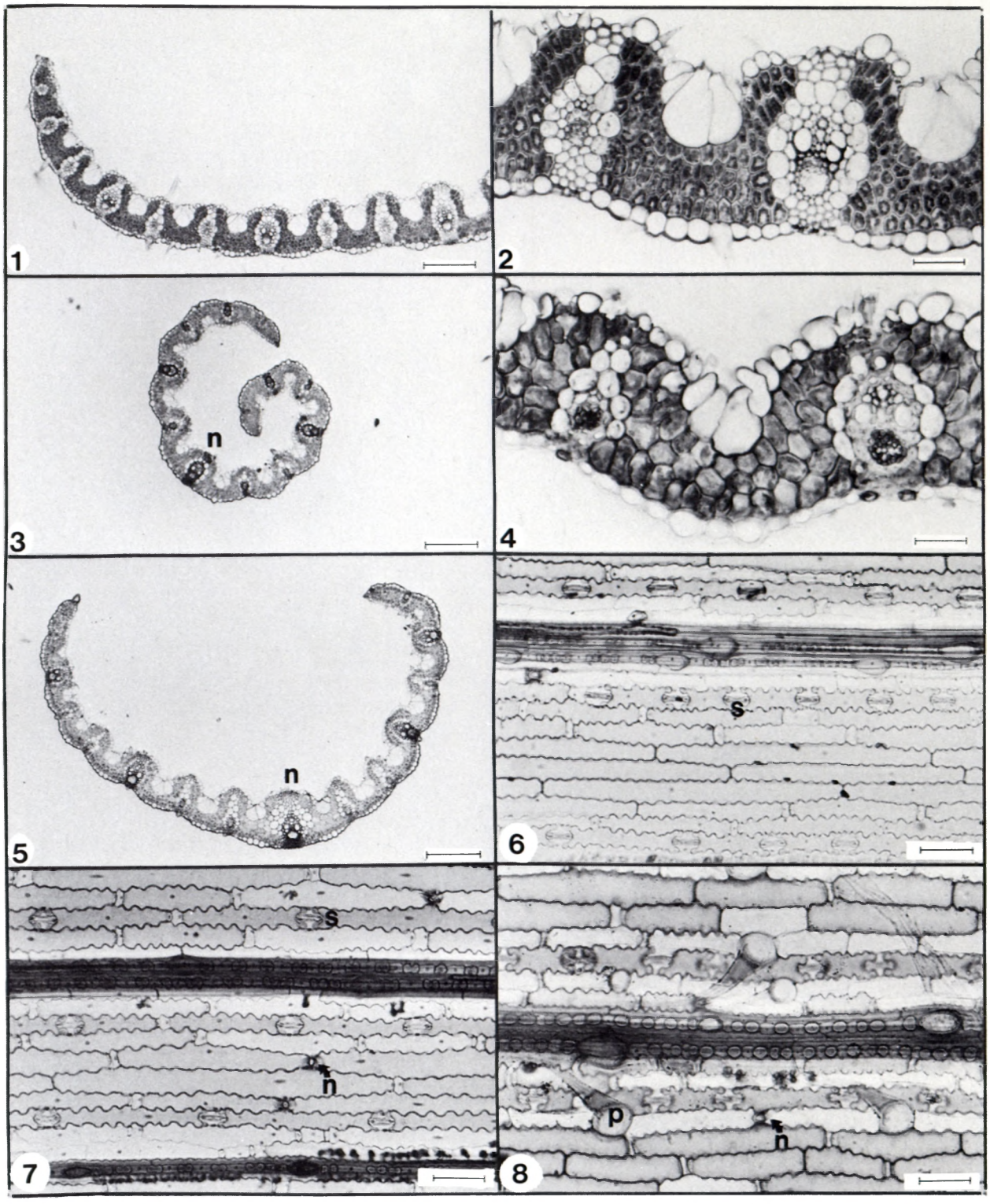

FIGURE 5. — Leaf anatomy of *Ehrharta thunbergii*. 1–5, leaf transections; 6–8, abaxial epidermides. 1–2, *Ellis 1152*: 1, median bundle not structurally distinct, scale bar = 20 μm; 2, chlorenchyma cell detail and arrangement typical of that of the Villosa group, scale bar = 5 μm. 3–4, *Ellis 708*: 3, inrolled blade with slight keel (n), scale bar = 20 μm; 4, detail showing less pronounced radiate and palisade chlorenchyma arrangement and abaxial ribs, scale bar = 5 μm. 5–6, *Ellis 1145*: 5, leaf outline showing small but definite keel (n), scale bar = 20 μm; 6, elongated intercostal long cells, stomata obscured by flanges (s), scale bar = 5 μm. 7, *Ellis 708* with elongated stained and unstained intercostal long cells with slightly undulating walls, microhairs (n) and flanged stomata (s), scale bar= 5 μm. 8, *Ellis 1152*; note silica bodies, costal and intercostal prickle hairs (p), stained and unstained long cells, microhairs (n) and flanged stomata, scale bar = 5 μm.

Abaxial epidermis

Costal and intercostal zones are always distinguishable (Figures 5.6–5.8, 6.2, 6.4, 7.2, 7.4–7.6). Cell size and shape differ markedly between these two zones on all the specimens examined. The intercostal long cells are often much more elongated than in *E. villosa* but this character is variable with Figures 5.6, 5.7 and 6.4 representing the two extremes encountered in this species. The long cell shape is usually rectangular but may be diamond-shaped (Figure 7.4). The markedly elongated long cells may also stain with safranin (Figures 5.7, 5.8).

Stomata occur in 2–3 files on either side of each costal zone but are absent from the central files of the intercostal zones. These stomata are always sunken and overlapped by cuticular flanges although these are not always easily visible with the light microscope (Figures 5.6, 5.7). The specimens with thinner leaves and