

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

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ABSTRACT

The leaf blade anatomy of the taxa of the Setacea group of species of the genus *Ehrharta* is described and illustrated. This group includes *E. rupestris* Nees ex Trin. subsp. *rupestris*, subsp. *tricostata* (Stapf) Gibbs Russell and subsp. *dodii* (Stapf) Gibbs Russell, as well as *E. setacea* Nees subsp. *setacea*, subsp. *scabra* (Stapf) Gibbs Russell, subsp. *uniflora* (Burch. ex Stapf) Gibbs Russell and subsp. *disticha* Gibbs Russell. All these taxa share a very characteristic leaf anatomy with inrolled or infolded leaves without keels and have adaxial ribs with interlocking prickles. The chlorenchyma is dense and compact with inwardly projecting invaginations visible in all taxa except *E. setacea* subsp. *setacea*. In *E. setacea* subsp. *scabra* typical arm cells are present. Abaxial costal and intercostal zones are not differentiated and stomata are absent. The long cells are hexagonal or inflated with sinuous walls. Silica bodies are single or paired and rounded in shape. Small hook-like prickles with short barbs are common. Microhairs with a short, truncated distal cell occur. This leaf anatomical structure differs considerably from that of the other species groups recognized in African *Ehrharta* and the Setacea group appears to be more distinct from the other groups than they are from each other.

UITTREKSEL

Die blaarskyfanatomie van die taksons van die Setacea-spesiegroep van die genus *Ehrharta* word beskryf en geïllustreer. Hierdie groep sluit *E. rupestris* Nees ex Trin. subsp. *rupestris*, subsp. *tricostata* (Stapf) Gibbs Russell en subsp. *dodii* (Stapf) Gibbs Russell asook *E. setacea* Nees subsp. *setacea*, subsp. *scabra* (Stapf) Gibbs Russell, subsp. *uniflora* (Burch. ex Stapf) Gibbs Russell en subsp. *disticha* Gibbs Russell in. Al hierdie taksons het 'n baie kenmerkende blaaranatomie gemeen. Die blare is ingerol of ingevou, sonder 'n kiel en het adaksiale ribbe met ineensluitende dorings. Die chlorenchiem is dig en kompak met instulpings van die selwande sigbaar in alle taksons behalwe *E. setacea* subsp. *setacea*. In *E. setacea* subsp. *scabra* is tipiese vertakte selle teenwoordig. Die abaksiale kostale en interkostale sones is nie onderskeibaar nie en huidmondjies is afwesig. Die langselle is seshoekig of opgeblaas en met gekartelde wande. Silikaliggaampies is enkel of gepaard en het 'n ronde vorm terwyl die stekelhare met kort weerhake toegerus is. Mikrohare met 'n kort afgeknotte distale sel kom voor. Hierdie anatomiese struktuur verskil aansienlik van dié van al die ander spesiegroepe in *Ehrharta* in Afrika en die Setacea-groep blyk 'n afsonderlike groep te wees wat meer van die ander groepe verskil as wat hulle van mekaar verskil.

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INTRODUCTION

The African species of *Ehrharta* fall into two natural groups: those with the first sterile lemma similar to the second, and the fertile lemma differing from both; and those with the first sterile lemma reduced and scale-like,

and the fertile lemma similar to the second sterile lemma (Gibbs Russell 1984). About 20 species belong to the first group, but the second group, to which the Setacea group belongs, contains only two species: *E. rupestris* Nees ex Trin. and *E. setacea* Nees, together with seven subspecific taxa. These two species, therefore, differ considerably in spikelet structure from the other species groups in the genus and, morphologically, the Setacea group appears to be rather isolated from the rest of the genus. This paper will examine whether the leaf anatomy of the representatives of this group confirms this observation, and will discuss the affinities of this group by reference to the anatomical evidence.

Chippindall (1955) recognized five species with a short sterile lemma but Gibbs Russell (1984, 1987) has combined these into only two species, each with several subspecies. Within each species there are parallel trends for reduced size and spikelet number, for rolled, folded or flat, erect or spreading leaf blades and for suffrutescence. This apparently reticulate pattern of relationships, which generally applies to the genus *Ehrharta*, results in parallel or convergent trends in vegetative parts occurring in different taxa recognized on the basis of spikelet differences. It is of interest to determine whether the leaf anatomical variation parallels that exhibited by the spikelets and whether it substantiates the morphological classification based on relative glume length. This paper will copiously illustrate, describe briefly and evaluate the leaf anatomy of each of the seven subspecies of the two species of this group with reference to the systematic position of these taxa and of the group as a whole relative to the genus and the higher classification of the Poaceae.

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E. rupestris Nees ex Trin. subsp. *rupestris*

Transverse section

The median vascular bundle is indistinguishable structurally from the lateral first order bundles (Figure 1.1), as is the case throughout this group. Smaller third order bundles occur on either side of the median bundle and near the margin (Figure 1.1; 1.3) and, perhaps, second order bundles should be distinguished in this taxon. However, if these irregular and ill-defined additional bundles are excluded then only two smaller bundles separate consecutive first order bundles, as is the case in all other taxa in this group. The presence of these additional bundles is not considered to be taxonomically significant and probably only represents individual variation in the specimen studied.

Rounded adaxial ribs and narrow furrows are present (Figure 1.2; 1.3), the furrows having interlocking adaxial prickles (Figure 2.1). Similar prickles also occur on subsp. *tricostata* but are absent on subsp. *dodii*.

The chlorenchyma tissue is compact, consisting of small round cells with dense chloroplasts (Figure 1.2). These cells do not have straight, isodiametric sides but do have slight, but clearly discernible wall invaginations (Figure 1.2; 1.3). According to the generally accepted definition of arm cells, these must be considered as such and, in fact, they do closely resemble the arm cells of the Oryzaceae and some of the other bambusoid grasses. These invaginations are better developed in subsp. *rupestris* than in either subsp. *tricostata* or subsp. *dodii* and a definite reduction series is evident in these three subspecies.

Abaxial epidermis

The epidermis conforms very closely to the type diagnostic for this group, with the costal and intercostal zones being structurally undifferentiated and with the long cells being very short and inflated to hexagonal with sinuous walls (Figure 1.4; 1.5). Abaxial stomata were not detected with the light microscope, neither in

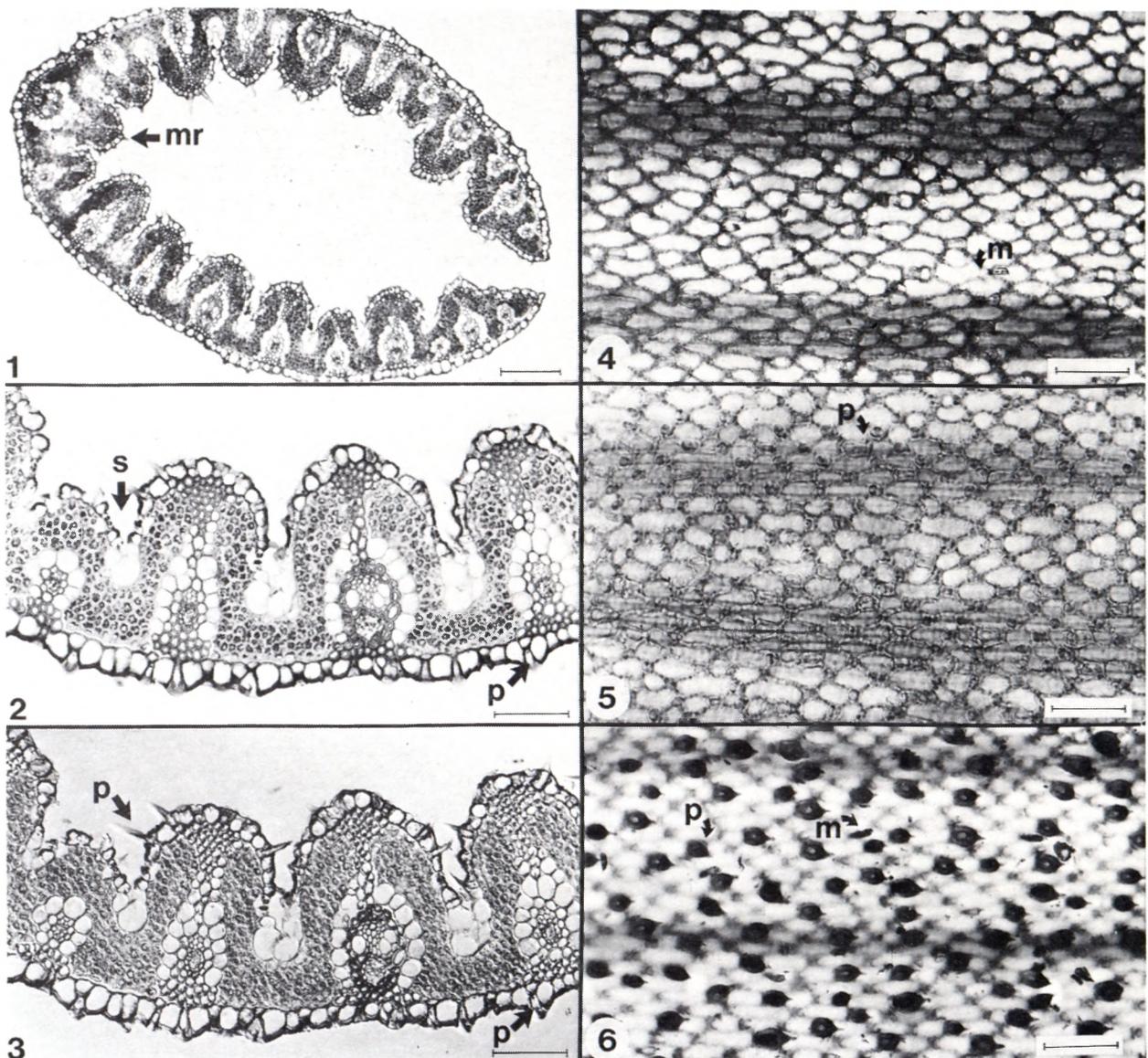


FIGURE 1.—Leaf anatomy of *Ehrharta rupestris* subsp. *rupestris*. 1–5, Ellis 4685. 1–3, leaf transverse sections; 1, infolded leaf blade with median vascular bundle (mr) only, scale = 20 μm ; 2, compact mesophyll with chlorenchyma cells with slight wall invaginations, adaxial stomata (s) only and abaxial hooks (p) with short barbs, scale = 10 μm ; 3, interference contrast showing long barbs of adaxial prickles (p) and short barbs of abaxial hooks (p), scale = 10 μm . 4–5, abaxial epidermis: 4, costal and intercostal zones of similar cells, note microhair (m), scale = 10 μm ; 5, costal and intercostal long cells separated by hooks, prickles (p) or silica bodies, scale = 10 μm . 6, abaxial epidermis of *Van Breda 4436* showing costal and intercostal hooks (p) and microhairs (m), scale = 10 μm .

