

# Taxonomy of the genus *Ehrharta* (Poaceae) in southern Africa: the *Villosa* group

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**Keywords:** Fynbos, Capensis, *Ehrharta*, Poaceae, Succulent Karoo, taxonomy

## ABSTRACT

The *Villosa* species group in the genus *Ehrharta* Thunb. is differentiated morphologically by very large, profusely hairy, bearded and aristate spikelets and by a suffrutescent habit, with culms woody at the base and with reduced leaf blades. The *Villosa* group is composed of two species, one with a variety: *E. thunbergii* Gibbs Russell, nom. nov., *E. villosa* Schult. f. var. *villosa* and *E. villosa* var. *maxima* Stapf. Members of the group occur on sandy soils in the Succulent Karoo and Fynbos Biomes, along the west coast in Strandveld and on the southern coast as far east as the Fish River. Morphologically, the group appears to be related to the *Calycina* and *Capensis* groups.

## UITTREKSEL

Die *Villosa*-groep in die genus *Ehrharta* Thunb. word morfologies onderskei deur baie groot, dig behaarde, bebaarde en skerppuntige blompakkies asook halfstruikagtige habitus, met halms houtagtig aan die basis en met gereduseerde blaarlaminas. Die *Villosa*-groep sluit twee spesies in, een met 'n varieteit: *E. thunbergii* Gibbs Russell, nom. nov., *E. villosa* Schult. f. var. *villosa* en *E. villosa* Schult. f. var. *maxima* Stapf. Lede van die groep kom voor op sanderige gronde in die Sukkulente Karoo- en Fynbosbiome, langs die westkus in die Strandveld en aan die suidelike kus so ver oos as die Visrivier. Morfologies vertoon die groep verwantskap met die *Calycina*- en *Capensis*-groepe.

## INTRODUCTION

Previous papers in this series have outlined the seven species groups of *Ehrharta* Thunb. in southern Africa (Gibbs Russell & Ellis 1987), and dealt in detail with the morphology and anatomy of the taxa in the Setacea group (Gibbs Russell 1987; Ellis 1987a). In the *Villosa* group, as in all the groups except the Setacea group, the first and second sterile lemmas are of similar size and ornamentation (Figure 1). The *Villosa* group is distinguished morphologically by large spikelets 10–18 mm long that have sterile lemmas with conspicuously bearded bases, profusely hairy sides and mucronate to aristate tips; and by a suffrutescent habit with culms woody at the base and with reduced leaf blades. Besides these characters of habit and spikelet, the two species share features in leaf anatomy (Ellis 1987b). Within the group, the species differ mainly in spikelet size, relative glume length, rhizome structure, and in habitat and distribution, as well as in anatomical characters (Ellis 1987b). All the taxa are robust and have long, stout rhizomes. They occur only in sandy soil, and are the only species of *Ehrharta* to grow on seaside dunes.

Because of the spikelet similarities, Chippindall (1955) questioned the level of treatment of the three taxa, and only described *E. villosa* in detail, including within it some of the distinctive vegetative characters of *E. thunbergii*. However, previous treatments from Schultes (1830) to Stapf (1900) distinguished two taxa (*E. villosa* Schult. f. and *E. gigantea* Thunb.) on spikelet and rhizome characters similar to those used here.

It is unfortunate that a new name was required for the species previously known as *E. gigantea* Thunb. For 194 years, since 1794, the epithet 'gigantea' has been applied to the smaller, inland specimens of the *Villosa* group. However, this name is based on the same type, the specimen in the Thunberg herbarium, as Linnaeus the Younger's (1781) *Aira villosa*, and therefore, as a superfluous name, was illegitimate when published. The epithet 'villosa' cannot be taken up, however, because the new combination was not made in *Ehrharta* before Schultes (1830) published his own *Ehrharta villosa*, based on a different type. No other name has been applied to the species, so a new name is necessary. It is fortunate that 'villosa' was already occupied in *Ehrharta*, or the species previously known as *E. gigantea* would have had to become *E. villosa*, and *E. villosa* would have required a new name, an even more unsatisfactory situation.

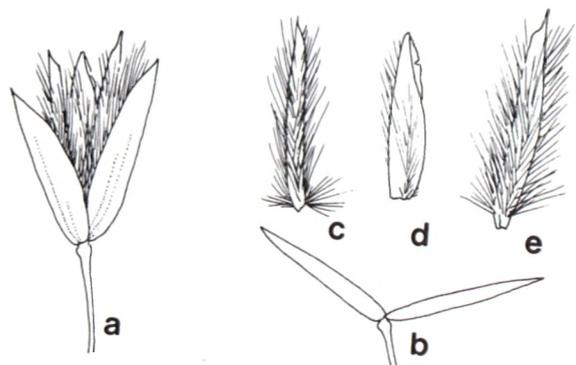


FIGURE 1. — Spikelet of *E. villosa* var. *villosa* (Crook 2260, PRE): a, whole spikelet; b, glumes; c, first sterile lemma; d, fertile lemma; e, second sterile lemma; all  $\times 2$ .

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## METHODS

The descriptive data for the species and infraspecific taxa has been recorded through the DELTA computer system, originated by Watson and Dallwitz (Dallwitz 1984, Watson & Dallwitz 1980, 1985) and used previously at species level by Webster (1983). The system has the advantage of recording comparable character states for each taxon in a form that can be used to generate descriptions, keys and an online identification facility, and that can be used directly for classificatory studies. Because of this change in methodology, the descriptions given from now on include more characters than were previously recorded, and are strictly comparable.

## KEY TO SPECIES IN THE VILLOSA GROUP

- Glumes  $\frac{1}{2}$ – $\frac{3}{4}$  as long as spikelet, 5-nerved, upper glume to 8 mm long; spikelets 8–10 mm long; rhizomes densely covered with hairy cataphylls, internodes often sub-bulbous..... 1. *E. thunbergii*
- Glumes  $\frac{3}{4}$  as long to about equalling spikelet, 5–9-nerved, upper glume 8–13 mm long; spikelets (10–) 11–18 mm long; rhizomes naked, neither sub-bulbous nor bulbous..... 2. *E. villosa*

1. *Ehrharta thunbergii* Gibbs Russell, nom. nov. Type: *Thunberg*, (sheet 8851, UPS, holo.-PRE, microfiche!).

*Aira villosa* L. f., Supplementum plantarum: 109 (1781). *Melica gigantea* Thunb.: 21 (1794). *Ehrharta gigantea* (Thunb.) Swartz: 58 (1802); Thunb.: 339 (1818); Schrader: 2079 (1821); Thunb.: 336 (1823); Schult.: 1375 (1830); Trinius: 16 (1839); Nees: 216 (1841); Steudel: 5 (1855); Stapf: 680 (1900); Chippindall: 45 (1955). Type: *Thunberg*, (sheet 8851, UPS, -PRE microfiche!).

*Ehrharta gigantea* (Thunb.) Swartz var. *neesii* Stapf: 680 (1900). Type: *Drège*, near Riebeecks Castle, among shrubs (K, holo.!).

*Ehrharta gigantea* (Thunb.) Swartz var. *stenophylla* Stapf: 881 (1900). Type: *Schlechter* 9058 (K, holo.!).

Perennial, tufted, erect, long-rhizomatous, robust, suffrutescent. *Rhizomes* often with internodes sub-bulbous, clad with imbricate, thickened, hairy cataphylls. *Culms* several, to 1.5 m tall, 3 mm across, woody, solid, sometimes geniculate at lower nodes, crowded, branched at base, sometimes branching in fascicles above, nodes usually black, rarely with ascending hairs, the lowest internode sometimes sub-bulbous, the 'bulb' pale orange, polished, shining. Young shoots intravaginal. *Leaves* mostly basal, persistent, culm leaves usually with blades reduced, often auriculate from mouth of sheath, the auricles rarely accrescent, to 10 mm long, with bristly edges; basal sheaths loose, papery, often splitting into fibres, grey or whitish; culm sheaths not overlapping; ligule a fringed membrane 0.5 mm long; blades persistent, linear, to 5 mm across, flat or rolled, gradually tapering at the tip, erect or spreading, herbaceous, usually glabrous, but sometimes hairy. *In-florescence* a fascicled panicle, narrow, often sinuous, to 160 mm long, somewhat overtopping leaves, exerted from uppermost leaf sheath, of numerous spreading spikelets. *Spikelets* pedicellate on filiform curled pedicels, laterally compressed, 8–10 mm long, 2–3 mm across above glumes. Glumes keeled, subequal,  $\frac{1}{2}$ – $\frac{3}{4}$  as long as the spikelet, translucent, sometimes purple-tinged; lower glume to 6 mm long, 5-nerved, acute; upper glume to 8 mm long, 5-nerved, acute. *Florets* with lemmas decidedly

firmer than the glumes, keeled. Sterile lemmas slightly rounded on sides, similar in shape and texture. First sterile lemma  $\frac{2}{3}$ – $\frac{3}{4}$  length of second sterile lemma, with keel and margins parallel; base substipitate, conspicuously bearded; sides with profuse long spreading white hairs, otherwise smooth and unornamented, dull; tip abruptly aristate from keel, aristae to  $\frac{1}{3}$  length of lemma, usually dark purple. Second sterile lemma similar to first sterile lemma, but larger and distinctly stipitate. *Fertile floret* shorter than second sterile lemma, lemma differing from sterile lemmas, strongly laterally compressed, sides apparently nerveless, sparsely hairy, tip truncate; palea  $\frac{2}{3}$  or more as long as lemma, keeled, 1-nerved. Lodicules 2, membranous, 2-lobed. Stamens 6, anthers 5 mm long, white. Stigmas white. *Caryopsis* not seen.

This species is distinguished from other *Ehrharta* species by the large hairy spikelets with short, translucent glumes and the sub-bulbous rhizomes with hairy cataphylls. It is the most widespread and abundant of the members of the *Villosa* group, and its distribution is shown in Figure 2. Unlike most *Ehrhartas*, which tend to have an 'eastern' or 'western' distribution, its range extends both northwards through Fynbos, Strandveld, and Succulent Karoo to the southern border of South West Africa/Namibia and eastward along the coastal ranges as far as Mossel Bay. However, it appears to be less common in the eastern part of the range.

Stapf's two varieties are not recognized because they intergrade with the more common and widespread form, and because they are not distinguished by a separate range or habitat. However, each of these forms shows an interesting link to the *Capensis* group. 'Bulbous' basal internodes (var. *stenophylla*) are characteristic of most species in the *Capensis* group, and the specimens with many-noded geniculate culms with small flat leaf blades (var. *neesii*) are similar in habit to the only non-bulbous member of the *Capensis* group, *E. barbinodis*. There is in addition a form with broad and often hairy leaves (for example, *Gibbs Russell* 5619) that occurs from Calvinia to Lambert's Bay and Piketberg. A few specimens intermediate to *E. villosa* var. *villosa* are discussed under that variety.

*E. thunbergii* grows in sandy or sandy gravel soils, mostly on hill slopes, but also in coastal sand and

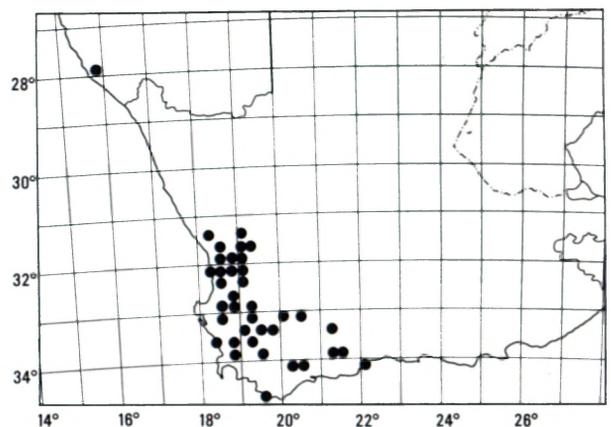


FIGURE 2. — Distribution of *E. thunbergii*.

occasionally beside watercourses. Flowering occurs from September to December.