elongated long cells have less conspicuous flanges associated with more superficial stomata. Those specimens tending toward *E. villosa* in leaf anatomy have this characteristic well developed (Figures 6.2, 6.4), as do the specimens showing similarities with the Calycina group (Figure 7.4) or the Ramosa group (Figures 7.5, 7.6). Although variable, this attribute is evident on all the specimens studied and is confirmed by the SEM (Figures 4.5–4.7).

Costal silica bodies are generally well differentiated, being conspicuous and rounded and alternating along the costal files (Figures 5.8, 6.4, 7.2). Crescent-shaped, enfolding cork cells do not appear to occur in this species. Abaxial costal prickles are common and were observed on all specimens with two specimens *(Ellis 1152* and *5102)* even possessing large intercostal prickles associated with the stomatal bands (Figure 5.8). Microhairs, although very small, were detected on all specimens, even those resembling *E. villosa* in other anatomical characteristics. Ultrastructurally these hairs are seen to have a tapering distal cell (Figures 4.6, 4.8).

Specimens examined

CAPE.—3118 (Vanrhynsdorp): Vanrhynsdorp Dist., Gifberg (–DD), *Ellis 5102.* 3119 (Calvinia): Nieuwoudtville Dist., Van Rhyn's Pass (–AC), *Ellis 1145, 4626.* 3218 (Clanwilliam): Clanwilliam Dist., Pakhuis Pass (–BB), *Ellis 1700*; Langvlei Valley, Sandberg Station (–BC), *Ellis 4642*; Piketberg Dist., Versveld's Pass (–DD), *Ellis 5130.* 3219 (Wuppertal): Cedarberg, Pakhuis Pass (–AA), *Ellis 708, 1152, 4633, 4635*; Kouebokkeveld, Skurweberg, Op-die-Berg (–CD), *Ellis 4648.* 3318 (Cape Town): Malmesbury Dist., Paardeberg (–DB), *Boucher 4724.* 3321 (Ladismith): Langeberge, Cloete's Pass, Bergkloof (–DC), *Ellis 4693.*

Comments

The diagnostic anatomical attributes of the Villosa group are all present in *E. thunbergii* although they may be somewhat modified on some specimens.