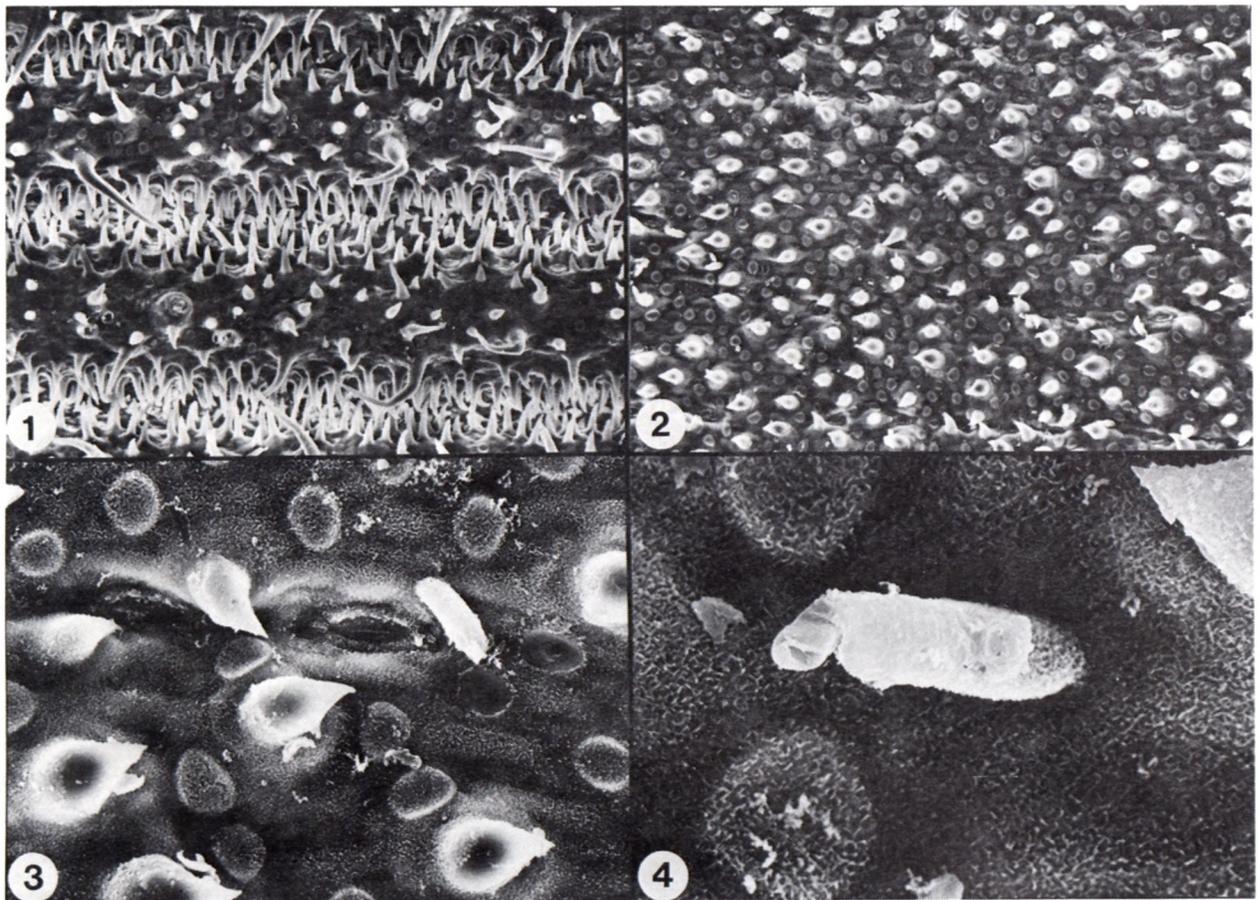


FIGURE 2.—Epidermal ultrastructure of *Ehrharta rupestris* subsp. *rupestris*. 1–4, Ellis 4685. 1, adaxial epidermis showing ribs and furrows with interlocking prickles, $\times 60$; 2–4, abaxial epidermis: 2, epidermal zonation not evident and prickle hairs are widespread, $\times 60$; 3, detail of prickles, stomata and papilla-like silica bodies, $\times 340$; 4, microhair and silica bodies, $\times 1000$.

transverse sections (Figure 1.2; 1.3) nor in epidermal preparations (Figure 1.4–1.6). However, the SEM revealed a few isolated stomata deeply sunken between the inflated long cells and obscured by hooks (Figure 2.3).

Silica bodies are structurally identical throughout the epidermis and appear as single, rounded bodies located between the long cells (Figures 1.4; 1.5). Under the SEM these are clearly seen to be raised, rounded structures covered with epicuticular wax (Figure 2.3; 2.4). As such they are indistinguishable from papillae and do not resemble the usual silica bodies with their concave faces devoid of wax platelets. Their refractive nature is visible with the light microscope (Figure 1.5) and they can also be seen to be raised (Figure 1.6). They are undoubtedly silica bodies but they are highly unusual and their exact nature and structure remains somewhat uncertain. Comparable structures have not been described elsewhere in the literature and they deserve further study. Similar structures also occur in *E. setacea* and they appear to be a unique characteristic of this group of *Ehrharta* species.

The entire abaxial epidermis is densely covered in shortly barbed hooks occupying the same locations between the long cells as the silica bodies (Figure 1.6). These hooks can occupy up to 50% of the available localities (Figure 1.6) but may be fewer in number (Figure 1.4; 1.5). The hooks with their reduced barbs may be difficult to distinguish from the silica bodies with the light microscope but are definitely distinct structures as seen under the SEM (Figure 2.2; 2.3).

The microhairs of subsp. *rupestris* are also of interest in that they are very short, with a blunt distal cell which does not taper to a point (Figure 2.3; 2.4). They are common throughout the epidermis (Figure 1.4; 1.6) and are an important distinguishing feature between this group and all the other groups of *Ehrharta*.

Specimens examined

CAPE.—3118 (Van Rhynsdorp): Vredendal Distr., Koekenap (–CB), Van Breda 4436. 3319 (Worcester): Riviersonderend Mts, Jonas Kop (–DC), Ellis 4685.

Discussion

A small and inadequate sample was studied anatomically and, consequently, little information on variation in this subspecies can be deduced. However, the specimen from the Van Rhynsdorp District in Succulent Karoo comes from an atypical habitat and is particularly robust (Gibbs Russell 1984) and yet closely resembles the specimen from the Mountain Fynbos in leaf anatomy. It, therefore appears as if the leaf anatomy of this taxon is stable and consistent despite differing environmental conditions.

E. rupestris subsp. *rupestris* is obviously very closely related to subsp. *tricostata* and the two can hardly be separated anatomically and, with a larger study sample, can be expected to grade into one another. The cross-sectional anatomy tends to support the diagnostic difference of folded (Figure 1.1) versus rolled (Figure 3.1; 3.4) leaf blades (Gibbs Russell 1984, 1987) even though subsp. *tricostata* is not rolled in the same way as subsp.

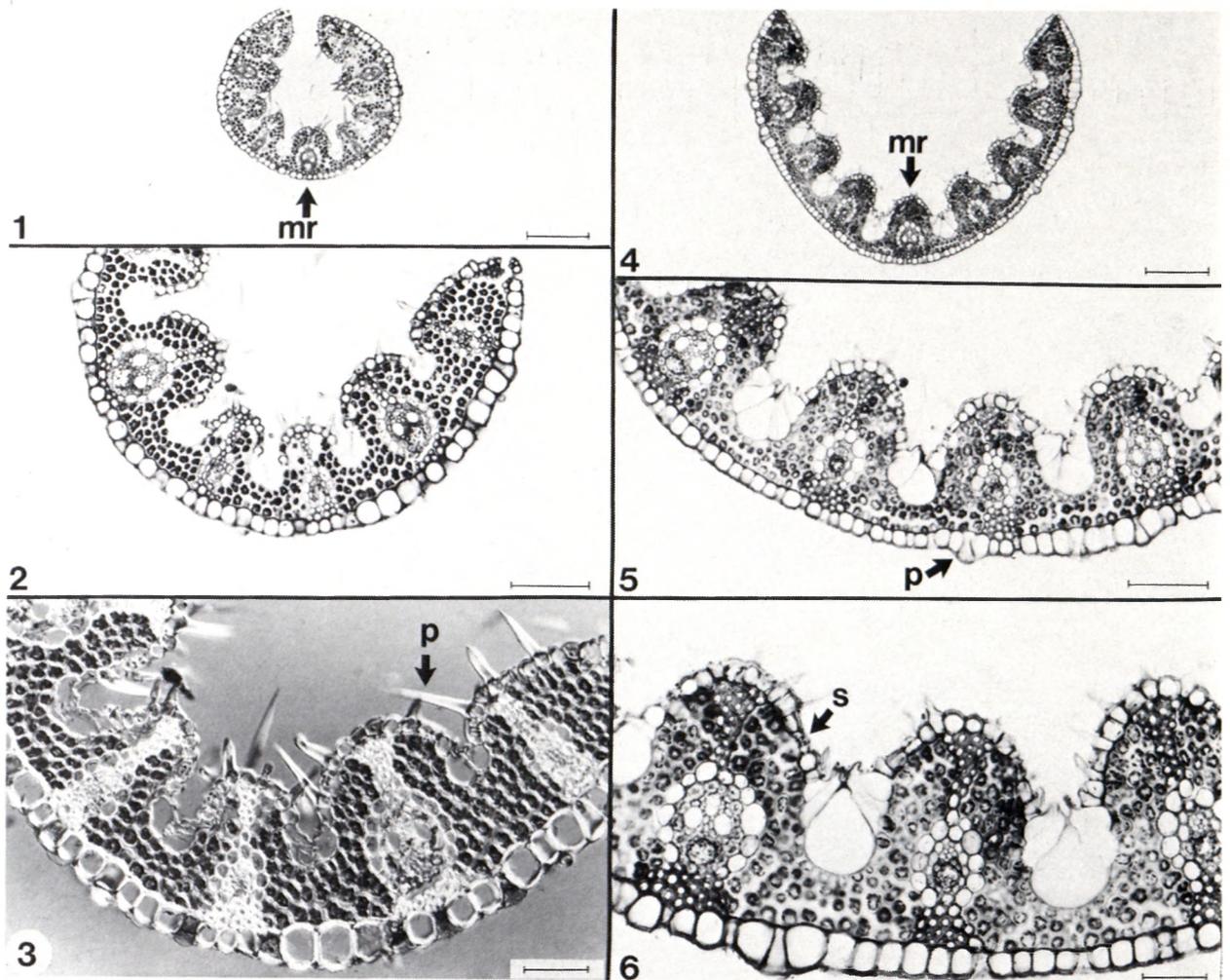


FIGURE 3.—Transsectional leaf anatomy of *Ehrharta rupestris* subsp. *tricostata*. 1–3, *Ellis 4700*: 1, inrolled leaf outline with median vascular bundle (mr), scale = 20 μm ; 2, compact mesophyll with cells densely packed with chloroplasts, scale = 10 μm ; 3, interference contrast showing very slight inward projections of walls of chlorenchyma cells and long barbs of adaxial prickles (p), scale = 5 μm . 4–6, *Ellis 4690*: 4, infolded leaf outline, scale = 20 μm ; 5, arrangement of first and third order vascular bundles, scale = 10 μm ; 6, detail of chlorenchyma with some cells showing slight indentations and adaxially located stomata (s) only, scale = 5 μm .

dodii (Figure 6.1; 6.3). This morphological difference is, therefore, not very convincing when it is analysed structurally. Further anatomical studies are required to confirm whether these two taxa are anatomically distinct; all indications are that only infraspecific separation is justified. This study, therefore, supports the decision of Gibbs Russell (1984, 1987) to reclassify *E. tricostata* as a subspecies of *E. rupestris*. It must also be noted that these two subspecies show greater similarities with each other than either does to subsp. *dodii*.