Vouchers: *Acocks* 23393; *Andreae* 1314; *Boucher* 4724; *Liebenberg* 6551; *Schlechter* 10208.

2. *Ehrharta villosa* Schult. f. in *Systema vegetabilium* 7,2: 1374 (1830). *Trinius*: 16 (1839); *Nees*: 213 (1841); *Steudel*: 5 (1855); *Stapf*: 681 (1900); *Chippindall*: 45 (1955); *Smook & Gibbs Russell*: 55 (1985). Type: *Ecklon*, Promont. b. spei, in *arenosis maritimis* (P, holo.).

Perennial, tufted, erect, long-rhizomatous, robust, suffrutescent. *Rhizomes* woody, naked. *Culms* several, to 1,5 m tall, woody, solid, branched at base, branching in fascicles above, nodes glabrous, lowest internode never bulbous. Young shoots intravaginal. *Leaves* not basally aggregated, culm leaves with blades reduced, often auriculate from mouth of sheath, the auricles not accrescent; basal sheaths loose, papery, grey or whitish; culm sheaths not overlapping; ligule a fringed membrane 0,5 mm long; blades deciduous or persistent on basal sheaths and culm sheaths, linear, to 8 mm across, but rolled and appearing setaceous, gradually tapering at the tip, herbaceous, glabrous. *Inflorescence* a fascicled panicle, narrow, sometimes sinuous, 40–260 mm long, somewhat overtopping leaves, exserted from or sometimes closely subtended by uppermost leaf sheath, of numerous spreading spikelets. *Spikelets* pedicellate on filiform curled pedicels, laterally compressed, (10–) 11–18 mm long, 3–4 mm across above glumes. Glumes keeled, more or less equal,  $\frac{3}{4}$  as long to slightly longer than rest of spikelet, opaque white, sometimes purple-tinged; lower glume 8–13 mm long, 5–9-nerved, acute; upper glume 9–18 mm long, 5–9-nerved, acute. *Florets* with lemmas decidedly firmer than the glumes, keeled. Sterile lemmas slightly rounded on sides, similar in shape and texture. Sterile lemmas similar to *E. thunbergii*, but first sterile lemma with tip abruptly mucronate or aristate from keel, purple or pale. Second sterile lemma similar to first sterile lemma, but larger and distinctly stipitate. *Fertile floret* similar to *E. thunbergii* but anthers 6–8,5 mm long, brownish yellow. *Caryopsis* 5,5 mm long, ovate, flattened.

This species grows on sea dunes from Lambert's Bay to Port Alfred, and is our only indigenous grass that behaves as a 'marram'. It is distinguished from *E. thunbergii* by its naked rhizomes and longer spikelets with comparatively longer glumes.

KEY TO VARIETIES

- Inflorescence exserted from uppermost leaf sheath, the sheath usually not inflated; upper glume 9–13 mm long; culms to 3 mm across ..... 2a. *E. villosa* var. *villosa*
- Inflorescence closely subtended or enveloped by inflated uppermost leaf sheath; upper glume (10–) 13–18 mm long; culms to 5 mm across ..... 2b. *E. villosa* var. *maxima*

2a. var. **villosa**. *Stapf*: 681 (1900); *Chippindall*: 45 (1955); *Smook & Gibbs Russell*: 55 (1985).

Culms robust, to 3 mm across. *Inflorescence* interrupted, to 150 mm long, usually exserted from uppermost leaf sheath, the sheaths usually not inflated. *Spikelets* 11–14 mm long, to 3 mm across laterally above glumes. Glumes  $\frac{3}{4}$  as long to slightly shorter

than rest of spikelet; lower glume 8–12 mm long; upper glume 9–13 mm long. *Florets* with sterile lemmas mucronate or aristate. Anthers 7,5–8 mm long.

Variety *villosa* is distinguished from var. *maxima* by its exserted inflorescences, smaller stature and somewhat smaller spikelets. The two varieties are sympatric throughout most of their distribution (Figures 3 & 4), although this one extends farther north on the west coast and is more common in the southwestern Cape.

A few intermediate specimens occur, always near the sea but not on seaside dunes, that have small glumes and spikelets like *E. thunbergii*, but naked rhizomes like *E. villosa*: *Ellis* 4640 from Lambert's Bay; *Gibbs Russell* 5670 from the Cape Peninsula; and *Liebenberg* 4015 from Mossel Bay. Most of the specimens from Mossel Bay, to the east of the range of both this variety and of *E. thunbergii*, appear to be of this intermediate type, although these intermediates are few and sporadic elsewhere. Inland, rare intermediate specimens show a different pattern of variation. *Ellis* 4693, from the roadside at Cloete's Pass, has the hairy rhizome cataphylls of *E. thunbergii* and the larger spikelets with long glumes of *E. villosa*. *Emdon* 200, from disturbed Fynbos, has large glumes that are translucent.

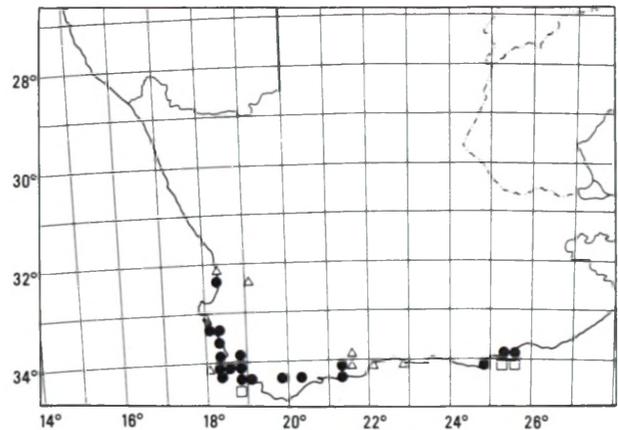


FIGURE 3. — Distribution of *E. villosa* var. *villosa*. Intermediates to *E. thunbergii* are shown by triangles,  $\Delta$ . Intermediates to *E. villosa* var. *maxima* are shown by squares,  $\square$ . Where symbols would be superimposed, those for intermediates are shown apparently in the sea directly below or to the left of the correct quarter degree.

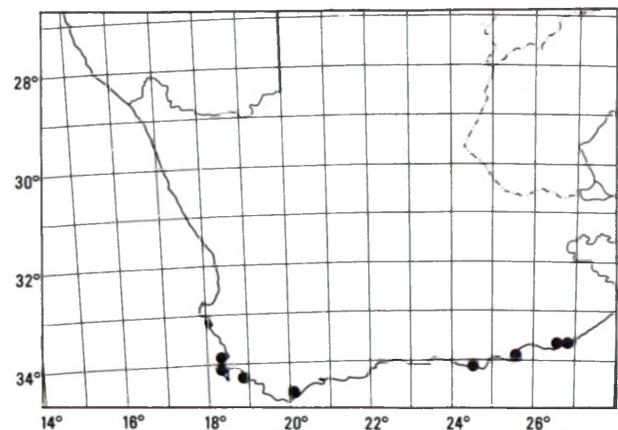


FIGURE 4. — Distribution of *E. villosa* var. *maxima*.

The intermediates, all mapped in Figure 3 with *E. villosa* var. *villosa*, occur either at the extremities of the distribution of this variety, or in disturbed habitats, and all occur within the range of *E. thunbergii*. Furthermore, no intermediates are known from the part of the range of *E. thunbergii* that lies outside that of *E. villosa*. Therefore, the hypothesis that most likely accounts for the intermediates is that they are the result of hybridization between the two taxa.

Variety *villosa* grows most commonly on seaside dunes, but has been collected as far as 1 km inland on the limestone ridges at De Hoop, although still in sandy soil. It flowers from October to December.

Vouchers: *Bohnen 4541; Cleghorn 3122; Crook 2260; Marloth 3046; Smith 4649.*

2b. var. **maxima** Stapf in *Flora capensis* 7: 681 (1900). Chippindall: 45 (1955); Smook & Gibbs Russell: 55 (1985).

Culms very robust, to 5 mm across. *Inflorescence* dense, to 260 mm long, closely subtended or enveloped by uppermost inflated leaf sheath. *Spikelets* (10-) 12-18 mm long, to 4 mm across laterally above glumes. Glumes slightly shorter to slightly longer than rest of spikelet; lower glume 9-13 mm long; upper glume (10-) 13-18 mm long. *Florets* with first sterile lemma tip mucronate. Anthers 6-8,5 mm long.

The distribution of this variety is shown in Figure 4. It extends as far east as Port Alfred, where it is the only *Ehrharta* on the dunes, but extends no farther than the Cape Peninsula. It is less common than var. *villosa* in the western part of its range, where it is known from a few specific sites, such as Robben Island. It is recognized at varietal rather than sub-specific rank because of the close similarity between the two taxa in morphology, anatomy, distribution and habitat.

Variety *maxima* occurs only on seaside dunes, and flowers from September sporadically to March.

Vouchers: *Boucher 1689; Britten 778; Theron 1108; Tyson Herb. Marl. No. 8598; UPE Staff 158.*

#### CONCLUSION

This closely related group of species shows a cline in size, from the smaller, aristate forms of *E. thunbergii* on Namaqualand hillsides, to the robust, short-mucronate, dune-binding *E. villosa* var. *maxima* at Port Alfred. *E. villosa* var. *villosa*, which is concentrated geographically in the middle part of the distribution of the group, also has morphological and anatomical (Ellis 1987b) intermediates to both the other taxa. The rhizome differences between the species may be related to habitat differences. In the shifting dune sands there are no cataphylls and no bulb-like structures.

Relationships of the Villosa group to other species groups appear somewhat different when examined morphologically and anatomically. Morphologically, the Villosa group is linked to the Calycina group by the hairy spikelets with long glumes, and to the Capensis group by the large spikelets with short-awned or mucronate and stipitate sterile lemmas, and by

the 'bulbous' internodes. Ellis (1987b) reports anatomical links to the Calycina group, which is similar anatomically to the Capensis group. However, the suggested anatomical link to the Ramosa group is shown morphologically in only one species in the Ramosa group, which has long glumes and suffrutescens culms.