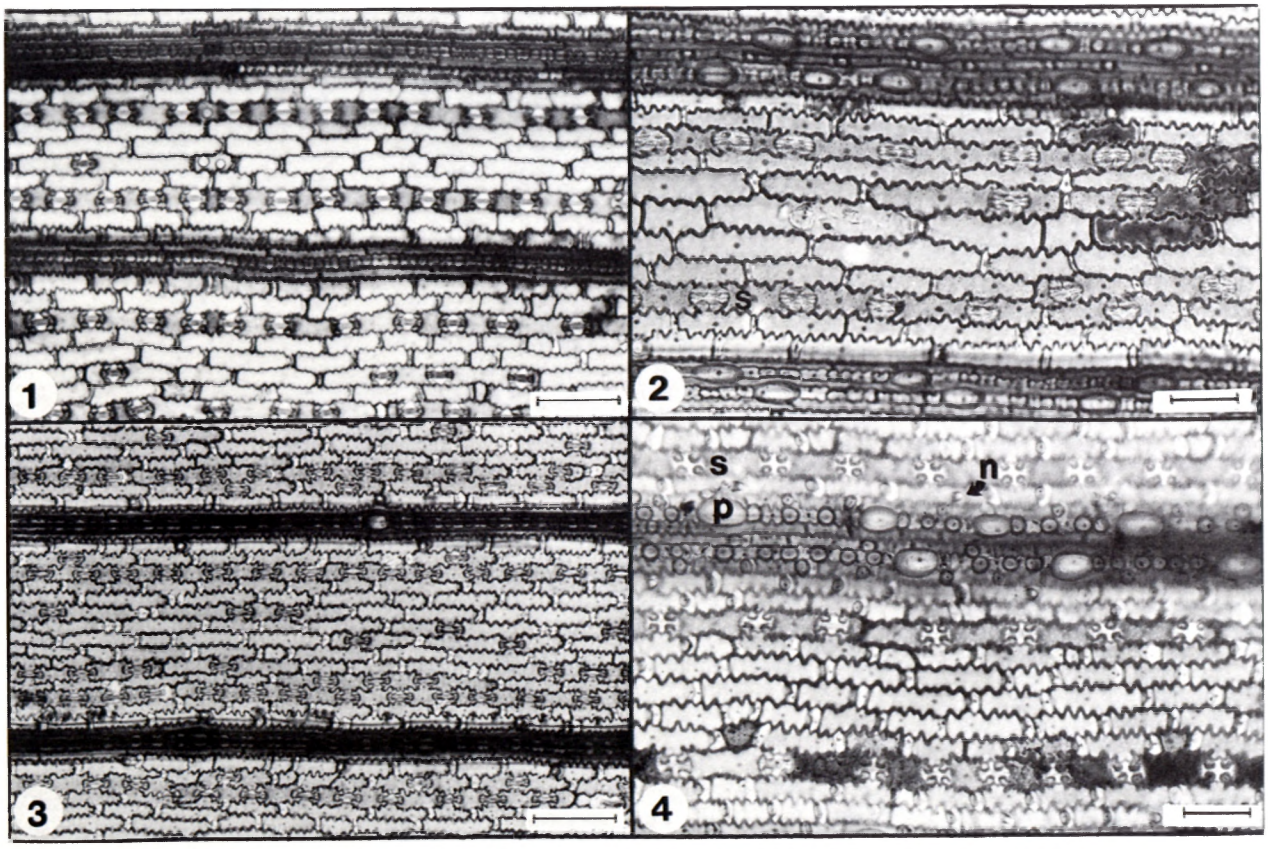

FIGURE 6. — A comparison of the abaxial leaf epidermis of *Ehrharta villosa* (1 & 3) and *Ehrharta thunbergii* (2 & 4). 1, *E. villosa, Ellis 4640,* showing short intercostal long cells with slightly sinuous walls; microhairs and prickles absent, scale bar = 10 μm. 2, *E. thunbergii, Ellis 4635,* with very sinuous long cell walls, intercostal microhairs and costal prickles, scale bar = 5 μm. 3, *E. villosa, Ellis 1651,* short, slightly sinuous long cells, flanged stomata, scale bar = 10 μm. 4, *E. thunbergii, Ellis 4648,* prominent, round costal silica bodies and prickles. Intercostal microhairs (n) and stomata (s) overarched by flanges from interstomatal long cells, scale bar = 5 μm.