E. rupestris Nees ex Trin. subsp. *tricostata* (Stapf)
Gibbs Russell

Transverse section

No keels or midribs are present (Figure 3.1; 3.4) and successive first order vascular bundles are separated by two third order bundles (Figure 3.2; 3.5). The outline of the lamina is very similar to that of subsp. *rupestris* and these two taxa differ only in subsp. *rupestris* having considerably wider leaf blades which are infolded but with the arms of the lamina curved outwards. In subsp. *tricostata* the leaf blades are narrower and setaceous with no angle being present at the median bundle (Figure 3.1; 3.4) and these leaves can be considered as being inrolled

although the margins do not overlap as in subsp. *dodii*. This distinction between subsp. *tricostata* and subsp. *rupestris* is only minor and intermediates can be expected when a larger sample is studied. Both these subspecies also possess a ribbed adaxial surface with interlocking prickles overlying the furrows (Figure 3.3).

The mesophyll is compact, of small regular cells. The cells are rounded and very tightly packed (Figure 3.3) and closer inspection reveals very slight inward projections on only a few cell walls (Figure 3.3; 3.6). These cells resemble arm cells but cannot be considered to be typical and may result from reduction of the type of invagination described in subsp. *rupestris*.

Abaxial epidermis

The epidermal structure is virtually identical to that of subsp. *rupestris* as illustrated in Figure 4.1–4.4. The prickles are not always very common and may lack barbs (Figure 4.4) but the solitary, round silica bodies are clearly visible (Figure 4.2). Ultrastructurally these bodies are also seen to be raised and papilla-like (Figure 5.3) and not concave as typical silica bodies usually are. The microhairs have a short, blunt distal cell (Figure 5.4)

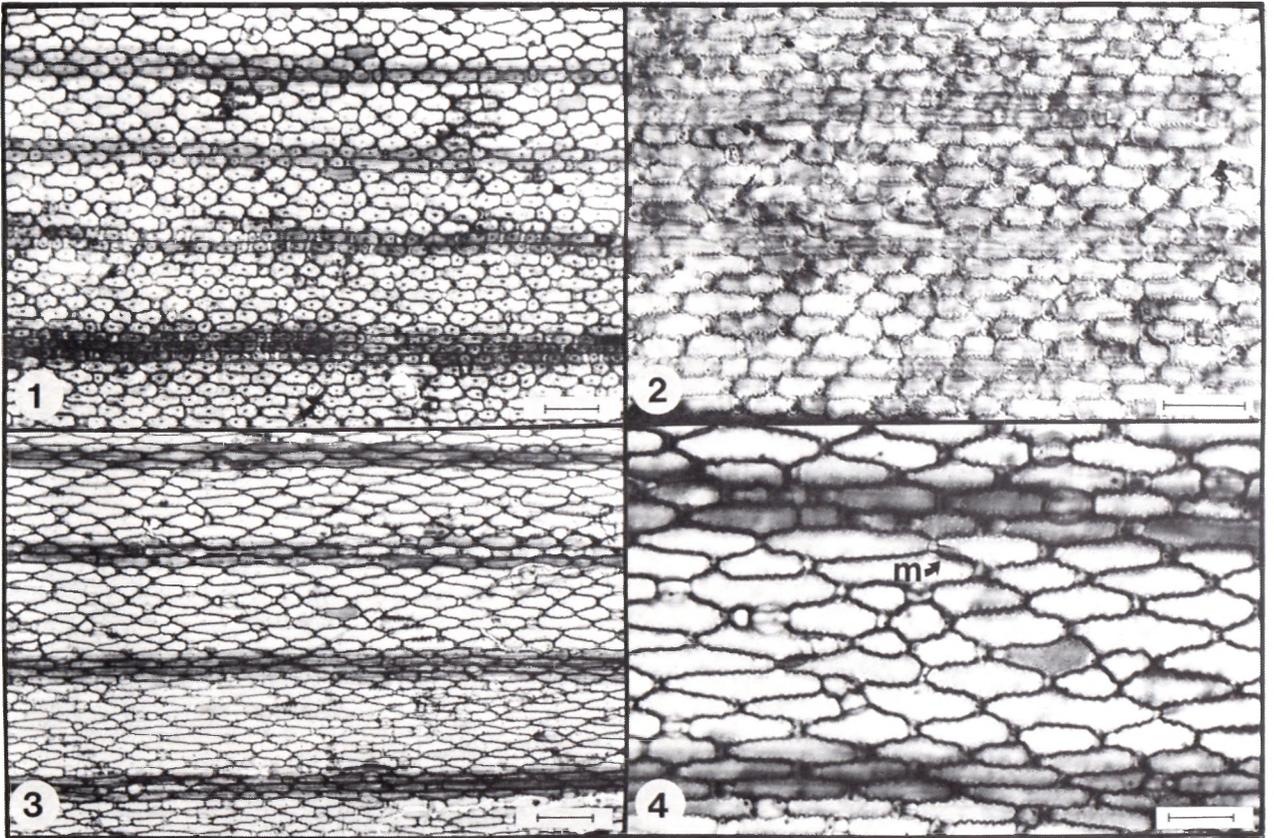


FIGURE 4.—Abaxial epidermis of *Ehrharta rupestris* subsp. *tricostata*. 1–2, *Ellis 4700*: 1, costal and intercostal files of similar composition, scale = 10 μm ; 2, interference contrast showing silica cells or hooks between all long cells, scale = 10 μm . 3–4, *Ellis 4690*: costal and intercostal long cells diamond shaped, scale = 10 μm ; 4, intercostal long cells with thickened, pitted walls, note microhair (m), scale = 10 μm .

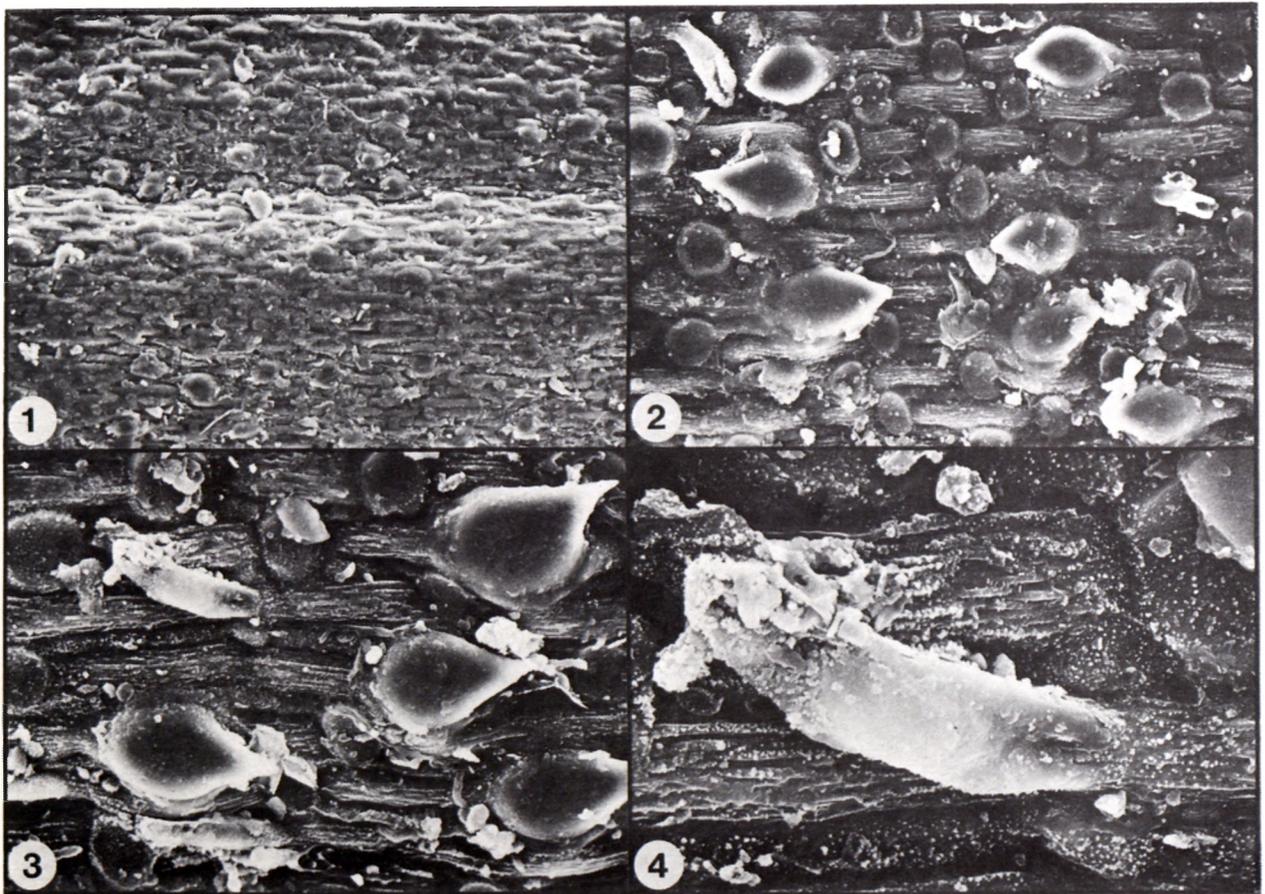


FIGURE 5.—Abaxial epidermis of *Ehrharta rupestris* subsp. *tricostata*. 1, *Ellis 4690* showing absence of costal and intercostal zonation, $\times 60$. 2–4, *Ellis 4700*: 2, prickles common and short long cells separated by raised silica bodies, $\times 200$; 3, prickles with short barbs, microhairs and long cells, $\times 300$; 4, detail of microhair and cuticular striations on long cells, $\times 1000$.

and are unusual in this regard in the genus. The epicuticular wax layer in subsp. *tricastata* is very thick with distinct horizontal striations (Figure 5.3; 5.4) and not of fine platelets as in subsp. *rupestris* (Figure 2.3; 2.4).

Specimens examined

CAPE.—3321 (Ladismith): Riversdale Distr., Langeberg, Garcia's Pass (-CC), *Ellis* 4690. 3322 (Oudtshoorn): Outeniqua Mts, Robinson's Pass (-CC), *Ellis* 2547, 4700.