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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-opeeninge 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 nou verwant 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) synonymize *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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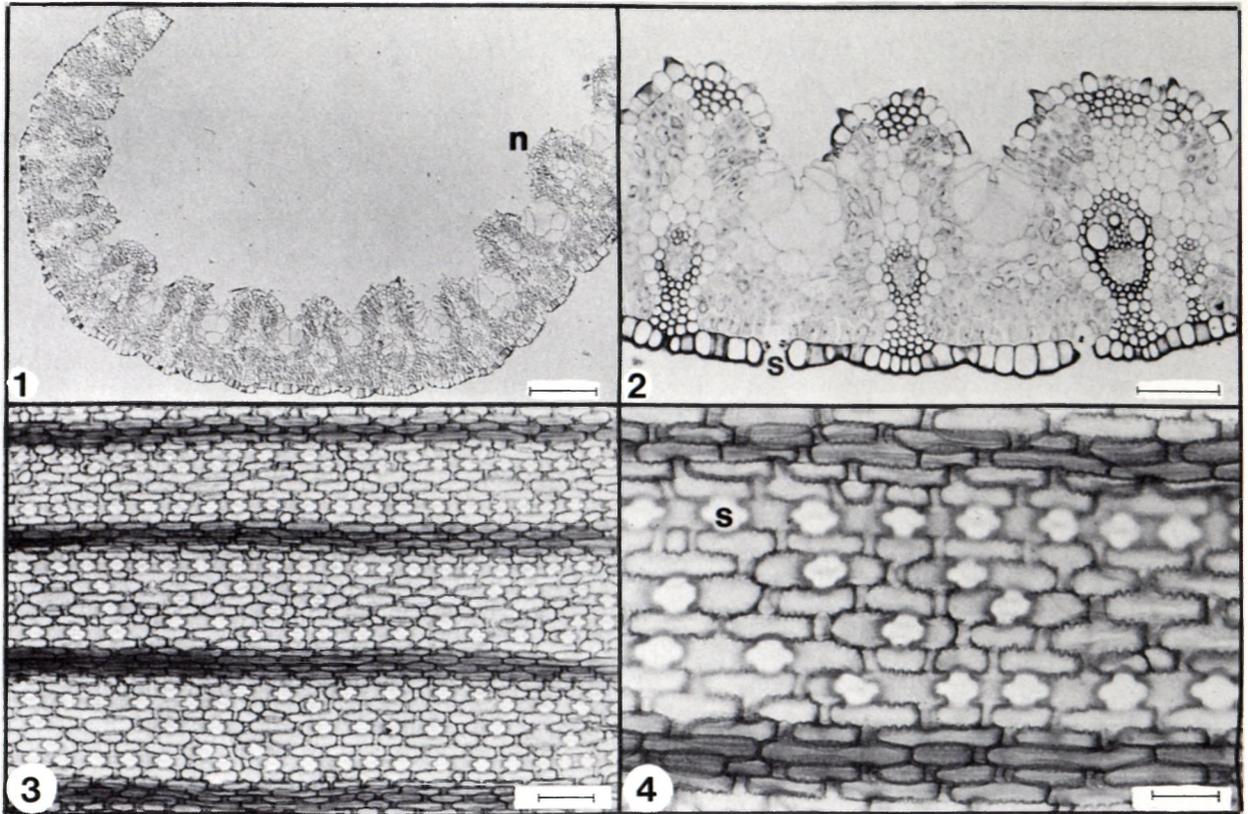


FIGURE 1. — Leaf anatomy of *Ehrharta villosa* var. *maxima*, Ellis 601: 1–2, leaf in transverse section: 1, vascular bundle arrangement and absence of keel (n), scale bar = 20 µm; 2, anatomical detail with sunken abaxial stomata (s) and mesophyll with adaxially located chlorenchyma cells radiately arranged 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 semi-radiate 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*).

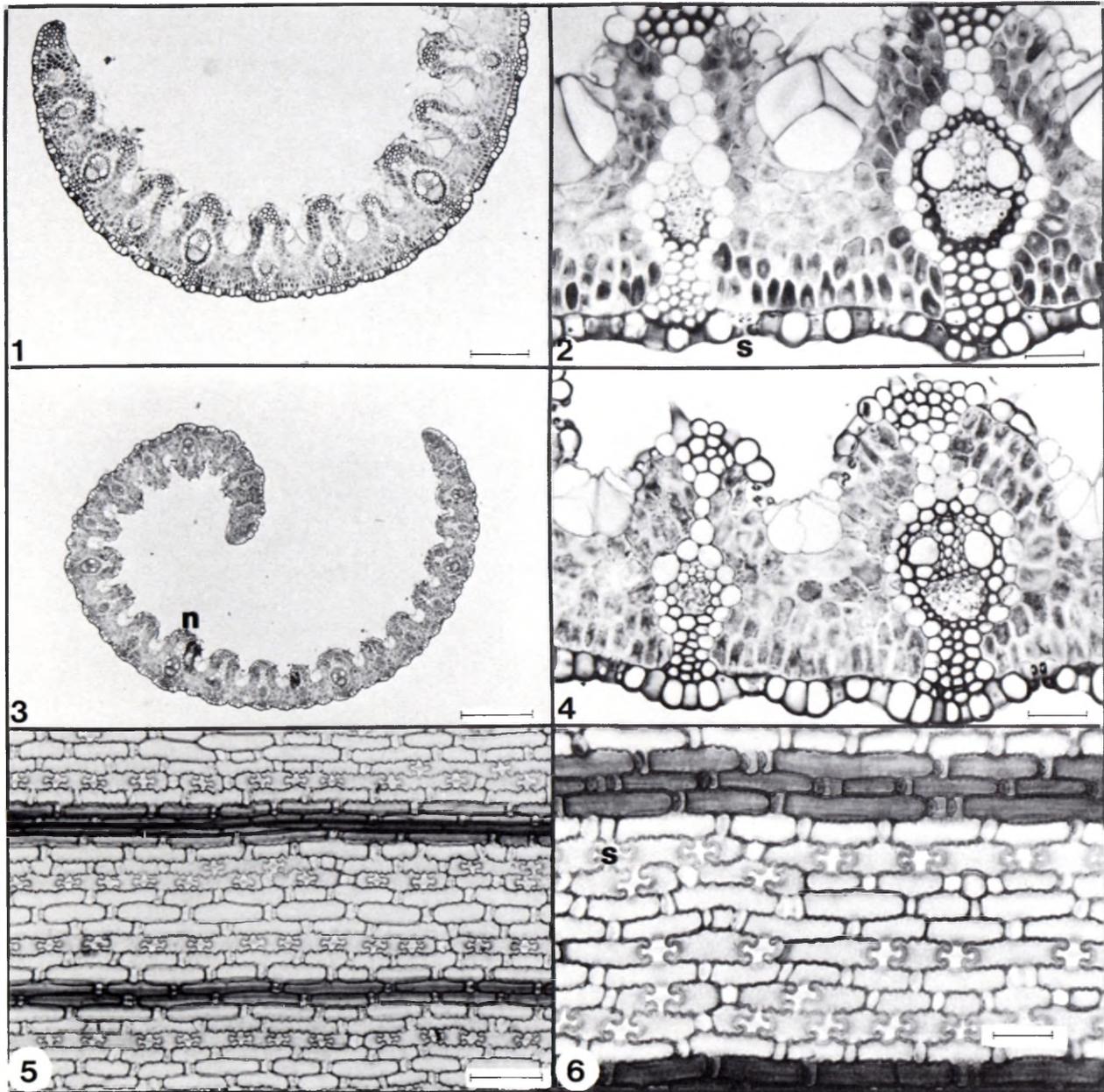


FIGURE 2. — Leaf anatomy of *Ehrharta villosa* var. *villosa* specimens resembling var. *maxima* in structure. 1–2, *Ellis 1686*, leaf blade transection: 1, loosely inrolled blade without a keel, scale bar = 20  $\mu$ m; 2, detail of the chlorenchyma showing dense abaxial palisade-like cells; note sunken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

#### *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-

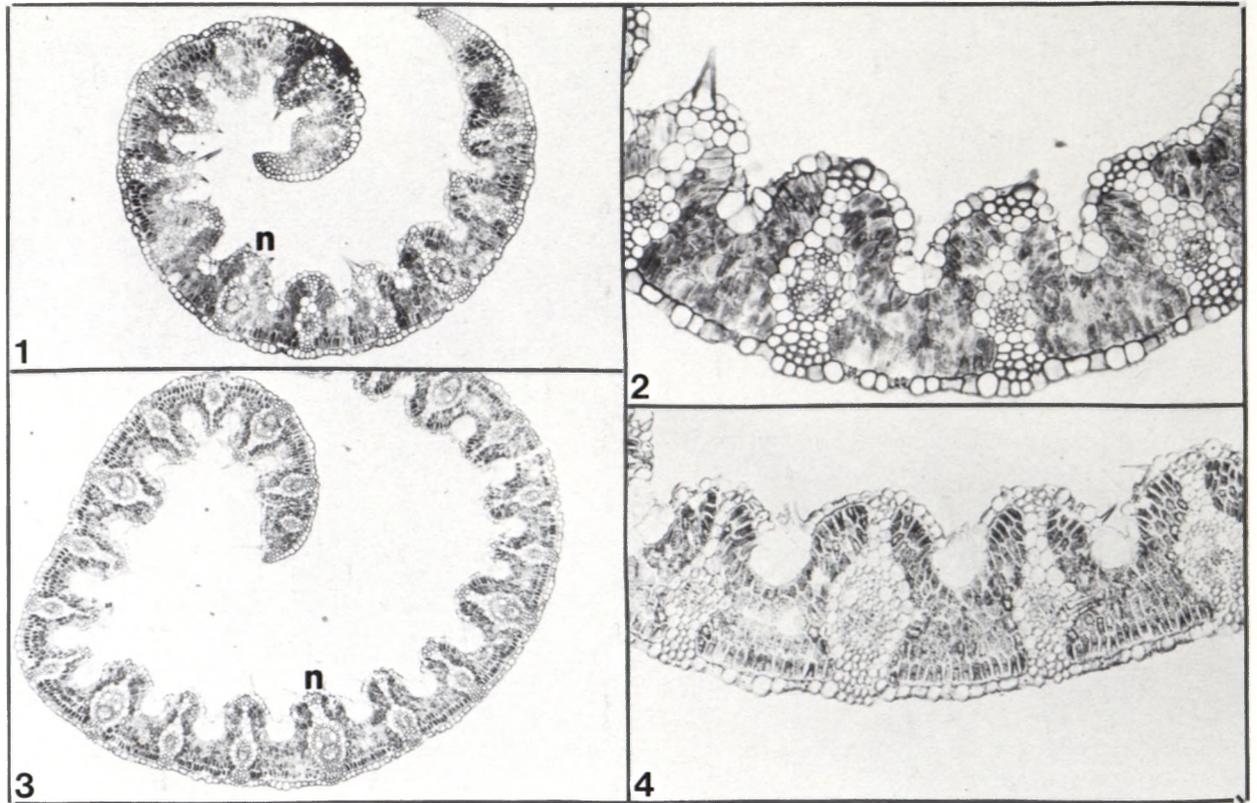


FIGURE 3. — Trans sectional leaf anatomy of *Ehrharta villosa* var. *villosa*. 1–2, *Ellis 4665*: 1, inrolled outline with median bundle (n) only, scale bar = 20 µm; 2, anatomical detail showing rather angular chlorenchyma cells with radiate adaxial layers and palisade-like abaxial layers, scale bar = 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).