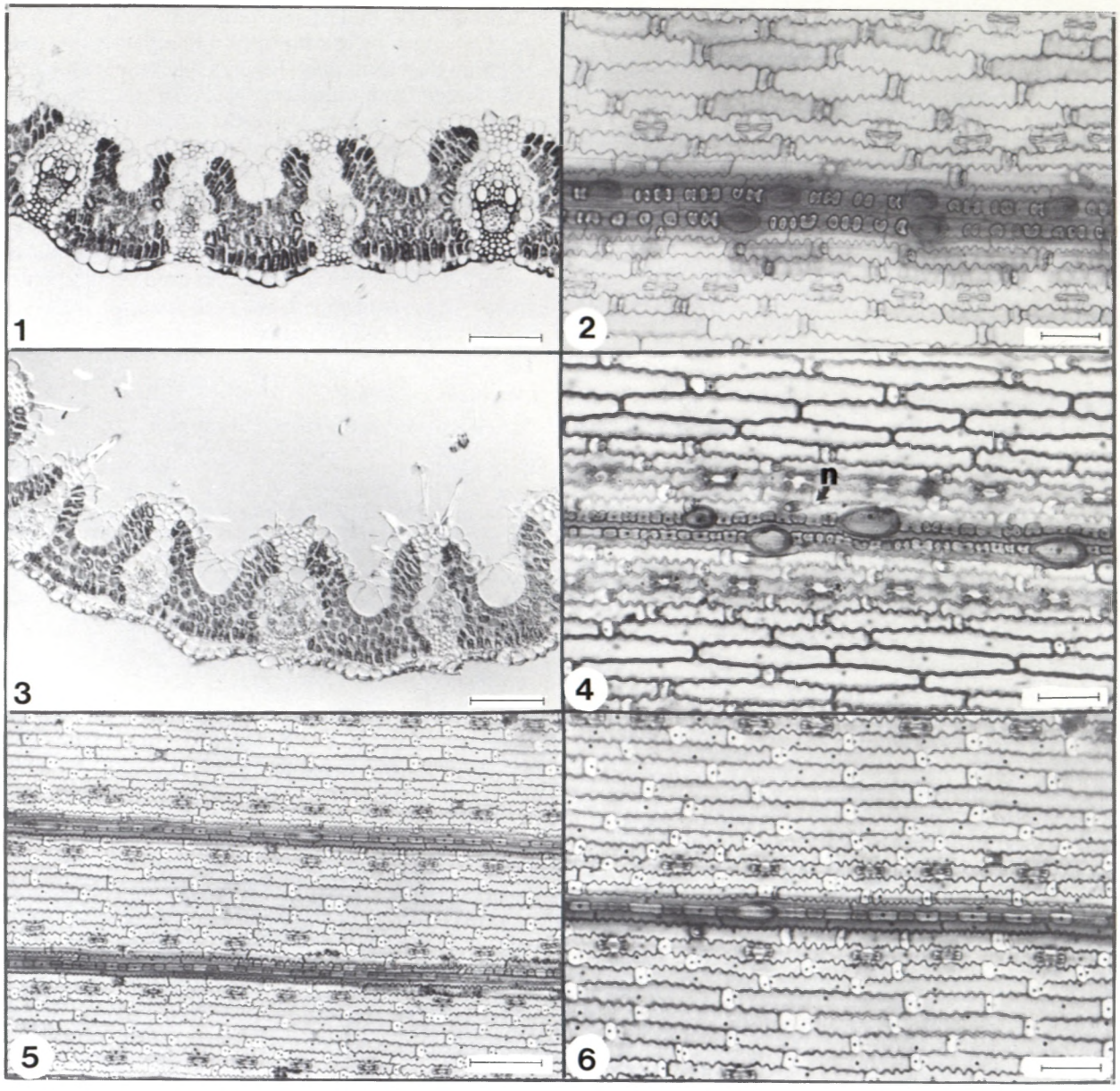

FIGURE 7. — Anatomical variation in *Ehrharta thunbergii*. 1–2, *Ellis 1700* resembling *E. villosa*: 1, transverse section with radiate and palisade-like mesophyll cells, scale bar = 10 μm; 2, abaxial epidermis with rectangular, sinuous-walled long cells but stomatal flanges not conspicuous, scale bar = 5 μm. 3–4 *Ellis 4626* resembling the Calycina group: 3, normal transverse section but note the enlarged abaxial epidermal cells in the centres of the intercostal zones, scale bar = 10 μm; 4, central intercostal long cells markedly elongated and diamond-shaped but stomata retain characteristic flanges, scale bar = 5 μm. 5–6, *Ellis 4693* resembling the Ramosa group: 5, conspicuous intercostal short cell pairs separate successive long cells, scale bar = 10 μm; 6, nucleate epidermal long and short cells but stomata flanged, scale bar = 5 μm.