Discussion

Anatomically subsp. *tricastata* is very similar indeed to subsp. *rupestris* and these two taxa cannot be satisfactorily distinguished on anatomical criteria. This is supportive of their separation at only the subspecies level (Gibbs Russell 1984) and the leaf anatomy confirms the extremely close relationship of these two taxa. The recognition of two separate species is not corroborated by the anatomical evidence.

E. rupestris Nees ex Trin. subsp. *dodii* (Stapf) Gibbs Russell

Transverse section

No keel is present (Figure 6.1; 6.3) and the adaxial ribs and furrows are not well developed and interlocking prickles are absent (Figure 6.2). Of particular interest is the convolute inrolling of the leaf blade (Figure 6.1; 6.3). This type of inrolling does not occur in either subsp. *rupestris* or subsp. *tricastata* and appears to be a significant anatomical difference between these two subspecies and subsp. *dodii*.

The mesophyll tissue is compact, of small rounded and regular cells (Figure 6.2). These cells cannot be regarded as being typical arm cells as they possess only very slight invaginations.

Abaxial epidermis

The costal and intercostal zones are structurally undifferentiated although their relative positions can be determined due to the staining of the sclerenchyma girders underlying the costal zones (Figure 6.4). The long cells are considerably longer and less inflated than in either of the other two subspecies of *E. rupestris*. All three subspecies do have sinuous long cell walls and stomata are either very rare (subsp. *rupestris*) or absent from the abaxial surface. The silica bodies are also rounded but they are closely associated with a cork cell. Although these structures were not examined ultrastructurally, there can be little doubt that they are typical graminoid silica bodies and not the unusual type described in subsp. *tricastata* and subsp. *rupestris*. Prickles with prominent oval bases and very short barbs are common (Figure 6.4). Small microhairs, typical of those of the Setacea group, are also present (Figure 6.4).

Specimens examined

CAPE.—3418 (Simonstown): Hottentot Hollands Mts, Sir Lowry's Pass (-BB), *Ellis* 2286, 2287; Kogelberg State Forest, Platberg (-BD), *Boucher* 2039.

Discussion

In its leaf anatomy *E. rupestris* subsp. *dodii* differs more from subsp. *rupestris* and subsp. *tricastata* than

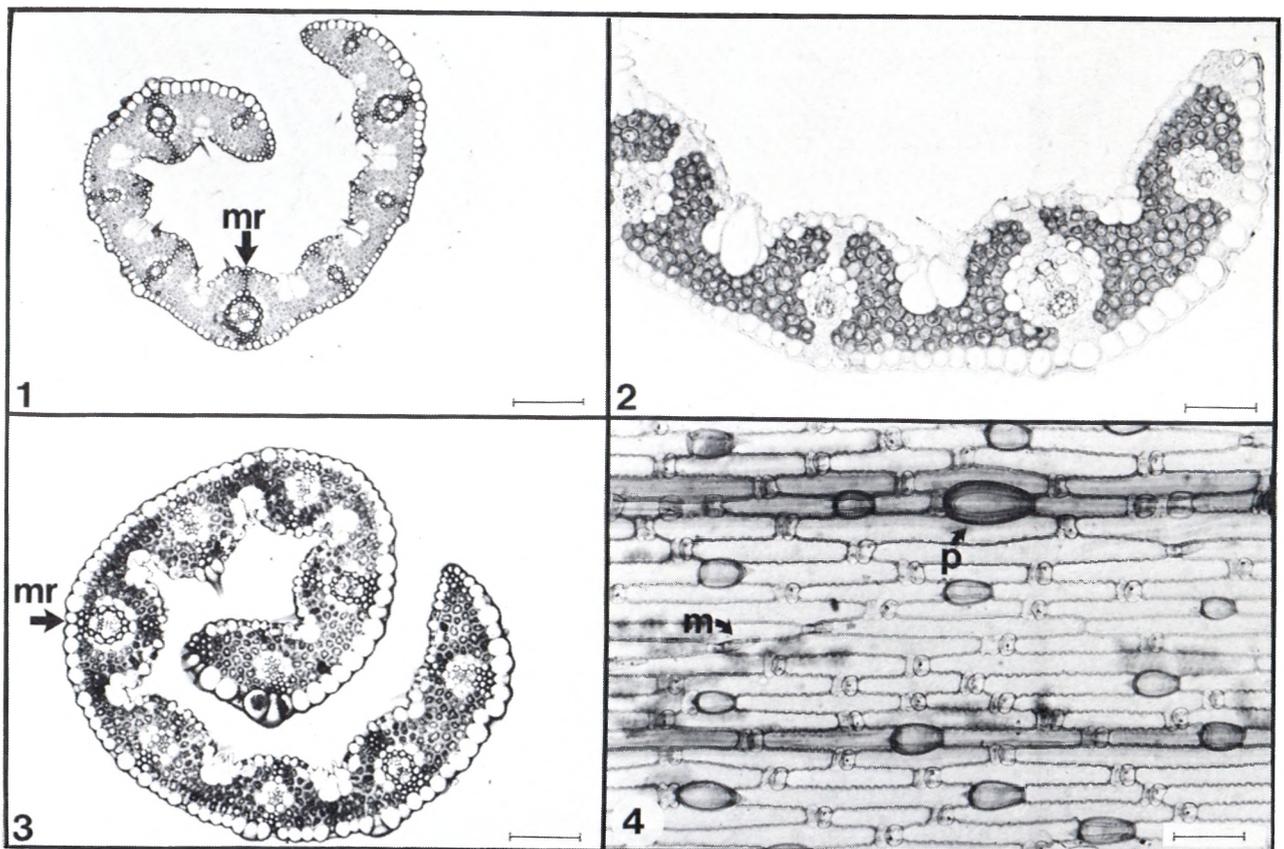


FIGURE 6.—Leaf anatomy of *Ehrharta rupestris* subsp. *dodii*. 1–3, leaf in transverse section. 1–2, *Ellis* 2286: 1, inrolled outline with simple median vascular bundle (mr), scale = 10 μ m; 2, compact mesophyll of rounded cells with slight wall indentations, scale = 5 μ m. 3, *Ellis* 2287, showing inrolled outline, few adaxial prickles and simple median bundle (mr), scale = 10 μ m. 4, abaxial epidermis, *Ellis* 2287, note absence of stomata, microhairs (m), costal prickles (p) and intercostal hooks, scale = 5 μ m.

these two subspecies differ from one another. The findings of this study, based on only a very small sample, appear to indicate that subsp. *dodii* is sufficiently distinct from *E. rupestris* to warrant separate specific status. Additional anatomical material may reveal anatomical intermediates with subsp. *tricostata* but this appears rather unlikely in view of the entirely different nature of the involution of the blades of these two taxa. The convolute type of inrolling in subsp. *dodii* may indicate a different type of bud veneration to that of subsp. *tricostata* where inrolling is of the involute type. If this proves to be true then the case for separation at the species level will be strengthened.

Although subsp. *dodii* differs somewhat from subsp. *rupestris* and subsp. *tricostata* in leaf anatomy, their anatomy is still typical of the Setacea group and different from that of all the others of *Ehrharta* (Gibbs Russell & Ellis 1987). Subsp. *dodii*, therefore, unquestionably belongs to this very distinct group.

The less acicular type of leaf transection and the elongation of the epidermal long cells seems to be paralleled in *E. setacea* in subsp. *disticha* and subsp. *uniflora*. This trend may be related to the milder climate of the Cape Peninsula and Caledon District to which these three taxa are restricted. These three subspecies do not occur at higher altitudes in the mountain ranges further inland as do *E. rupestris* subsp. *rupestris* and subsp. *tricostata* and *E. setacea* subsp. *setacea* and subsp. *scabra*. This trend, associated with a more mesophytic type of anatomy and elongated epidermal cells with costal and intercostal zones and with abaxial stomata, may represent the convergent trends so evident in this group. Alternatively this pattern may reflect the reticulate nature of relationships which also characterizes this group. It is therefore an academic decision whether subsp. *dodii* should be recognized as a separate species or not. Whatever basis is used to define species in this group, other characters will not necessarily follow the same pattern. The decision is also dependant on a similar decision being made for subsp. *disticha* and subsp. *uniflora* in *E. setacea*.

E. setacea* Nees subsp. *setacea

Transverse section

This taxon has the leaf outline which typifies this group: the blades are setaceous, without midribs or keels (Figure 7.1; 7.3) and with well developed abaxial ribs and furrows (Figure 7.2; 7.4). Subsp. *setacea* is notable in having acicular leaf blades of the permanently in-folded type with the abaxial epidermal cells being very large and regular in size as seen in transection (Figure 7.2; 7.4).

The chlorenchyma is exceptionally compact and consists of straight-walled, isodiametric cells (Figure 7.2; 7.4). The chloroplasts are dense, peripherally arranged and with a central vacuole. No invaginations are visible. This chlorenchyma is identical in appearance to the type so common in the Danthonieae in genera such as *Merxmuellera*, particularly *M. disticha* (Schrad.) Nees (Ellis 1980), *Pseudopentameris* (Ellis 1985a) and some species of *Pentameris* (Ellis 1985b,c).

Abaxial epidermis

Costal and intercostal zones are not differentiated (Figure 7.5; 7.7), the long cells are short and fusiform

(Figure 7.6; 7.8) and separated by a single, raised silica body (Figure 12.1). Abaxial stomata are absent as are hooks and prickles. Microhairs are infrequent (Figure 7.8) or absent (Figure 7.6) but when present are short with rounded distal cells (Figure 12.2).

Specimens examined

CAPE.—3418 (Simonstown): Hottentots Holland Mts, Sugarloaf Peak (—BB), *Ellis* 2273; Sir Lowry's Pass (—BB), *Ellis* 2294; Landrostkop, Somerset Sneeuwkop (—BB), *Ellis* 4679.

Discussion

The leaf anatomy conforms closely to that typical of the Setacea group, and subsp. *setacea* resembles *E. rupestris* subsp. *rupestris* and subsp. *tricostata* very closely in leaf anatomy. It differs mainly in the absence of abaxial prickles. Other slight differences, such as the chlorenchyma cell invaginations and the epidermal cells in transverse section which are regular in size, due to the absence of prickle hair bases, are only differences of degree. Anatomically, therefore, subsp. *setacea* clearly belongs to the Setacea group. Whether it should be separated from *E. rupestris* is debatable according to the anatomical evidence and *E. setacea* subsp. *setacea* has more in common with *E. rupestris* subsp. *tricostata* than it has with any of the other subspecies of *E. setacea*. The leaf anatomy appears to indicate that these two taxa are conspecific and the relative glume length, which is used to separate *E. setacea* from *E. rupestris* (Gibbs Russell 1984), results in an apparently artificial anatomical grouping. This observation is particularly relevant when the anatomy of subsp. *setacea* is compared with that of subsp. *scabra*, as these taxa exhibit significant anatomical differences which would justify at least specific separation in other grass groups.