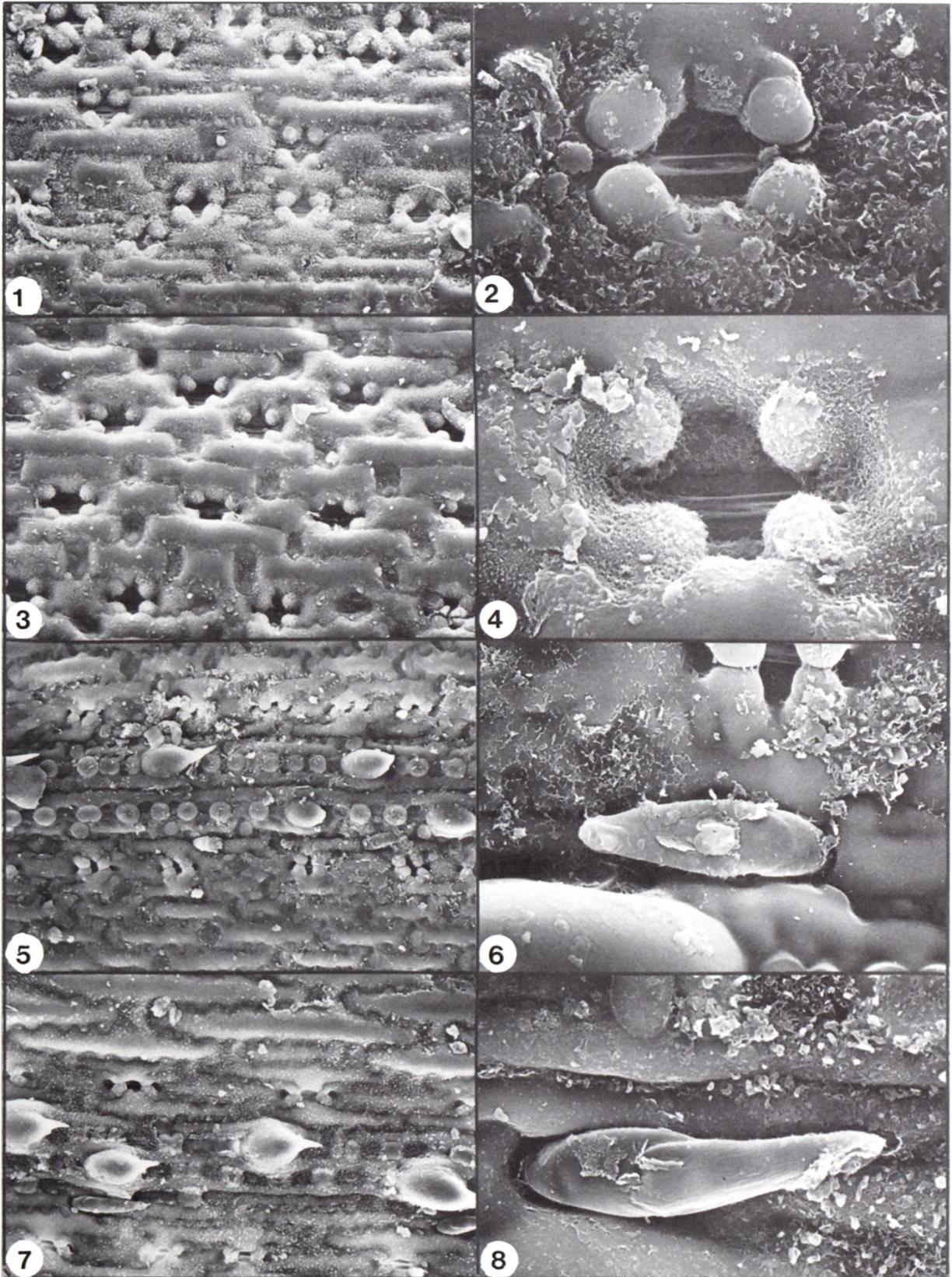


FIGURE 4. — Abaxial epidermal ultrastructure of representatives of the Villosa group. 1–4 *Ehrharta villosa* var. *villosa*. 1–2, *Ellis 4640*: 1, thickened epidermal cells, no microhairs and flanged stomata,  $\times 200$ ; 2, detail of the four papilla-like flanges over arching the stomatal apparatus with the guard cells visible below this aperture,  $\times 1000$ . 3–4, *Ellis 4665*: 3, thick cuticle, sunken stomata and microhairs absent,  $\times 200$ ; 4, guard cells beneath the overarching papillate flanges,  $\times 1000$ . 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,  $\times 200$ ; 6, detail of microhair with tapering distal cell and flanges obscuring adjacent stoma,  $\times 1000$ . 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,  $\times 200$ ; 8, microhair with tapering distal cell,  $\times 1000$ .

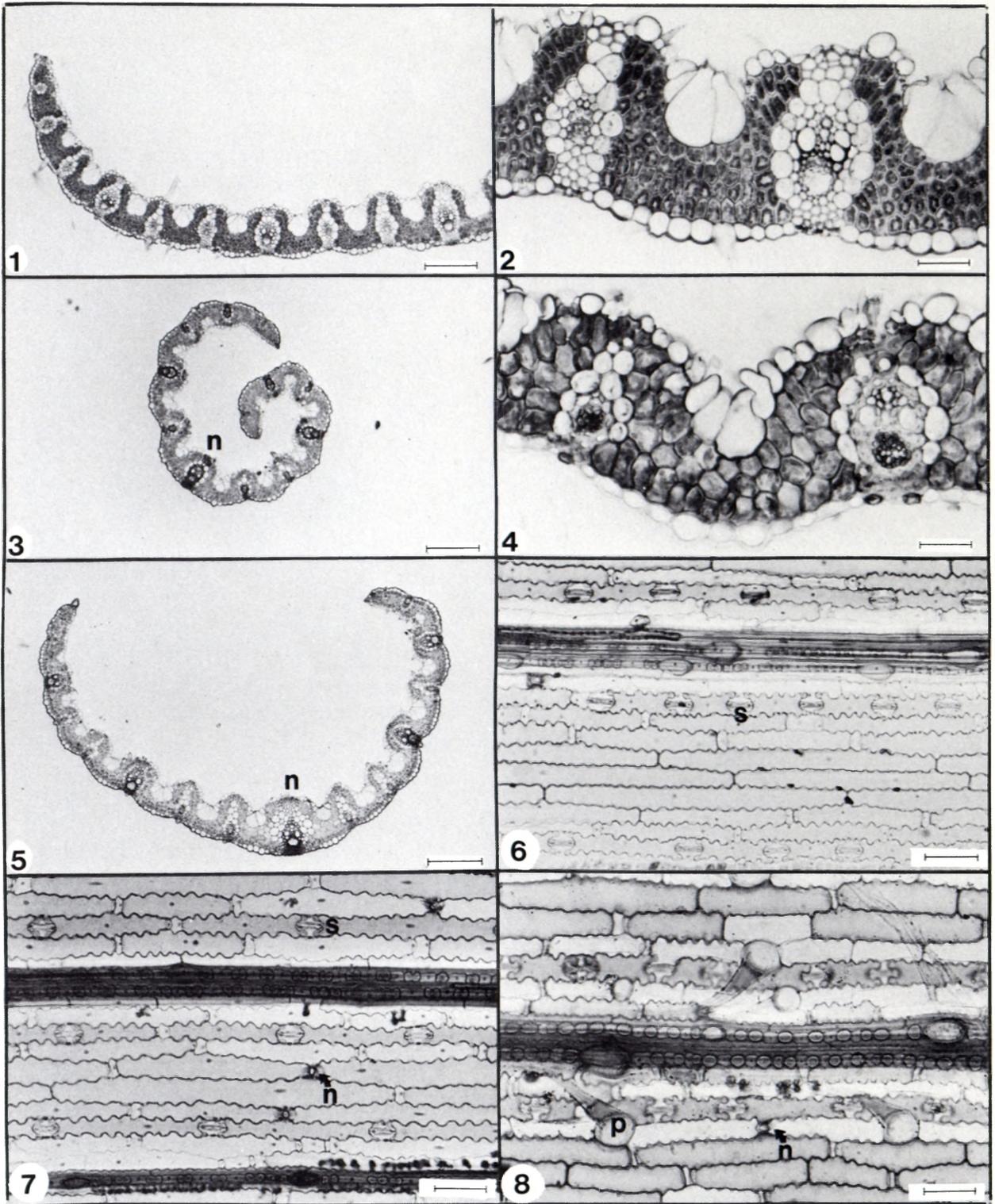


FIGURE 5. — Leaf anatomy of *Ehrharta thunbergii*. 1–5, leaf transections; 6–8, abaxial epidermides. 1–2, *Ellis 1152*: 1, median bundle not structurally distinct, scale bar = 20  $\mu$ m; 2, chlorenchyma cell detail and arrangement typical of that of the *Villosa* group, scale bar = 5  $\mu$ m. 3–4,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

### 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 (Vanhynsdorp): Vanhynsdorp Dist., Gifberg (–DD), *Ellis* 5102. 3119 (Calvinia): Nieuwoudtville Dist., Van Rhy'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; Kouebokkeweld, 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.

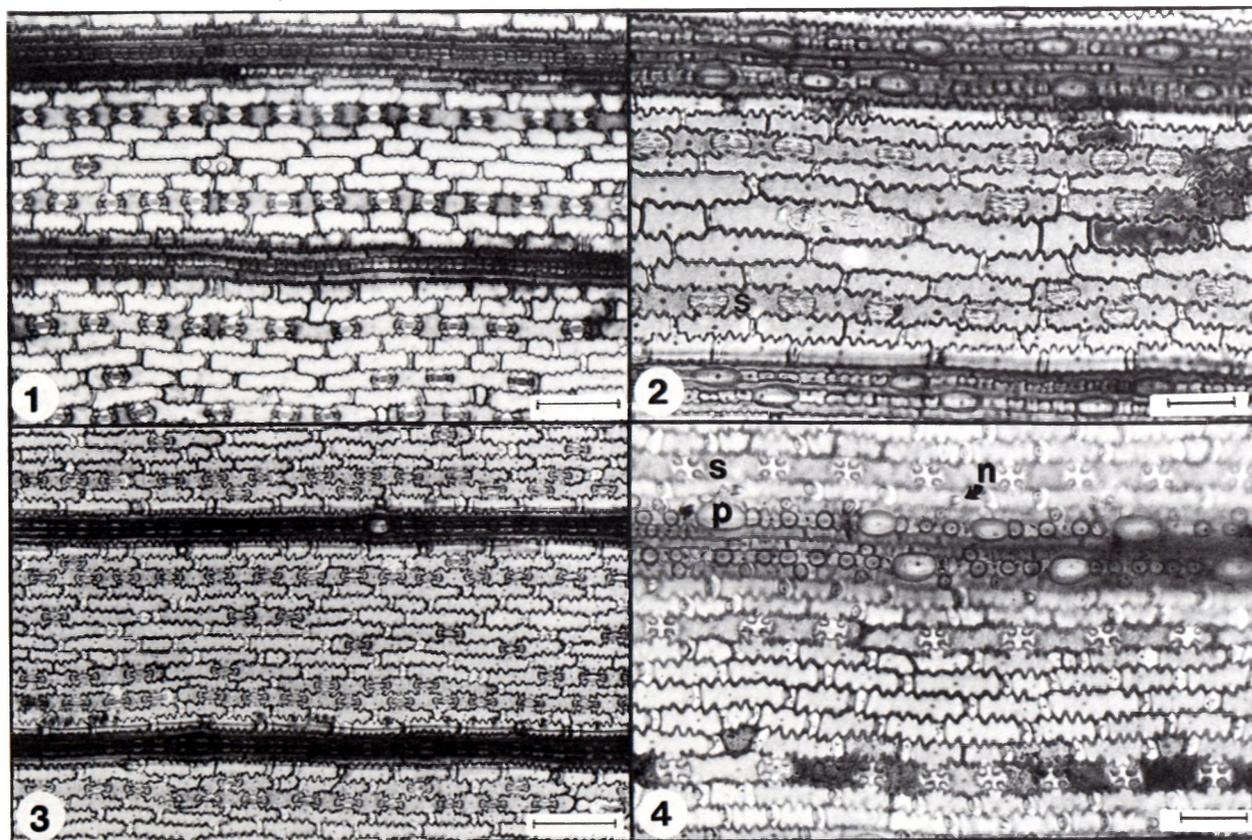


FIGURE 6. — A comparison of the abaxial leaf epidermis of *Ehrharta villosa* (1 & 3) and *Ehrharta thunbergii* (2 & 4). 1, *E. villosa*, *Ellis* 4640, showing short intercostal long cells with slightly sinuous walls; microhairs and prickles absent, scale bar = 10  $\mu$ m. 2, *E. thunbergii*, *Ellis* 4635, with very sinuous long cell walls, intercostal microhairs and costal prickles, scale bar = 5  $\mu$ m. 3, *E. villosa*, *Ellis* 1651, short, slightly sinuous long cells, flanged stomata, scale bar = 10  $\mu$ m. 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  $\mu$ m.