Thus only a median vascular bundle is normally present but in a few specimens additional colourless parenchyma is associated with the median bundle, which, by definition, constitutes a slight keel. The semi-radiate adaxial, and palisade-like abaxial mesophyll, so characteristic of this group, is evident in most specimens. However, in a few, particularly those with thinner leaves and with abaxial intercostal ribs, this pattern may be modified slightly. In all specimens the stomata are sunken and overlapped by four papillate epidermal flanges. However, in those specimens with elongate intercostal long cells the stomata may be almost flush with the level of the epidermis and the flanges are tiny. These diagnostic features are common to all taxa of the Villosa group and serve to unite *E. villosa* and *E. thunbergii* in a group separated from all the other species of *Ehrharta*.

In addition, several characters serve to separate *E. thunbergii* from *E. villosa,* although this distinction is not very clear-cut. Examples are the presence of microhairs and abaxial prickles, both of which are lacking in *E. villosa*. The costal silica bodies of *E. thunbergii* are also well differentiated and plentiful and alternate with costal short cells. They are not associated with cork cells as in *E. villosa*. These two taxa can, therefore, be distinguished anatomically.

Yet other attributes intergrade between the taxa of this species group, and the leaf anatomy of the *E. thunbergii* specimens studied shows a certain degree of variation. A distinct gradation is evident from

those specimens closely resembling *E. villosa* (Figures 6.2, 6.4, 7.1, 7.3) to the extreme type with thinner leaves and elongated long cells (Figures 5.3–5.7). The interface with *E. villosa* is indistinct. A continuum is discernible from those specimens resembling *E. villosa* to the extreme specimens which may display characteristics of some of the other *Ehrharta* species groups, the Calycina group in particular. Calycina type features observed are the fusiform intercostal long cells as in Figure 7.4, the tendency to stain with safranin (Figures 5.6–5.8) and the intercostal abaxial ribs (Figure 5.4) or the inflated central cells of the intercostal zones as illustrated for *E. villosa* (Figures 2.4, 2.5). A single specimen, *Ellis 4642,* although not illustrated, resembles *E. calycina* particularly closely, even having straight-walled fusiform long cells and intercostal macrohairs which were not observed on any other *E. thunbergii* specimen. However, flanged stomata indicate the true identity of this specimen.

One other interesting and deviant specimen is *Ellis 4693* (Figures 7.5, 7.6) which shows similarities with the Ramosa group of species. The sinuous, rectangular long cells, all separated by conspicuous cork/silica cell pairs and the irregular, dumbbell-shaped silica bodies, are reminiscent of the Ramosa group and were not seen in any other *E. thunbergii* specimens. However, this specimen also has distinctly flanged stomata.

The anatomical sample examined in this study is heavily biased toward the north-western parts of the distribution range of *E. thunbergii.* Those specimens from high altitudes in the extreme north at Van Rhyn's Pass *(Ellis 1145,* Figures 5.5, 5.6; *Ellis 4626,* Figures 7.3, 7.4) show anatomical similarities with *E. calycina.* A specimen *(Ellis 4642)* from lower altitude in the strandveld at Langvlei resembles *E. calycina* very closely indeed. On the other hand, few specimens from the east have been classified as *E. thunbergii* (these being mainly identified as *E. villosa)* and *Ellis 4693* from Cloete's Pass in the eastern Langeberge resembles the Ramosa group in certain respects. These observations may reflect transitions to these other *Ehrharta* species groups but a much more representative sample must be studied before this can be confirmed. Nevertheless, this does serve to demonstrate that the Villosa group is not discrete, and that characteristics of some other groups are evident, as is the case throughout the genus.

These observations are largely in agreement with the findings of Engelbrecht (1956) and the few exceptions noted will be briefly discussed. For the majority of specimens the epidermis is described as being homogenous with costal and intercostal zones not being distinguishable (Engelbrecht 1956). In the present study the condition is described where these zones are structurally identical, as in *E. villosa* var. *maxima* for example, but are distinguishable on account of their differential staining. Different staining procedures, therefore, may account for this apparently superficial difference between the findings of these two studies. Engelbrecht (1956) does record the absence of microhairs and prickles associated with the homogenous type of epidermis (which appears to be homologous with *E. villosa)* whereas the epidermis with distinct epidermal zonation was associated with the presence of these hairs. This correlation was observed in the present study and is considered to be a specific difference between *E. villosa* and *E. thunbergii* but Engelbrecht (1956) did not attribute any taxonomic significance to it. He also records cuticular stomatal flanges for all the specimens he examined and notes the uniqueness of this feature in the genus.