Once again the classification of taxa within the Setacea group presents problems with contradictory anatomical and morphological evidence. A possible explanation for this situation lies in different rates of evolution in different organs combined with a reticulate evolutionary pattern. Present knowledge indicates that, whatever characters are used to distinguish taxa in this group, heterogeneity of other character sets will result. This makes a generally acceptable classification almost impossible to achieve.

The anatomical resemblance between subsp. *setacea* (and *E. rupestris* subsp. *tricostata* as well) and many of the winter rainfall danthonoid grasses deserves further mention. Both in section and epidermis subsp. *setacea* closely resembles species of *Pseudopentameris* (Ellis 1985a), and *Pentameris* (Ellis 1985b,c) in particular. These similarities may only be coincidental but it is more probable that they result from convergent evolution. Convergent and parallel patterns appear to be common in Cape fynbos grass species. Most species of the mountain regions, where nutrients are severely limiting, have evolved a structurally complex, long-lived leaf, in contrast to the lowland species in which the leaves are deciduous (or the plants annual) with a much simpler internal structure, with thinner cell walls, less sclerenchyma and larger air spaces. This general pattern cuts across phylogenetic lines at the generic level and does not appear to be taxonomically significant. What is of importance, however, is that here taxa from different subfamilies have responded identically to similar environmental conditions.

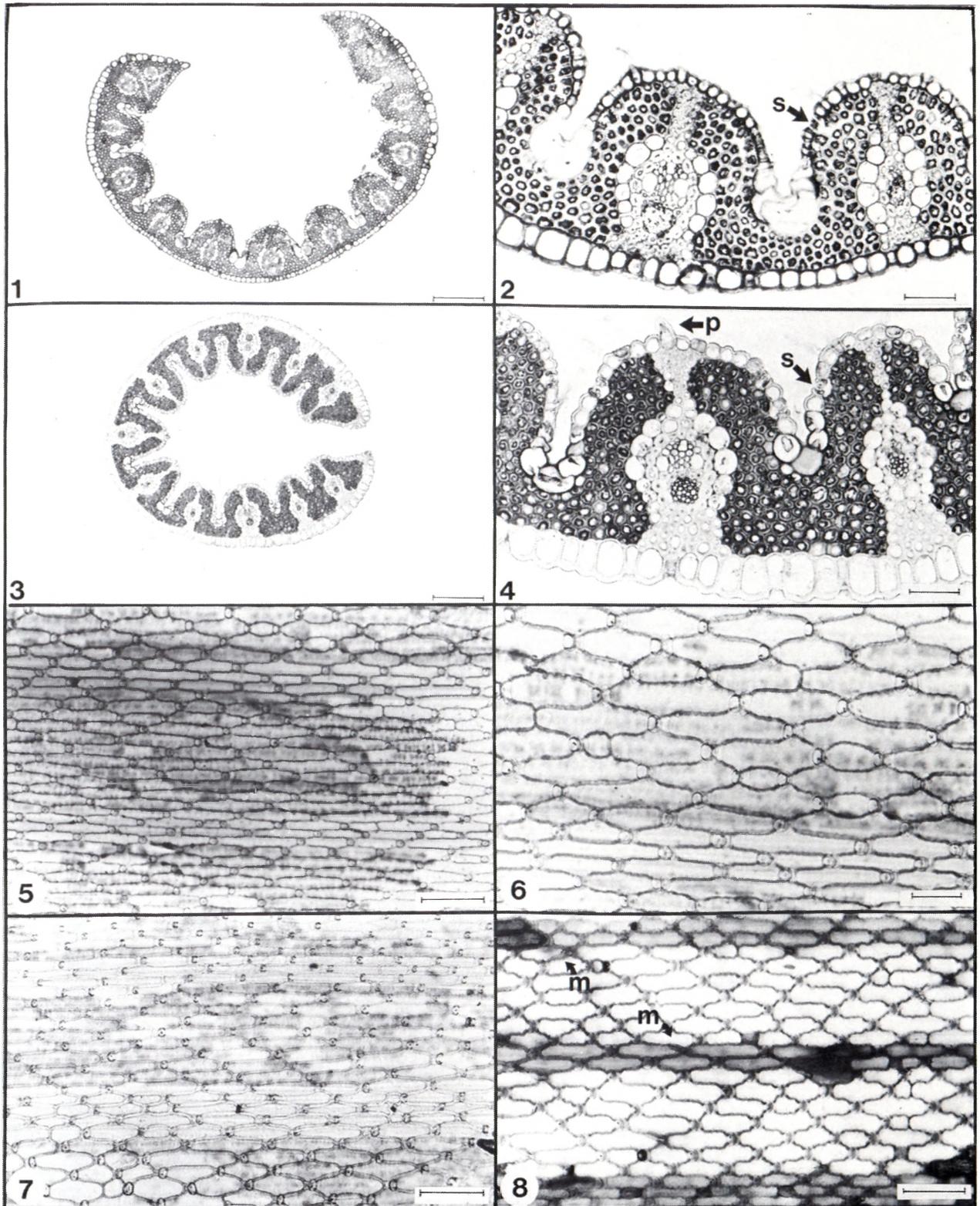


FIGURE 7.—Leaf anatomy of *Ehrharta setacea* subsp. *setacea*. 1–2, *Ellis 4679*: 1, leaf outline showing inrolling and undifferentiated midrib, scale = 20 μm ; 2, anatomical detail with compact chlorenchyma and adaxial stomata (s), scale = 5 μm . 3–4, *Ellis 2273*: 3, inrolled outline, scale = 20 μm ; 4, isodiametric chlorenchyma cells without wall invaginations, scale = 5 μm . 5–6, *Ellis 2294*, abaxial epidermis: 5, costal and intercostal zone cell structure similar, scale = 10 μm ; 6, hexagonal long cells separated by cork-silica cell pairs, scale = 5 μm . 7, *Ellis 2273*, costal and intercostal zones not clearly differentiated, scale = 10 μm . 8, *Ellis 4679*, note small, indistinct microhairs (m), scale = 10 μm .

E. setacea Nees subsp. *scabra* (Stapf) Gibbs Russell

Transverse section

This subspecies has a wide, expanded type of lamina (Figure 8.1; 8.3) which is not of the setaceous type of subsp. *setacea*. In all specimens, even those in which the blade is almost flat, there are indications of convolute infolding (Figures 8.1; 8.3). This is reminiscent of the condition in *E. rupestris* subsp. *dodii*. Slight adaxial ribs and wide, open furrows (Figures 8.2; 8.4; 8.6) resemble the subsp. *dodii* condition more than subsp. *setacea*.

The single most significant anatomical feature of subsp. *scabra* is the possession of definite arm cells in the mesophyll (Figures 8.2; 8.4; 8.5; 8.6). These are typical arm cells with distinct invaginations of the cell walls visible in all chlorenchyma cells (Figures 8.2; 8.4) and the chloroplast pattern is also indented, indicating the presence of these inward projections of the cell walls (Figures 8.5; 8.6). Typical arm cells are, however, sometimes lacking in subsp. *scabra* (Ellis 4653). Arm cells do not occur in subsp. *setacea* but indications of their existence are evident in all other taxa of the Setacea group.

Abaxial epidermis

The structure of the epidermis is very similar to that of *E. rupestris*. Absence of zonation, short fusiform long cells, no stomata, rounded silica bodies and hook-like prickles (Figure 9.1–9.4) occur in subsp. *scabra* and characterize the taxa of the Setacea group. Ultrastructurally this similarity is confirmed by the raised papilla-like silica bodies (Figure 12.3) and short microhairs with rounded distal cells (Figure 12.4). This epidermal structure differs somewhat from that of subsp. *setacea* and subsp. *uniflora* but is virtually identical to that of *E. rupestris* subsp. *rupestris* and subsp. *tricostata*.

Specimens examined

CAPE.—3320 (Montagu): Barrydale Distr., Tradouw's Pass (–DC), Ellis 1678, 1679, 4652, 4653 (varies anatomically). 3321 (Ladismith): Riversdale Distr., Langeberge, Garcia's Pass (–CC), Ellis 2544, 4689.

Discussion

Arm cells are considered to be a very important character in the systematics of the Poaceae and the presence of these cells in subsp. *scabra* may be taxonomically meaningful. Arm cells are a diagnostic characteristic of

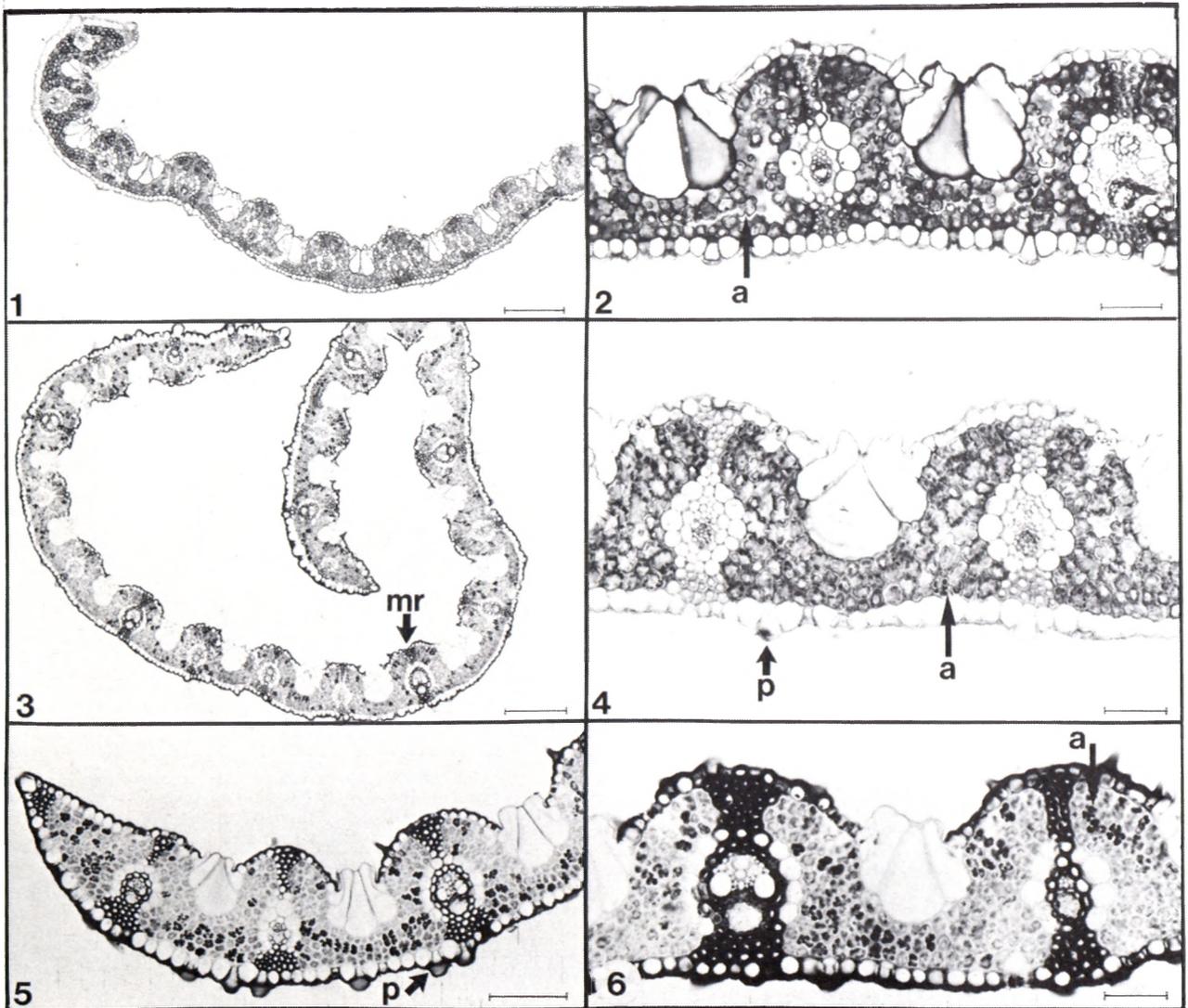


FIGURE 8.—Cross-sectional leaf anatomy of *Ehrharta setacea* subsp. *scabra*. 1–2, Ellis 4689: 1, broad, expanded outline, scale = 20 μ m; 2, anatomical detail clearly showing arm cells (a), scale = 5 μ m. 3–4, Ellis 2544: 3, inrolled but broad leaf with median vascular bundle (mr) only, scale = 20 μ m; 4, arm cells (a) with distinct cell wall invaginations, scale = 5 μ m. 5, Ellis 1679, leaf margin showing arm cells and abaxial prickles (p), scale = 10 μ m. 6, Ellis 1678, arm cells (a) of chlorenchyma densely filled with chloroplasts, scale = 10 μ m.