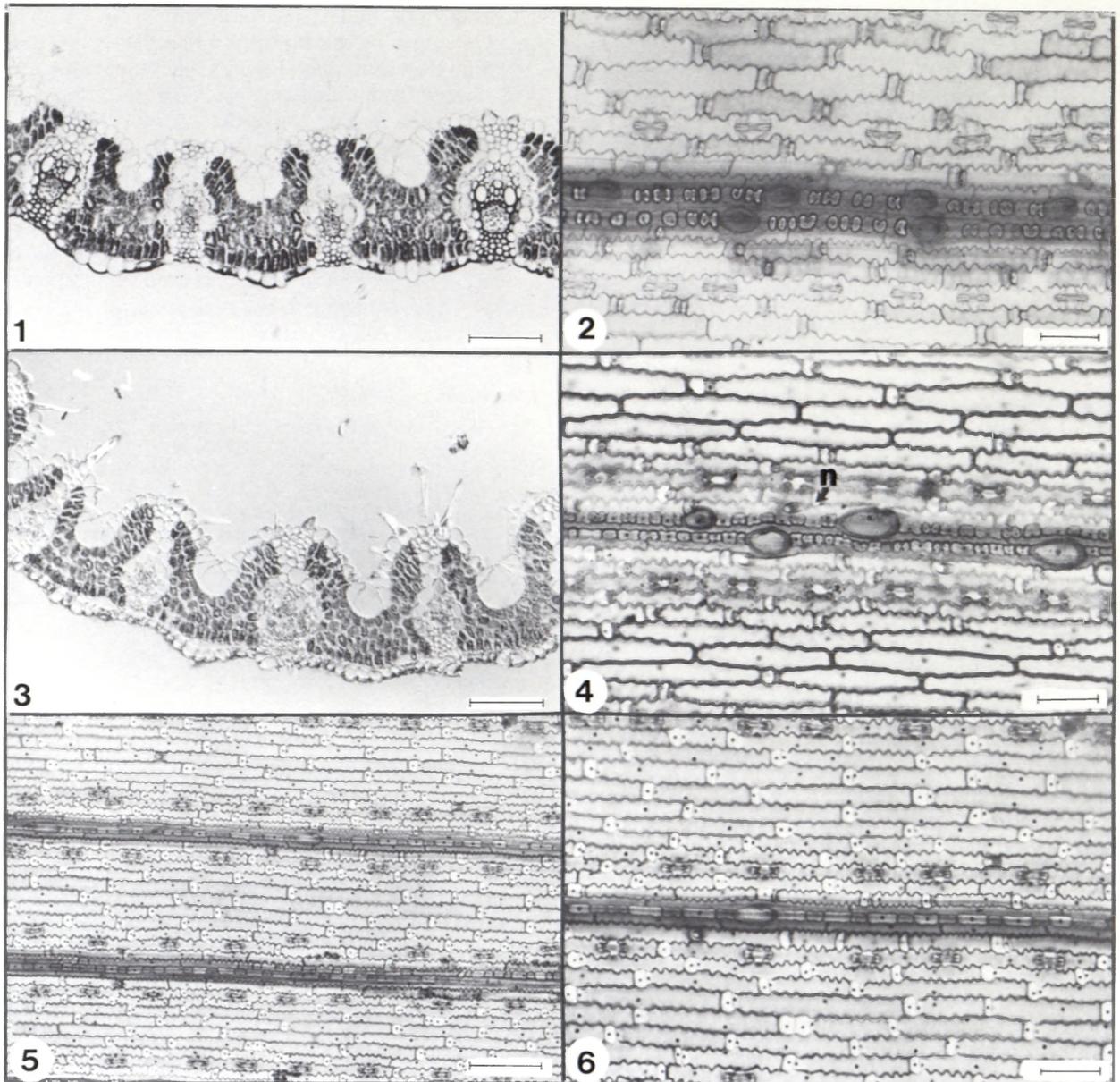


FIGURE 7. — Anatomical variation in *Ehrharta thunbergii*. 1–2, *Ellis 1700* resembling *E. villosa*: 1, transverse section with radiate and palisade-like mesophyll cells, scale bar = 10  $\mu\text{m}$ ; 2, abaxial epidermis with rectangular, sinuous-walled long cells but stomatal flanges not conspicuous,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

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 unfixed 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 synonymy 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 vestiture, 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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# Phytogeography of the subtribe Leipoldtiinae (Mesembryanthemaceae)

H. E. K. HARTMANN\*

**Keywords:** ecology, Leipoldtiinae, Mesembryanthemaceae, phytogeography, winter rainfall

## ABSTRACT

An investigation of distribution and species frequency of the nine genera of the subtribe Leipoldtiinae shows that two centres of diversity can be distinguished. These coincide more or less with the 'Gariiep centre' in the north and the 'Vanrhynsdorp centre' in the south (both sensu Nordenstam 1969). Speciation seems to have occurred in both centres. The subtribe may have evolved in an arid winter rainfall area which could have been situated outside its present distribution area. The centres of distribution coincide with those observed in both subfamilies of the Mesembryanthemaceae.

## UITTREKSEL

'n Ondersoek na verspreiding en spesie-frekwensie van die nege genusse van die subtribus Leipoldtiinae toon dat twee sentrums van diversiteit onderskei kan word. Hierdie twee kom min of meer ooreen met die 'Gariiepsentrum' in die noorde en die 'Vanrhynsdorpsentrum' in die suide (albei sensu Nordenstam 1969). Dit wil voorkom asof spesiasie in albei sentrums plaasgevind het. Die subtribus kon moontlik in 'n dorre winterreëngedebied wat buite die huidige verspreidingsgebied geleë kon gewees het, ontwikkel het. Die verspreidingsentrums kom ooreen met dié wat in albei subfamilies van die Mesembryanthemaceae waargeneem is.

## INTRODUCTION

The subtribe Leipoldtiinae of the Mesembryanthemaceae comprises nine genera with a total of 81 species. Members of the subtribe can be recognized by their rather hard xeromorphic leaves (the outer epidermal wall always contains calcium oxalate crystals) and their multilocular capsules (Figure 1) with valve wings, closing bodies and complete covering membranes. These membranes are distally recurved and radially traversed by a trace of spongy tissue which distally forms an additional closing device (closing bulge, ledge or rod, Hartmann 1983c). Dis-semination depends directly on the described internal structure (Funktionstyp 1 after Hartmann 1983c) and is effected in most taxa only by rain drops.

This is the first analysis of its kind within the Mesembryanthemaceae because this is the first group of genera for which adequate data are available. The phytogeography of the subtribe is of particular interest for two reasons: the distribution area of the Leipoldtiinae coincides with the centre of distribution of the entire family; and within this area, members of the subtribe form a major part of the vegetation.

## METHODS AND MATERIAL

The investigation is based on numerous field studies carried out between 1977 and 1986, about 6 000 relevant collections and about 800 additional herbarium sheets. Ecological data are derived partly from literature and partly from own observations; rainfall data were provided by the Weather Bureau, Pretoria. Information concerning morphology, anatomy, evolution and detailed distribution are taken

from the relevant genus monographs (see References).

## RESULTS

### *Distribution of the subtribe*

The subtribe is confined to the south-western Cape. Only one genus (*Cephalophyllum*) occurs in the entire range of the subtribe (see Figure 2), the other genera are restricted to smaller areas. The frequency distribution of genera is consequently uneven (Figure 3). Two main centres can be distinguished, a southern one, which will be referred to as 'Vanrhynsdorp centre' (sensu Nordenstam 1969), and a northern one, which agrees largely with the 'Gariiep centre' (sensu Nordenstam 1969). These centres stand out even more prominently when species distribution (Figure 4) is considered, and their significance will be discussed below.

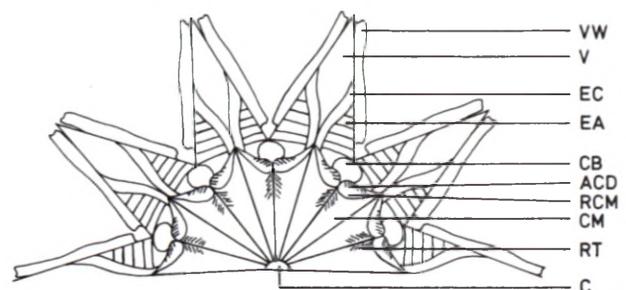


FIGURE 1. — Open fruit of Leipoldtiinae, schematic. ACD = additional closing device; C = columella; CB = closing body; CM = covering membrane; EA = expanding area; EC = expanding keel; RCM = recurved distal portion of covering membrane; RT = radial trace of spongy tissue; V = valve; VW = valve wing.

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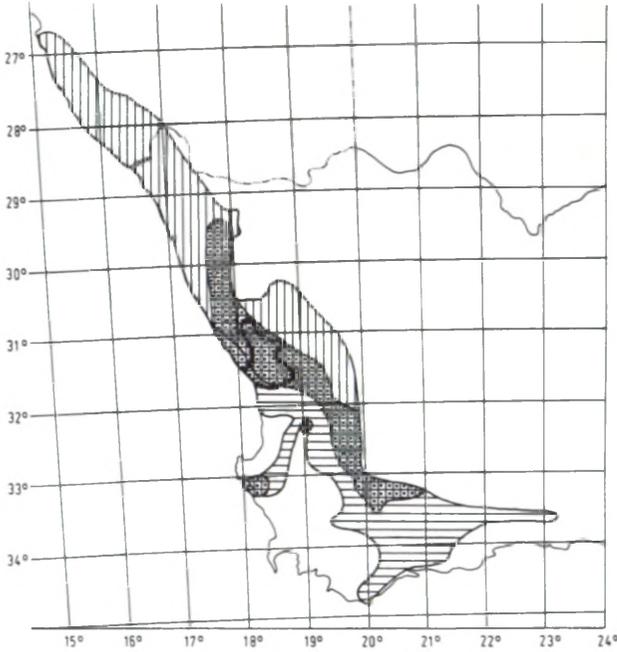


FIGURE 2. — Distribution areas of *Cephalophyllum* (thin lines) and *Argyroderma* (bold line). Horizontal lines = *Cephalophyllum* subgenus *Cephalophyllum*; vertical lines = *Cephalophyllum* subgenus *Homophyllum*; overlapping areas dotted.

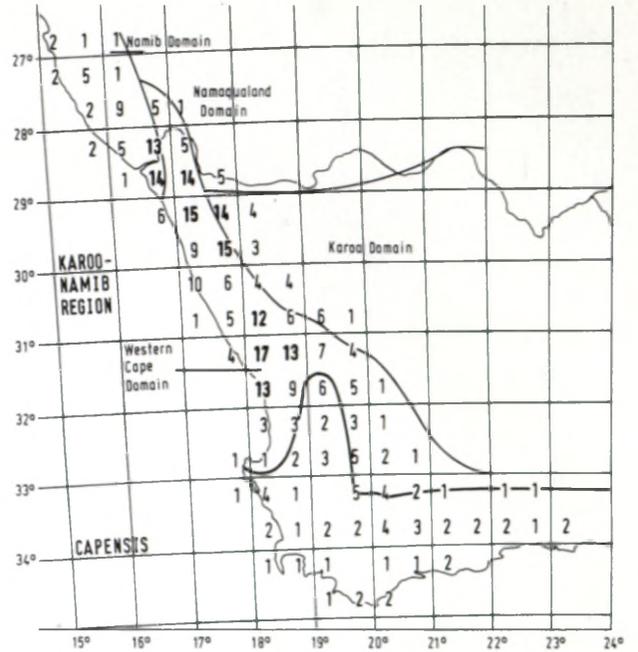


FIGURE 4. — Frequency of species of Leipoldtiinae (N = 81) per 30' x 30' square. The same two centres as in Figure 3 stand out (bold figures).