DISCUSSION AND CONCLUSIONS

The three taxa of the Villosa group, share a distinctive leaf anatomy characterized by a unique combination of attributes as well as similar vegetative morphology and a specific habitat. These distinguishing features correlate with the diagnostic large, hairy spikelets, and their assignment to the same small species group appears to be fully justified by the anatomical as well as the morphological evidence (Gibbs Russell 1987). This group also appears to represent a natural grouping.

The leaf anatomy is characterized by the absence of a keel, palisade-like mesophyll abaxially located, rectangular long cells and stomatal apertures which are overlapped by four cuticular flanges projecting from the two adjacent interstomatal long cells. This latter feature is unique to this species group in the genus *Ehrharta.*

Although Engelbrecht (1956) studied only unifixed leaf blade material he noted that the form of the cells of the abaxial chlorenchyma layer differed from the remainder, an observation confirmed in this study. However, he also reports cell wall invaginations as being present and characteristic of *E. villosa.* These invaginations were not observed on all chlorenchyma cells, however, but appeared to be confined to those cells adjacent to the vascular bundles or adjoining the adaxial epidermis. This observation was not confirmed in the present study, in which field-fixed material was examined, and appears to be an artefact probably resulting from imperfect rehydration of the mesophyll tissue.

Engelbrecht (1956) recognized two basic groups of species in *Ehrharta* — one with invaginated chlorenchyma and one without. *E. villosa* is placed in the group with invaginations together with taxa of the Setacea and Ramosa species groups as here constituted (Gibbs Russell & Ellis 1987). The present findings are in disagreement with Engelbrecht's (1956) grouping, as the Setacea group is the only group in which arm cells were observed (Ellis 1987) and the Setacea and Villosa groups are not considered to be closely related.

Although he examined a large sample, Engelbrecht (1956) was unable to distinguish *E. villosa* and *E. thunbergii* either anatomically or morphologically and concluded that they do not represent two separate species. The present study is not in full agreement with this conclusion as *E. villosa* and *E. thunbergii* were found to differ in several respects such as the presence of microhairs and prickles as well as differences in silica bodies. Although these differences appear to be consistent and diagnostic, it must be remembered that the interface between

these two species is not distinct as far as most other characters are concerned and a continuum is evident between them without clear character disjunctions. *E. villosa* and *E. thunbergii,* therefore, intergrade to a certain extent and, although their extremes are anatomically quite distinct, a small proportion of specimens are somewhat intermediate. The decision to consider these two taxa as being conspecific (Chippindall 1955; Engelbrecht 1956), therefore, has some merit. However, the placing of *E. thunbergii* in synonomy under *E. villosa* results in a very variable, polymorphic entity with a wide ecological tolerance. The recognition of three taxa seems to be a more practical solution which probably reflects the natural situation more accurately. However, a cline undoubtedly exists from *E. villosa* var. *maxima* through var. *villosa* to *E. thunbergii* with each of these taxa occupying slightly different habitats and differing in morphology and leaf anatomy.

The relationships of the Villosa group to the rest of the genus are not very clear from anatomical evidence alone. The group does not occupy such an isolated position within the genus as does the Setacea group (Ellis 1987) which possesses such taxonomically significant diagnostic features as arm cells and distinct microhairs and silica bodies. There are also no anatomical intermediates between the Setacea group and any of the other species groups. Although the Villosa group is readily diagnosed by its flanged stomata, this feature cannot be accorded the high taxonomic value that arm cells and microhair and silica body shape have in the classification of the Poaceae, because it is encountered independently in different subfamilies.

In addition, several *E. thunbergii* specimens display strong Calycina group attributes in their leaf anatomy, and both these groups have very similar microhairs. The Villosa and Calycina groups also share very similar hairy spikelets, which differ mainly in size and profuseness of vesture, but occur in no other *Ehrharta* species group. The indications are, therefore, that the Villosa group is more closely related to the Calycina group than to any of the other groups. However, as is common in this genus, a reticulate pattern of relationships can be expected and Ramosa group characteristics were also observed on a few specimens.

The Villosa group, although distinct in morphology, anatomy and ecology, does show certain affinities with the Calycina group and undoubtedly belongs to the genus *Ehrharta.* This group, therefore, appears to be a specialized perennial line with strong underground rhizomes and suffrutescent culms which has become adapted to a sandy habitat.

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