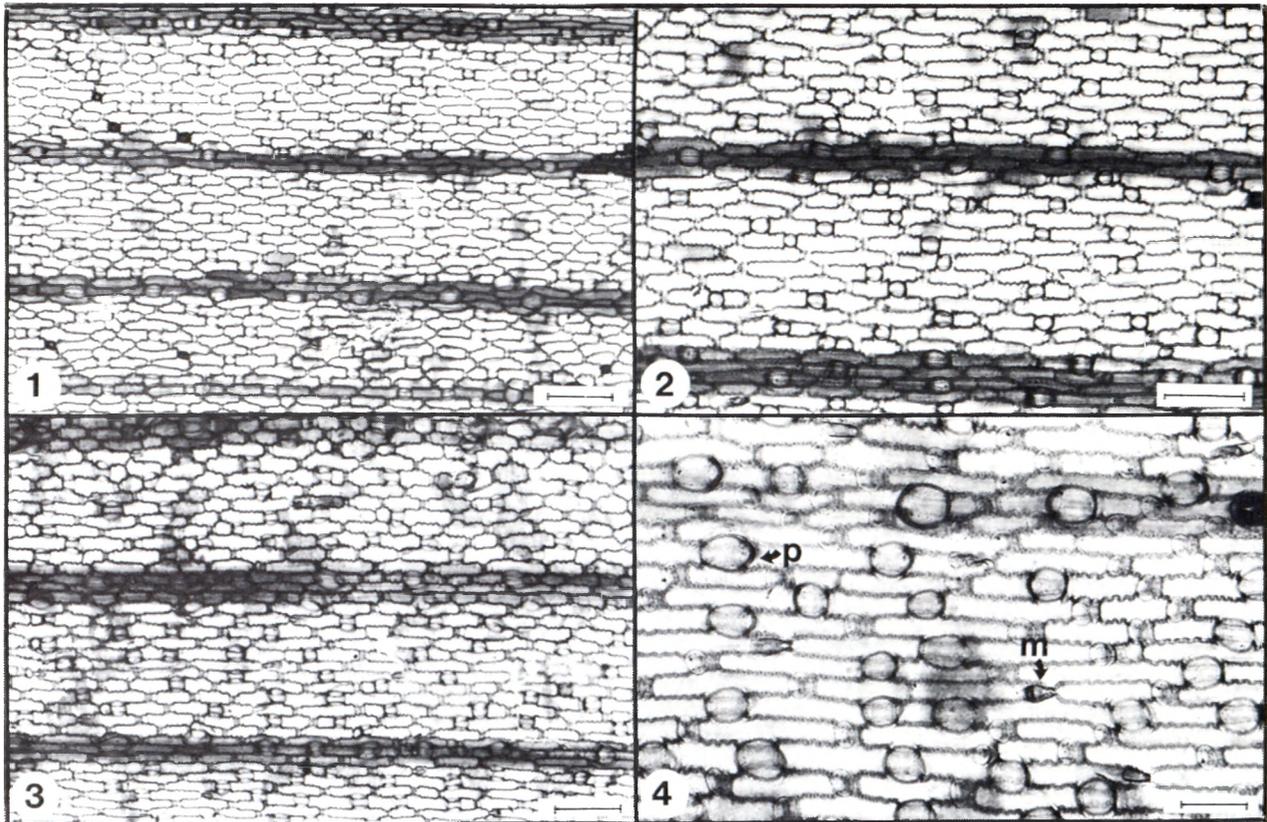


FIGURE 9.—Abaxial epidermal structure of *Ehrharta setacea* subsp. *scabra*. 1–2, *Ellis 4689*: 1, cell arrangement, scale = 10 μm ; 2, costal and intercostal zones only slightly differentiated, scale = 10 μm . 3–4, *Ellis 4652*: 3, cell pattern consistent throughout abaxial epidermis, scale = 10 μm ; 4, microhairs (m) and shortly barbed prickles (p), scale = 5 μm .

the Bambusoideae (including Oryzaceae) and, as such, are a feature of high taxonomic value. However, arm cells are known sporadically from non-bambusoid groups. Examples are *Phragmites* and *Thysanolaena* of the Arundinoideae and *Sclerodactylon* and the Triodeae of the Chloridoideae (Watson *et al.* 1985). This occurrence of arm cells in these apparently unrelated groups is impossible to explain but indicates that the presence of arm cells in the Setacea group of *Ehrharta* does not necessarily imply bambusoid relationships for the genus. However, their presence can undoubtedly be used to substantiate the arguments of those workers (Renvoize 1986) in favour of bambusoid affinities for *Ehrharta*. However,

the occurrence of fully developed arm cells in only one taxon of the genus *Ehrharta* urges caution in attaching too much importance to their presence.

A certain degree of anatomical variation was observed in this subspecies. This variation applies particularly to the presence of stomatal bands in the abaxial epidermis (Figure 10.3) with an associated development of clear structural differentiation between the costal and intercostal zones. The specimen displaying this type of structure (*Ellis 4653*) was collected growing together with *Ellis 4652*, which has the anatomy typical of subsp. *scabra*, whereas *Ellis 4653* is a much more robust plant with an

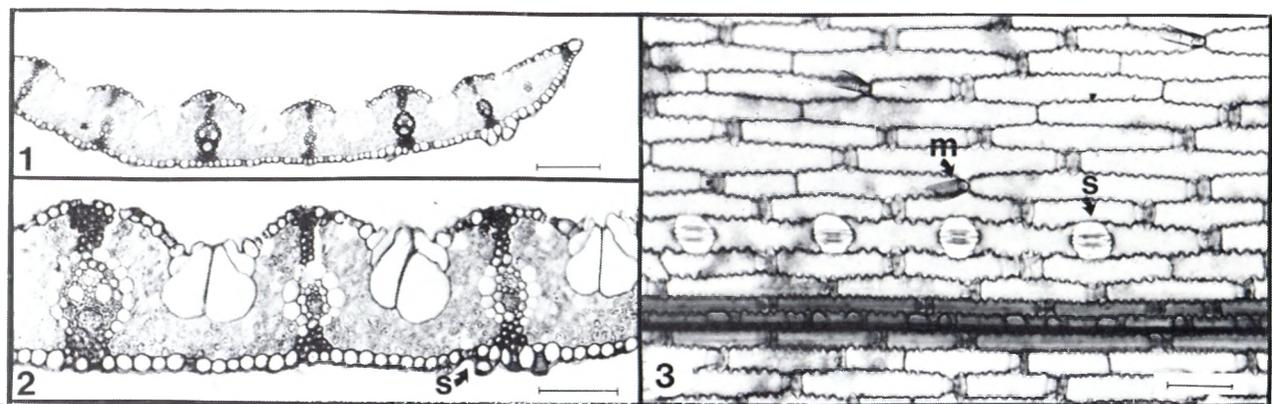


FIGURE 10.—Anatomical variation in *Ehrharta setacea* subsp. *scabra*, *Ellis 4653*. 1–2, leaf sections: 1, margin of open, expanded leaf, scale = 20 μm ; 2, mesophyll not compact and not comprised of distinct arm cells, note abaxial stomata (s), scale = 10 μm . 3, abaxial epidermis showing stomatal bands (s), microhairs (m) and clear cellular differentiation between costal and intercostal zones, scale = 5 μm .

extremely dense underground rhizome system. The anatomy of this specimen is illustrated in Figure 10 and it can be seen to differ from typical subsp. *scabra* in the presence of abaxial stomata, the epidermal zonation and by having elongated intercostal long cells (Figure 10.3) and by the absence of typical arm cells, with the invaginations being poorly developed (Figure 10.2). The microhairs are also more elongated (Figure 12.6) and there are fewer prickles (Figure 12.5). The anatomy of this specimen is, therefore, intermediate between that of subsp. *scabra* and subsp. *uniflora* which has abaxial stomata, no prickles and elongated, tapering microhairs (Figure 12.7; 12.8). A few isolated stomata were also observed on the epidermis of *Ellis 4689*, a rather robust specimen with wide leaves (Figure 8.1). However, in this specimen, the epidermal zones are not structurally differentiated (Figure 9.1; 9.2) and the arm cells are clearly developed (Figure 8.2). It is possible that a whole range of intermediates will be found between *E. setacea* subsp. *scabra* and subsp. *uniflora* and *disticha*. Unfortunately the latter two subspecies are poorly represented in this study and it was not possible to determine the exact pattern of variation between these taxa.

E. setacea Nees subsp. *uniflora* (Burch. ex Stapf)
Gibbs Russell

Transverse section

This subspecies has a narrow but flat and expanded leaf outline (Figure 11.1) with poorly developed ribs and furrows (Figure 11.3). This is not the setaceous type of leaf outline as in subsp. *setacea*, and abaxial stomata are clearly visible even in transection (Figure 11.3; 11.4). There is also no indication of convolute inrolling as in subsp. *scabra*.

The mesophyll of subsp. *uniflora* is also not as compact as in all the other taxa of the *Setacea* group (Figure 11.2; 11.4), a difference which appears to be associated with the development of an air-space system linked to the abaxial stomata. The mesophyll cells themselves cannot be considered to be classical arm cells (Figure 11.2; 11.4) although very slight invaginations are visible in some of the chlorenchyma cell walls.