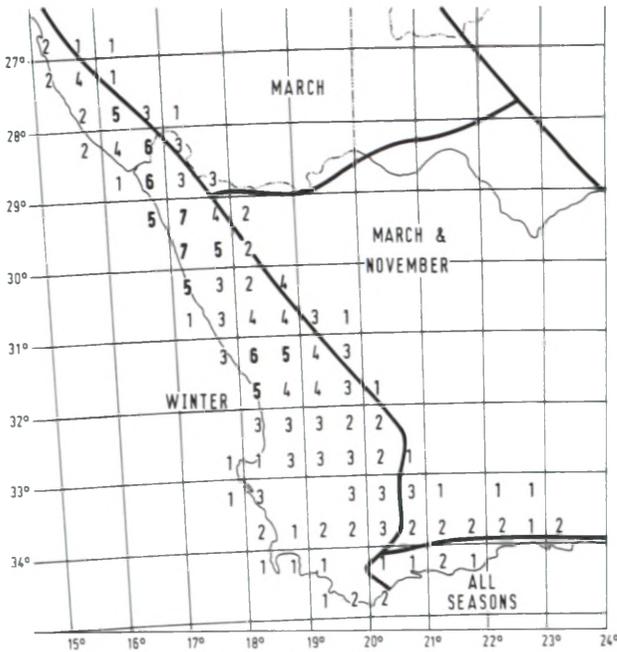


FIGURE 3. — Frequency of genera of Leipoldtiinae (N = 9) per 30' x 30' square. Two centres can be distinguished: 'Gariep centre' (bold figures between latitudes 27° and 31°); 'Vanrhynsdorp centre' (bold figures between latitudes 31° and 32°). Bold lines delineate the four main rainfall areas of the region.

The eastern limit of the distribution area of the Leipoldtiinae coincides for most of its extension with the eastern boundary of the winter rainfall area (defined here as the region receiving at least 60% of its annual precipitation between April and September, Figure 3). Only in the south, three genera (*Cephalophyllum*, *Jordaniella* and *Leipoldtia*) extend considerably into the March/November or all season rain-

fall areas. Only two species out of the 81 have their centre of distribution outside the winter rainfall region: *Cephalophyllum subulatoides* (Haw.) N.E. Br. (southern Little Karoo, 33°30'S, 21°–23°E) and *Cheiridopsis caroli-schmidtii* (Dinter & Berger) N.E. Br. (near Aus, 27°S, 16°E). The amount of annual precipitation decreases in the distribution area from south to north, and less markedly from west to east (Figure 5).

Phytochorologically, the main concentration of taxa falls into the Western Cape Domain of the Karoo-Namib Region as defined by Werger (1978), with extensions into the Namib Domain in the north, into the Karoo Domain in the north-east and even into Capensis in the south (Figure 4). Only a few species have their centre of distribution in Capensis *sensu* Werger (1978), namely *Cephalophyllum diversiphyllum* (Haw.) H. E. K. Hartm., *C. loreum* (L.) Schwantes, and *C. subulatoides* (Haw.) N.E. Br.

*Distribution of genera*  
*Cephalophyllum*

The largest genus of the subtribe, *Cephalophyllum* N.E. Br., with 30 species, has the largest distribution area (Figure 2) and grows in a wide range of ecological situations, from coastal to high mountain habitats, from monotypic open succulent associations to undergrowth in fynbos, and from the highest to the lowest rainfall regimes in different seasons. The two subgenera have different centres of distribution (Figure 2): subgenus *Cephalophyllum* dominates in the south and subgenus *Homophyllum* in the north, with a wide corridor in which they overlap.

A species frequency analysis (based on numbers of species per 30' x 30' square) reveals that the highest number of species occurs in the Vanrhynsdorp centre (Figure 6), which lies in the zone of overlap of the subgenera (Figure 2). A second centre of species

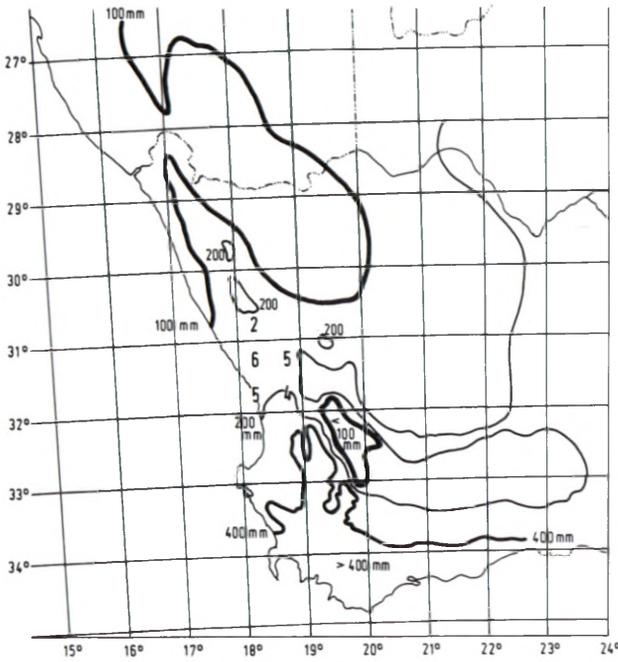


FIGURE 5. — Frequency of species of *Argyroderma* (N = 10) per 30' x 30' square and selected isohyets (bold line = 100 mm; medium line = 400 mm; thin line = 200 mm).

frequency lies in the north and coincides with the Gariiep centre of the subtribe (Figure 3). These centres cannot be correlated directly with the subgenera, as the centre of subgenus *Cephalophyllum* is situated near 33°S, 20°E (Figure 6 and Hartmann in press). In spite of the high species numbers per square, sympatry in *Cephalophyllum* is rare and speciation has been predominantly allopatric (Hartmann in press). Twelve species (40%) can be considered endemic: they occur in one to three 30' squares only (Figure 6). They are found near the two species centres but their frequency is low (1–3 per 30' square).

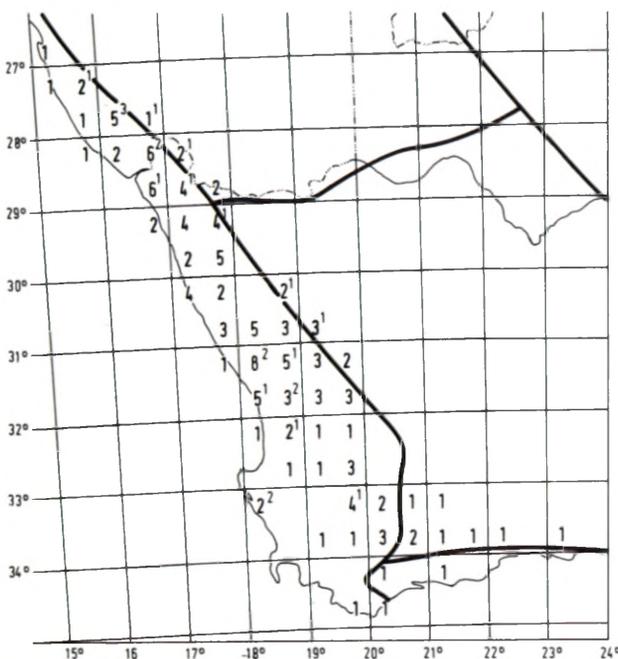


FIGURE 6. — Frequency of species of *Cephalophyllum* (N = 30) per 30' x 30' square. Small figures indicate frequency of endemic species.

Consequently, *Cephalophyllum* can be described as a genus with mostly widespread yet vicariant species, which have become adapted to a wide range of edaphic and climatic conditions: the genus occurs in 13 different vegetation types as defined by Acocks (1975) (Hartmann in press). The extended distribution area reflects the high degree of adaptability of the genus even today, supporting the hypothesis that the genus is at present in an active evolutionary phase (Hartmann in press).

*Argyroderma*

Closely related to *Cephalophyllum* is the genus *Argyroderma* N.E. Br. (Hartmann 1983c, in press) with ten species (Hartmann 1978a), restricted in distribution to the Knersvlakte in the Vanrhynsdorp centre (Figure 2), with a maximum of six species per 30' square (Figure 5). In contrast to *Cephalophyllum*, *Argyroderma* therefore presents a genus of narrow distribution which is due to the strict adaptation to the unique edaphic mosaic of the Knersvlakte.

*Leipoldtia*

With only eight species, *Leipoldtia* L. Bol. is one of the smaller genera of the subtribe, yet it is one of wide distribution (Figure 7). The predominantly shrubby plants often grow in conspicuous patches, mostly on gravelly and flat sedimentary soils. In contrast to the wide occurrence of subgenus *Leipoldtia*, the subgenera *Aureae* and *Cephalophylloides* inhabit only restricted areas overlapping with that of subgenus *Leipoldtia* (Figure 7). Only one species (*L. frutescens*, of the subgenus *Aureae*) grows in coastal plains (Strandveld sensu Acocks 1975). All other taxa inhabit higher altitudes, mainly in Namaqualand Broken Veld, Western Mountain Karoo and Karroid Broken Veld of the Little Karoo.

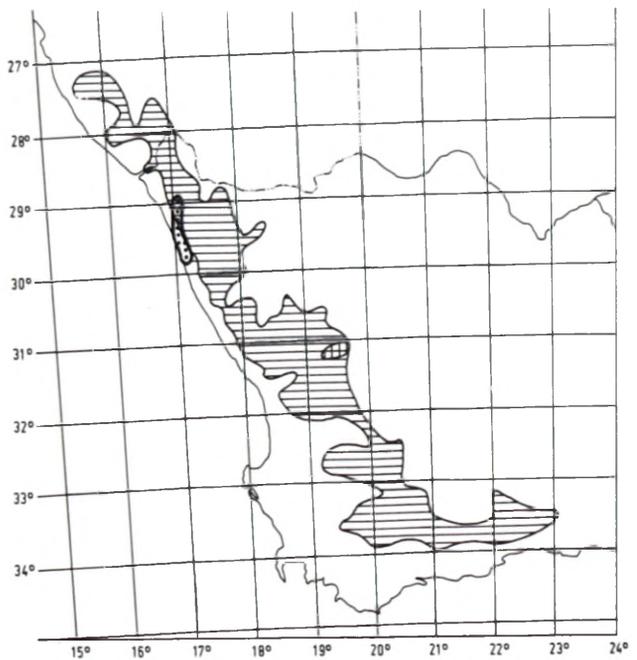


FIGURE 7. — Distribution area of *Leipoldtia*. Horizontal lines = subgenus *Leipoldtia*; vertical lines = subgenus *Cephalophylloides*; dots = subgenus *Aureae*.

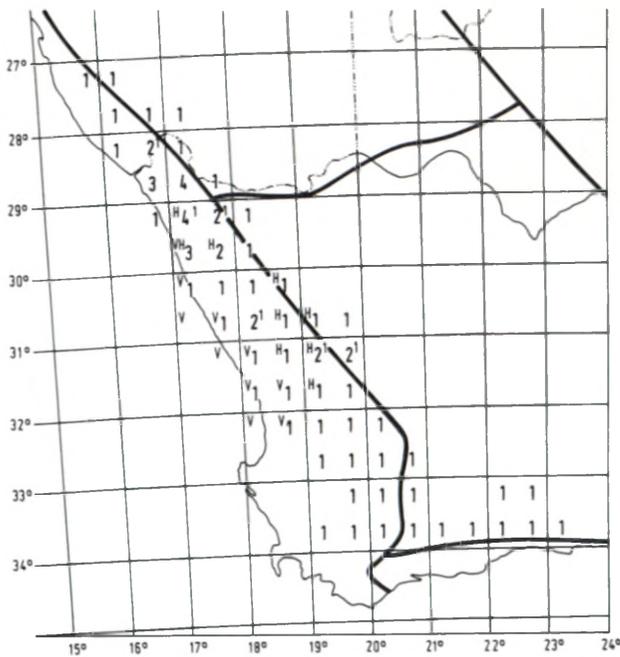


FIGURE 8. — Frequency of species of *Leipoldtia* (N = 8) per 30' × 30' square. H = occurrence of *Hallianthus*; V = occurrence of *Vanzijlia* in the square.

The highest species frequencies are found within the southern Gariep centre (Figure 8), where in certain localities up to three species occur sympatrically, each fitting into an ecological niche slightly different from those of the others (Hartmann & Rust in prep.). Since the same species can inhabit obviously different habitats in distant areas, a fine regulation of adaptation in regard to competition and isolation can be expected, but this is not yet understood (Rust unpublished).

Although 50% of all species of *Leipoldtia* occur in one 30' square, it cannot be simply assumed that this area presents a centre of origin. The scattered distribution of endemic species (Figure 8), and the varied character expressions in geographically separated areas of one species, point more towards an active phase of speciation by means of differentiation of semi-isolated, more or less marginal populations. The high species frequency in the Gariep centre could be the result of secondary invasions combined with the stabilization of hybrid derivatives as ecologically well adapted forms which have become isolated (Rust unpublished).

*Hallianthus* and *Vanzijlia*

Two monotypic genera with allopatric distribution are related to the genus *Leipoldtia* (Hartmann 1983c): *Hallianthus* H. E. K. Hartm. and *Vanzijlia* L. Bol. *Hallianthus* grows predominantly at altitudes above 300 m (Hartmann 1983b) in Namaqualand Broken Veld (sensu Acocks 1975) in associations of succulent shrubs. It extends northwards into the Gariep centre (Figure 8). *Vanzijlia*, as a mainly coastal genus, occurs around and in the Vanrhynsdorp centre (Figure 8). Most populations have been found in shrubby succulent associations of the Strandveld (sensu Acocks 1975), few inland in Succulent Karoo (Hartmann 1983a).

*Cheiridopsis* and *Odontophorus*

The genus *Cheiridopsis* N.E. Br. with 23 species, represents the third of the widespread genera of the subtribe. Like the genus *Odontophorus* N.E. Br., it can be recognized by its papillose leaf surface (Hartmann 1983c). As in *Cephalophyllum*, the two larger subgenera (subgenus *Cheiridopsis* and *Aequifoliae*) inhabit largely different geographical areas (Figure

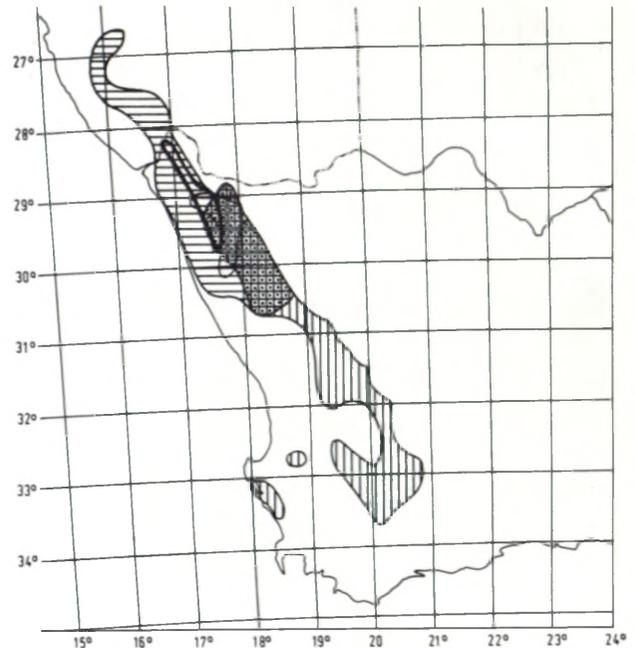


FIGURE 9. — Distribution of *Cheiridopsis* and *Odontophorus* (thin contour between latitude 28°55' and 30°10'). Horizontal lines = *C.* subgenus *Aequifoliae*; vertical lines = *C.* subgenus *Cheiridopsis*; dots = area in which subgenera *Aequifoliae* and *Cheiridopsis* overlap; bold contour = *C.* subgenus *Odontophoroides*.

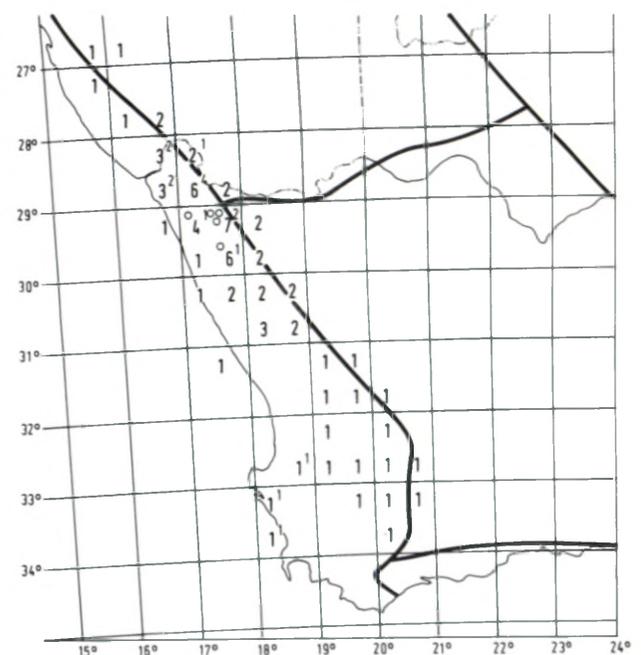


FIGURE 10. — Frequency of species of *Cheiridopsis* per 30' × 30' square (N = 23). Small figures indicate number of endemic species; O = *Odontophorus*; one symbol represents one species per square.

9) with an intervening zone in which they overlap. The third, smaller, subgenus *Odontophoroides*, as well as all species of the closely related genus *Odontophorus*, also occur in and near to this area of overlap. Consequently the number of species per 30' square is high (Figure 10) and contributes substantially to the formation of the southern Gariiep centre (Figure 4). Furthermore, most of the endemic species of *Cheiridopsis* (occurring in at most three adjacent 30' squares) are found here (Figure 10).

In and around the Gariiep centre, sympatry of different species of *Cheiridopsis* is frequent, but in most localities different, well defined microhabitats are colonized (Hartmann & Dehn 1987). The three species of *Odontophorus* occur allopatrically in disjunct areas (Hartmann 1976) as do the six species of subgenus *Odontophoroides* (Hartmann & Dehn 1987).

*Cheiridopsis* and *Odontophorus* constitute a genus pair similar in principle to *Cephalophyllum/Argyrodema* in so far as the genus of restricted distribution occurs in a centre of high species frequency of the widespread genus, but they differ in so far as *Cheiridopsis/Odontophorus* only possess one centre of diversity.

Another characteristic of the *Cheiridopsis/Odontophorus* complex is its nearly exclusive distribution along the eastern boundary of the area of the subtribe at altitudes above 300 m. Only three species, *C. brownii* Schick & Tischer and *C. robusta* (Haw.) N.E. Br. in the north and *C. rostrata* (L.) N.E. Br. in the south, occur on lower coastal plains. Nevertheless, the ecological amplitude of the genus is considerable. It occurs in eight veldtypes of Acocks (1975), with one species, *C. cigarettifera* (Berger) N.E. Br. in the south, growing in six different vegetation types (Hartmann & Dehn 1987). The adaptation to shrubby Renosterveld is particularly remarkable since this vegetation type is rather remote from Karoo types of vegetation.

#### *Jordaaniella* and *Fenestraria*

A distribution pattern different from the aforementioned ones is found in the genera *Jordaaniella* H. E. K. Hartm. and *Fenestraria* N.E. Br. (Figure 11), which are distinguished from the other genera of the subtribe by a considerable reduction of the closing body (Hartmann 1982, 1983c, 1984).

The plants grow exclusively on littoral aeolian sands, the distribution coinciding with Strandveld (sensu Acocks 1975) in the coastal fogbelt (sensu Nagel 1962) along the west coast. The occurrence along the south coast agrees well with the 'south coast Strandveld' as delineated by Moll *et al.* (1984), although the easternmost population exceeds these boundaries (Figure 11).

Only five species are recognized in the complex: one in *Fenestraria* and four in *Jordaaniella* (Figure 11). Sympatry is restricted to a section along the west coast (28°–30°30'S) with a maximum of three species near 30°S, 17°E. Both endemic species (*J. clavifolia* (L. Bol.) H. E. K. Hartm. and *J. longifolia*

(L. Bol.) H. E. K. Hartm.) occur in this region, but it is doubtful whether the centre of origin lies here (Hartmann 1984).

Clearly, the limited distribution areas of both genera are due to their very narrow ecological amplitudes leaving limited scope for speciation (Hartmann 1984).

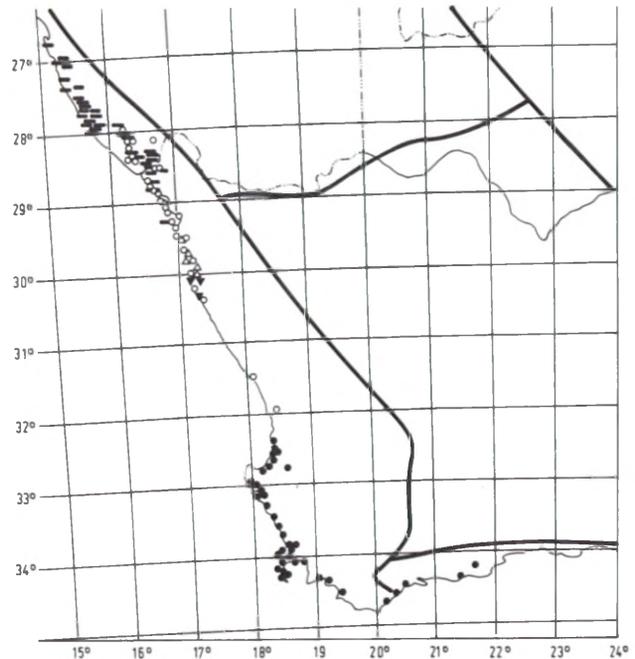


FIGURE 11. — Distribution of *Fenestraria* (solid bars) and *Jordaaniella* (open circles = *J. cuprea*; open triangles = *J. clavifolia*; full triangles = *J. longifolia*; full dots = *J. dubia*).

#### DISCUSSION

Interpretation of the phytogeographical data will concentrate on two different aspects: firstly the composition, development and meaning of the two geographical centres, and secondly the distribution of the genera and their possible evolution. In the process, ideas will be developed on the origin and the history of the Leipoldtiinae as a whole.

High species numbers in restricted geographical areas mostly reflect wide ecological diversity, and two processes can be distinguished: 1, specialization *in situ*, which can be recognized by a high percentage of endemic taxa; 2, overlapping of distribution areas of species which have their main (mostly wide) extension outside the centre of diversity; in the centre itself they colonize the ecologically and/or geographically extreme habitats to which they are adapted.