Abaxial epidermis

The presence of a single file of stomata on either side of each costal zone (Figure 11.5; 11.6) distinguishes the

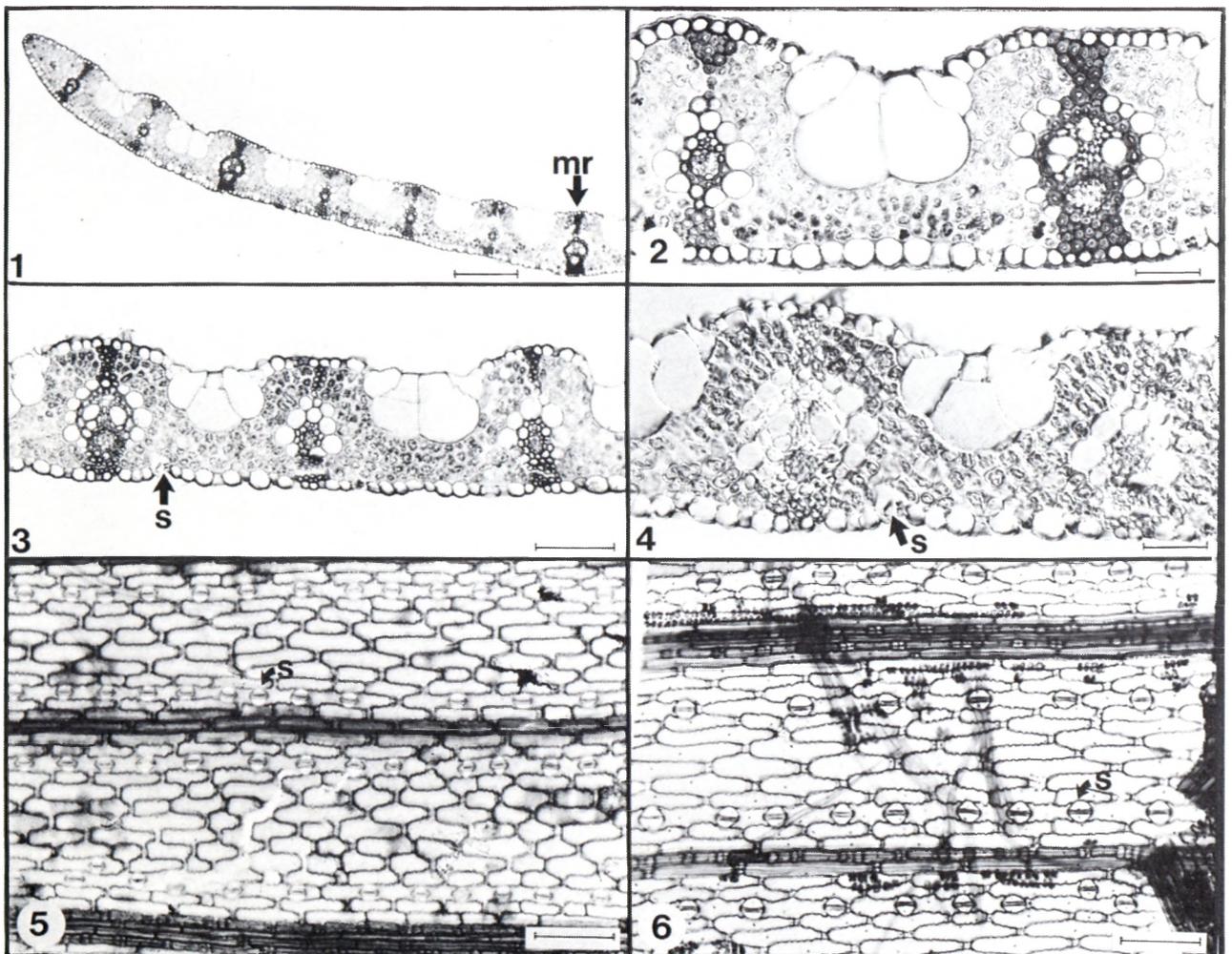


FIGURE 11.—Leaf anatomy of *Ehrharta setacea* subsp. *uniflora*. 1–2, *Ellis 4670*, transections: 1, open, expanded outline with median vascular bundle (mr) only, scale = 20 μm ; 2, anatomical detail showing chlorenchyma which is not composed of typical arm cells, scale = 5 μm . 3–4, *Ellis 4669*, transections: 3, abaxial stomata (s) common, scale = 10 μm ; 4, interference contrast showing only slight wall indentations and abaxial stomatal aperture (s), scale = 5 μm . 5, abaxial epidermis, *Ellis 4670*, with single file of stomata (s) on either side of each costal zone, scale = 10 μm . 6, abaxial epidermis, *Ellis 4669*, showing stomata (s) and clearly differentiated costal zones, scale = 10 μm .

epidermis of this subspecies from all the other taxa of the Setacea group (except subsp. *disticha*). There is also a definite tendency for the costal zones to be structurally different from the intercostal zones (Figure 11.6) with the silica bodies being different. The intercostal long cells are not separated by raised silica bodies as in the other subspecies of *E. setacea* (Figure 12.1; 12.3; 12.5; 12.7). In this respect subsp. *uniflora* differs from all other members of the Setacea group. Other differences are the tapering microhairs (Figure 12.8) and the presence of epicuticular wax (Figure 12.7).

Specimens examined

CAPE.—3418 (Simonstown): Cape Peninsula, Chapman's Peak (-AB), *Esterhuysen* 34039. 3419 (Caledon): Olifantsberg, Hermanus (-AD), *Ellis* 4669, 4670, *Esterhuysen* 31039.

Discussion

The leaf anatomy of subsp. *uniflora* appears to be intermediate between that of the Setacea group and some of the other groups of the genus *Ehrharta*. This contention is supported by the epidermal zonation with abaxial stomata, the presence of epicuticular wax, the absence of raised silica bodies, the tapering microhairs and the less compact mesophyll tissue. These features are all characteristic of the Setacea group and subsp. *uniflora* differs from the other taxa in this group in all these attributes which tend toward the condition found in several of the other infrageneric groupings in *Ehrharta*.

The leaf anatomy of subsp. *uniflora* is very similar indeed to that of *Ellis* 4653, an atypical subsp. *scabra* specimen (Figure 10). *Ellis* 4653 is a much more robust plant with wider leaf blades than any subsp. *uniflora* specimen. This is not reflected in the leaf anatomy, however, and leaf thickness and epidermal cell size are comparable. Only the width of the lamina is different. It appears that the loss of the setaceous, acicular type of leaf results in a very similar anatomy, irrespective of which subspecies this occurs in. The development of abaxial stomata appears to be the most significant change and it is associated with several other anatomical features such as the zonation of the epidermis and the presence of an extensive air-space system accompanied by less compact mesophyll. The loss of the Setacea type of silica body and the possession of tapering microhairs is not explained by the development of abaxial stomata, however, and they appear to be additional differences not linked to the presence of these stomata.

Subsp. *uniflora* grows at very low altitudes, from 10–500m (Gibbs Russell 1984) and this is a possible reason for the development of these abaxial stomata. Temperatures are less extreme at these lower altitudes with an equable maritime climate and the nutritional status of the soil is considerably better than the leached soils at higher altitudes. More material of subsp. *uniflora* is required to gain a better understanding of the interrelationships of these taxa.

E. setacea Nees subsp. *disticha* Gibbs Russell

Transverse section

No fresh material of this taxon was available for anatomical study and, consequently, the transectional anatomy was not examined.

Abaxial epidermis

The epidermal structure is very similar to that described for subsp. *uniflora*, with stomatal files and

clearly differentiated costal and intercostal zones (Figures 13.1; 13.2). Intercostal hooks are absent and the intercostal silica bodies appear to be of the raised type typical of the Setacea group but they are associated with cork cells (Figure 13.2). Microhairs are common and appear to be longer than the type usually found in this group (Figure 13.2).

Specimens examined

CAPE.—3419 (Caledon): Caledon Distr., Vogelgat (-AD), *Williams* 3086.

Discussion

The epidermal anatomy of subsp. *disticha* is virtually identical to that of subsp. *uniflora* and it is predicted that the leaf anatomy of these two taxa will also be very similar. This supports their classification as subspecies of the same species (Gibbs Russell 1984). Freshly fixed material for anatomical study is required to confirm the prediction.

DISCUSSION

The leaf anatomy of several species of *Ehrharta* has been studied by various authors (Metcalf 1960; Jacques Felix 1962; Renvoize 1985) but none of these studies, except those of Tateoka (1963) dealt with any representatives of the Setacea group. Tateoka (1963) included four species of this group but did not notice any arm cells. Consequently, the unique anatomy of this most interesting group has received very little attention. If the presence of these arm cells had been reported earlier, it is certain that it would have had a profound influence on the classification of the genus in the Poaceae. On the evidence of spikelet morphology and embryo anatomy (Reeder 1957, 1962) *Ehrharta* has been placed in the Oryzaceae (Stebbins & Crampton 1961). However, the leaf blade anatomy of the representatives studied to date showed no affinity with the Bambusoideae (Tateoka 1963). The genus has therefore been retained in the Arundinoideae, with which it conforms in leaf anatomy (Renvoize 1981). Awareness of the arm cells in the Setacea group would undoubtedly have strengthened the argument for retention of the genus in the Bambusoideae.

For these reasons it is regrettable that the detailed and comprehensive study of the genus by Engelbrecht (1956) was never published. In this thesis, 26 species of *Ehrharta* were studied in detail and their structure interpreted with considerable insight. Unfortunately, this work has remained virtually unknown and has not been considered in the taxonomy of the genus to date.