In the first case close relationship between the taxa is common, whereas in the second, relationship is irrelevant, the effect being simply accumulative. In both centres of multiplicity of the Leipoldtiinae, a core of closely related species, including several endemics, is found (Figures 2, 5–11). In the Gariiep centre, the genera *Cephalophyllum* (Figure 6) and *Cheiridopsis* (Figure 10) represent the major portion (60–70%) of the occurring species. In the Vanrhynsdorp centre, species of *Cephalophyllum* (Figure 6)

and *Argyroderma* (Figure 5) contribute largely to the formation of the centre (up to 14 out of 17 species in one 30' square). Of the additional taxa occurring in these centres, some clearly reach the limit of their distribution here: *Vanzijlia* and *Hallianthus* in the Vanrhynsdorp centre (Figure 8); and *Hallianthus* (Figure 8), *Jordaaniella* and *Fenestraria* (Figure 11) in the Gariep centre.

Obviously, in both centres speciation and overlapping of distribution areas contribute to the high degree of diversity, and it can be suggested that several subsequent events contributed to bring about the present situation. A similar case has been reported in the eastern Cape, for which Gibbs Russell & Robinson (1981) stress the accumulative effect of different phytochoria meeting, whereas Cowling (1982) points out certain groups with high endemism.

Both centres of the Leipoldtiinae exhibit extreme variation in geology and soils, often in island pattern distribution, a condition considered favourable for speciation of semi-isolated populations. In addition, the dense mosaic of different ecological niches in both centres permits short-distance migration under changing climatic conditions, thus allowing persistence of taxa within the area.

Consequently, it is not surprising that both phytogeographical centres have been traced in other groups as well (e.g. Nordenstam (1969) who named the Vanrhynsdorp centre, and circumscribed a 'Gariep centre' in the north). Of the two, the less prominent Vanrhynsdorp centre seems the more uniform, its undulating surface suggesting differentiation mainly in edaphic factors (e.g. Nordenstam 1969). Yet, on close investigation a wealth of ecological niches is found and is reflected in the vegetation (Jürgens 1986).

The Gariep centre has been accepted more readily as a phytogeographical centre because its geological differentiation is complimented by a large relief formation into which the extensions of the surrounding widespread plains reach (e.g. Tölken pers. comm.; Nordenstam 1969; Goldblatt 1976; Moffett 1979). The Gariep centre of the Leipoldtiinae covers a wider area (Figures 3 & 4) than the one circumscribed by Nordenstam (1969) and receives varying amounts of annual precipitation. It is not surprising, therefore, that not a single species occurs over the entire range. Distinct subcentres of genera can be seen: In *Cephalophyllum* (Figure 6), species numbers decrease from northwest to southeast, in *Cheiridopsis* (Figure 10) an increase occurs in the same direction, and *Leipoldtia* has its highest species frequency in the two central 30' squares (Figure 8). Yet, it seems impossible to subdivide the centre into smaller entities, and it seems possible that within the area migration movements could have taken place.

Six species of five genera occur in both phytogeographical centres: *Cephalophyllum inaequale* L. Bol., *Cephalophyllum pillansii* L. Bol., *Hallianthus planus* (L. Bol.) H. E. K. Hartm., *Jordaaniella cuprea* (L. Bol.) H. E. K. Hartm., *Leipoldtia schultzei* (Schltr. & Diels) Friedrich and *Vanzijlia annulata* (Berger) L. Bol. As can be expected, all of them have their main distribution areas outside the

centres, thus contributing to the 'overlapping effect' (see above).

All nine genera have different distribution patterns, and three main types can be distinguished: A — restricted distribution, B — wide distribution with one distinct centre, C — wide distribution without a distinct centre.

The genera *Argyroderma* (Figure 5) and *Odontophorus* (Figure 9) represent examples of pattern A and their restricted geographical occurrence is correlated with marked ecological adaptations (Hartmann 1976, 1978a).

Edaphic factors seem to play important roles in both genera, indicating that speciation may have occurred in the present areas of distribution. This would suggest that appropriate climatic conditions have prevailed for a considerable period allowing extensive radiation processes to take place.

A genus of wide distribution with one distinct centre of diversity (pattern B) is *Cheiridopsis*, where highest species numbers and occurrence of all three subgenera coincide (Figures 9 & 10). Based mainly on morphological data, Hartmann & Dehn (1987) suggest that the centre of origin of the genus (and of the closely related genus *Odontophorus*) lies here, speciation having been promoted by the varied ecological conditions within the southern Gariep centre (see above). Marginal speciation (via semi-isolated populations) in extreme habitats seems to have been rare and has been recorded for *Cheiridopsis carolischmidtii* (Dinter & Berger) N.E. Br. in the north on weathered gneiss in the March rainfall area, and *Cheiridopsis rostrata* (L.) N.E. Br. in the south-west on sandy soils in West Coast Strandveld (sensu Moll *et al.* 1984). *Leipoldtia* can be taken as another example of distribution pattern B, but the centre is less prominent and marginal speciation (Figure 8) more frequent — both smaller subgenera colonize the border areas. The genus could therefore also be seen as an example of pattern C, which lacks a distinct centre. The predominantly shrubby habit and generally low expression of succulence in leaf, stem and root indicate that *Leipoldtia* may have evolved under slightly wetter conditions than it experiences today, perhaps even outside its present distribution area.

The widespread monotypic genera *Fenestraria* (Figure 11), *Hallianthus* and *Vanzijlia* (Figure 8) naturally lack centres of species richness, and even surveys for character multiplicity (Hartmann 1982, 1983a, 1983b) have not yielded positive results. Differentiation patterns can be correlated with geographical distribution (flower characters in *Fenestraria*, Hartmann 1982) or ecological factors (germination in *Vanzijlia*, Hartmann 1983a) or they can occur incidentally (flower characters in *Hallianthus* with island-type distribution, Hartmann 1983b). Adaptation to rocky habitats restricts the distribution of *Hallianthus*. The genus could well have occurred over wider conjunct areas at a time when sedimentary plains covered less ground.

Assessment of the widespread genus *Jordaaniella* is complicated by the strict adaptation to coastal habitats (Figure 11) over several climatic ranges. Ex-

tensive migration along the coast could have taken place, and although three of the four species occur in close proximity (near 30°S, 17°E, Figure 11) it does not seem justified to conclude that this region is the centre of origin (see also Hartmann 1984). Nevertheless, the creeping habit and prolonged germination indicate that the genus probably originated in a coastal habitat.

The large genus *Cephalophyllum* exhibits a complex distribution pattern which cannot be assigned to one of the types mentioned above. Following the character analyses of Hartmann (1978b, in press), the most primitive capsule types and least specialized growth forms occur in species in the Vanrhynsdorp centre, where the highest species frequencies of the genus are found as well (Figure 6). But the number of endemics is low, suggesting that the present species richness is mainly due to overlapping of distribution areas.

In contrast, the species of the Gariiep centre show a high degree of uniformity in capsule morphology, differing mainly in habitat and seed characters, so that this region can be considered to represent a centre of origin for part of the genus (Hartmann in press).

In contrast to *Cheiridopsis* (above), relations between the two subgenera cannot be elucidated from distribution data alone (Figure 2). This is mainly due to the more or less strict allopatric occurrence of the nine species of *Cephalophyllum* subgenus *Cephalophyllum*, in which highest frequencies per 30' square (three species, Hartmann in press) are attained mainly by overlapping of wide distribution areas (only two species of restricted distribution are known, one of them isolated in the south-west, see Figure 6). Speciation in this subgenus seems to have followed predominantly the parapatric model (sensu Wiley 1981) in which narrow contact zones existed between diverging populations.

Some speculations can be made on the phyto-geographical development of *Cephalophyllum*. The predecessor of this genus (and *Argyroderma*?) could have existed in the Vanrhynsdorp centre, but a major part of the genus would have occurred in (or migrated to ?) adjacent areas. Differentiation of the two subgenera possibly took place outside the present distribution range, probably followed by a phase of extensive geographical spreading — *Cephalophyllum* subgenus *Cephalophyllum* mainly into the wetter south, subgenus *Homophyllum* mainly into the drier north of the present distribution area. While parapatric speciation may have prevailed in subgenus *Cephalophyllum*, radiation of a considerable part of the subgenus *Homophyllum* could have taken place in the Gariiep centre. Distribution pattern B (above) can be applied to this species group.

At first sight it seems improbable that a common pattern for the biogeographical development of the Leipoldtiinae can be found. But the extensive meshing of character states, as demonstrated for the subtribe by Hartmann (1983c), clearly indicates that it constitutes a monophyletic group. The area of origin cannot be deduced from present distribution data and may well have lain outside the existing range.

Yet, it was probably not too far away because speciation processes are generally slow and many taxa of restricted occurrence (e.g. species of *Cheiridopsis* subgenus *Odontophoroides*) and/or with narrow ecological amplitude (e.g. *Argyroderma*, *Fenestraria*) can hardly be imagined to have migrated far.

With respect to ecology, the present data suggest that a winter rainfall regime with rather low annual amounts of precipitation (<200 mm, Figure 5) could have prevailed in the area of origin. The few extant exceptions could be seen as ecological fugitives. It is difficult though to localize an adequate region in the past, as opinions on past climates in South Africa are highly controversial (e.g. Van Zinderen Bakker Sr 1978; Deacon 1983), in particular with reference to the extent of the winter rainfall area (e.g. Van Zinderen Bakker Sr 1976, 1978; Lancaster 1979) in the late Pleistocene. In any case, it is accepted that higher precipitation prevailed in the west than at present (Kent & Griebnitz 1985). This leads some authors to the conclusion that the Namib is of rather recent origin (e.g. Tankard & Rogers 1978; Axelrod & Raven 1978) while others (e.g. Lancaster 1979) assume that arid 'isolated refuges along the Namib coast' or widespread deserts (e.g. Sarnthein 1978) existed during the wet phases of the late Pleistocene. Van Zinderen Bakker Sr (1978) also states that the Namib is 'ancient' and has only marginally been influenced by higher rainfall, retaining its 'hyper-arid centre' since the late Tertiary. An area like this could present an ideal cradle for speciation, permitting successive peripheral isolation of populations while re-migration could occur as well.

It seems possible therefore, that the predecessors of the extant genera of Leipoldtiinae originated on the fringes of an ancient Namib, probably under slightly higher rainfall regimes than today (based on the assumption that the less pronounced xeromorphic character expressions in *Leipoldtia*, *Cephalophyllum* and *Jordaniella* reflect the more primitive stages). The existence of strictly coastal taxa (*Jordaniella*, *Fenestraria*) suggests that similar habitats were already available during early speciation processes.

The origin of the Leipoldtiinae as a whole remains even more obscure than the diversification within the subtribe. By its unique morphological character set, the taxon is rather isolated within the family, although the xeromorphic leaf characters indicate that the closest relatives must be sought among the xeromorphic genera of the subfamily Ruschioideae. The main frequency centre of these genera lies around the mouth of the Orange River, coinciding with the Gariiep centre of the Leipoldtiinae. A less pronounced centre is found in the Little Karoo, and a third minor one in the Knersvlakte (Vanrhynsdorp centre), but genera of xeromorphic Ruschioideae occur as far east at 29°E, and as far north as 26°S in almost every degree square. Leipoldtiinae colonize a restricted area within the range of the Ruschioideae, thus emphasizing the relative isolation of the group. They contribute substantially to the formation of the western frequency centres (up to 50% of genera per 30' square), and present a typical 'arid winter rainfall' distribution.

The possibility cannot be excluded that this climatic regime presents the centre of origin of the xeromorphic members of the Ruschioideae, but in the absence of information from less derived subtribes no evidence can be offered for or against the suggestion.

With reference to the entire family, it may be important to note that distribution patterns of both subfamilies coincide almost completely, and that non-xeromorphic genera have their centres of frequency in the winter rainfall region as well. It can therefore be suspected that adaptation to winter rainfall with lower precipitation amounts could present a primary step of evolution within Mesembryanthemaceae, but the phylogeography of the Leipoldtiinae cannot be used as proof because of their specialized derived character set.

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