Engelbrecht (1956) observed wall invaginations in all members of the Setacea group except *E. setacea* subsp. *scabra* and subsp. *disticha* which were not examined by him. In addition, he reported the presence of arm cell-like invaginations in *E. rehmannii*, *E. ramosa*, *E. subspicata*, *E. gigantea* and *E. villosa*. These latter observations are not substantiated by the present study (Gibbs Russell 1987) and will be discussed fully in a later paper. Engelbrecht (1956) used the possession of these arm cells to divide the genus into two distinct groups of species. The group with arm cells was further subdivided into those without dumbbell-shaped silica bodies (the Setacea group) and those with dumbbell-shaped silica bodies (the Villosa and Ramosa groups). His circumscription of the Setacea group is, therefore, identical to the conclusions of the present study and it is

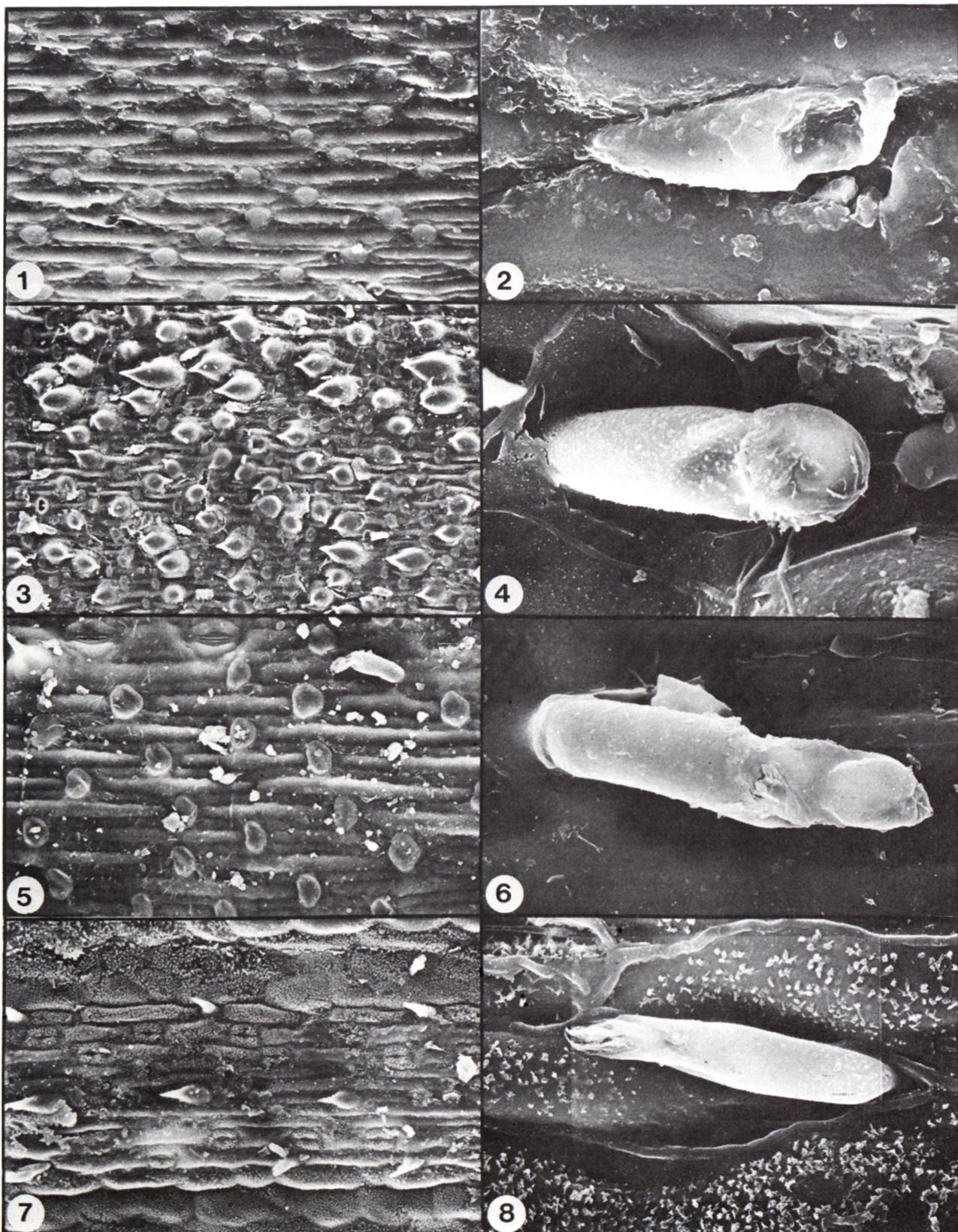


FIGURE 12.—Scanning electron micrographs of the abaxial epidermis of *Ehrharta setacea*. 1–2, *E. setacea* subsp. *setacea*, Ellis 4679: 1, all intercostal long cells interspaced by single, raised and rounded silica body, $\times 200$; 2, microhair with distal cell collapsed, $\times 1000$. 3–6, *E. setacea* subsp. *scabra*. 3–4, Ellis 4652: 3, prickles and asperites separating individual long cells, $\times 60$; 4, microhair with short, inflated distal cell, $\times 1000$. 5–6, Ellis 4653: 5, epidermis with few prickles, long cells separated by silica bodies and stomatal files present, $\times 200$; 6, microhair with slightly elongated distal cell, $\times 1000$. 7–8, *E. setacea* subsp. *uniflora*, Ellis 4670: 7, clear zonation with stomatal files and mid-intercostal long cells slightly inflated, $\times 100$; 8, microhair with tapering distal cell, $\times 1000$.

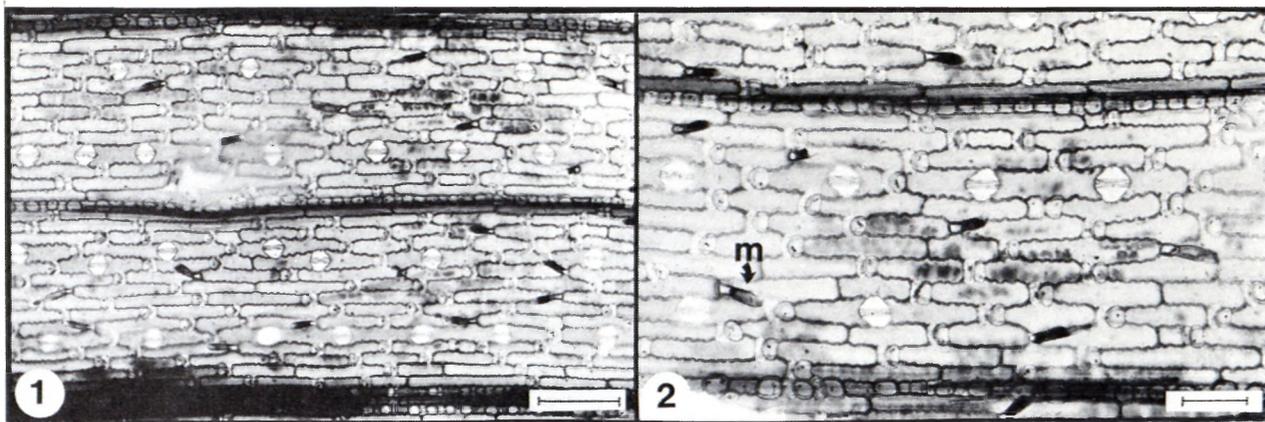


FIGURE 13.—Abaxial epidermis of *Ehrharta setacea* subsp. *disticha*, Williams 3086. 1, clearly differentiated costal and intercostal zones, scale = 10 μm ; 2, intercostal zones with microhairs (m) and stomata, scale = 10 μm .

truly unfortunate that these valuable observations have had to wait over 30 years before being confirmed and published.

Tateoka (1963), on the other hand, also examined the leaf anatomy of several representatives of the Setacea group (*E. dodii*, *E. rupestris*, *E. setacea* and *E. trico-stata*) but reported that 'the mesophyll cells do not seem to have an arm (a projection of cell membranes), as far as the present author can observe'. The fact that no *Ehrharta* species were seen to possess arm cells or complex midrib vasculature was used by Tateoka (1963) to convincingly argue the case for the phylogenetic separation of the Ehrharteae and Oryzeae into different tribes and subfamilies. If he had been aware of the arm cells in the Setacea group, this reasoning would not have been nearly so sound and would probably never have been propounded.

The present paper proves beyond doubt, with substantiating photographic evidence, that arm cells, comparable to those in most Oryzeae, occur in some of the taxa of the Setacea group, *E. setacea* subsp. *scabra* in particular. These invaginations, together with chlorenchyma cell size, appear to become progressively reduced in most of the other taxa and are difficult to observe, even in freshly fixed, fully hydrated material. In reconstituted dried material the invaginations are apparently easier to see (Engelbrecht 1956) but may be overlooked as being artefacts due to dehydration and subsequent wall shrinkage.

The Setacea group of species is obviously a closely related unit with very uniform leaf anatomy. The degree of modification of the arm cells which appears to have occurred in the different taxa of the group is, consequently, most unexpected. Two entirely different types of modification appear to have taken place which deviate from the *E. setacea* subsp. *scabra* condition. *E. setacea* subsp. *uniflora* from lower altitudes with more equable climates and possibly higher levels of soil nutrients seems to have developed a diffuse mesophyll with an extensive air space system associated with the possession of abaxial stomata. No invaginations are evident in the chlorenchyma cell walls of taxa with this type of mesophyll and all intermediate stages can be distinguished. Taxa from the opposite type of habitat, from high altitudes with extremes of temperature and a low level of soil nutrients, on the other hand, have a very different type of leaf anatomy which appears to be derived from

the basic subsp. *scabra* anatomy. This type of anatomy is probably linked to the perennial nature of these leaves and is characterized by the mesophyll cells becoming increasingly reduced in size until they are small, straight-walled and isodiametric with a corresponding almost total reduction in the air space system. This anatomical type is always associated with a setaceous type of leaf and with the absence of stomata. A clear reduction series is evident in *E. rupestris* and these two very different mesophyll structures can possibly be interpreted as different derivations of the *E. setacea* subsp. *scabra* type of anatomy. It may be relevant to this argument that *E. setacea* subsp. *scabra* itself is limited to the east of the range of most of the taxa of the Setacea group where summer rainfall becomes a significant factor. It can be postulated that the loss of the arm cell invaginations may be an adaptation to winter rainfall.

These two different anatomical types in the Setacea group mirror the situation prevailing in many of the Danthonieae of the Cape Fynbos region. Taxa from high altitudes, such as *Merxmuellera*, *Pseudopentameris* and *Pentameris* (Ellis 1980, 1985a,b,c), resemble the latter type, whereas species from the lowland Fynbos areas, such as some species of *Plagiochloa* and *Lasiachloa*, have a more diffuse type of mesophyll. It appears, therefore, that habitat has been more significant than phylogenetic relationships in the evolution of these anatomical features of the leaf blades in many Cape Fynbos grass taxa.

The fact that the typical arm cell type in the mesophyll of *E. setacea* subsp. *scabra* appears to be modified so easily suggests that caution must be exercised in attaching too much taxonomic significance to the presence of this single character. Watson *et al.* (1985) discuss the occurrence of arm cells in the family. They rightly consider them to be a feature of high taxonomic value but point out that they can occur sporadically in distant, unrelated groups. No satisfactory explanation can be given for this type of distribution. The presence of arm cells in the Setacea group of *Ehrharta* does not necessarily imply bambusoid affinities, particularly as they are not accompanied by fusoids and complex midrib vasculature. Rather, arundinoid links are suggested by the type of mesophyll seen in *E. setacea* subsp. *setacea* (Tateoka 1963) and perhaps the arundinoid type of leaf anatomy could have been derived in a similar manner to that described in the Setacea group of *Ehrharta* from a primitive bambusoid-like ancestor possessing arm cells. The

Setacea group, therefore, can be viewed as a primitive arundinoid type exhibiting some links to the peripheral groups of the bambusoids.

CONCLUSIONS

In both leaf anatomy and spikelet morphology the Setacea group differs more from all the other groups of *Ehrharta* than any of these differ from each other. Apart from arm cells, many other anatomical characters separate the Setacea group from the other groups (Gibbs Russell & Ellis 1987). Examples are microhair and silica body shape. Furthermore no anatomical intermediates were found linking this group to any of the other equivalent groups of *Ehrharta*. These other groups, on the other hand, are sometimes linked by intermediate specimens or taxa. This suggests that the Setacea group may deserve separate subgeneric or generic status but consideration of the generic and infrageneric classification of *Ehrharta* will be dealt with in the last of this series of papers.

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