Bothalia 17,1: 51–65 (1987)

Species groups in the genus *Ehrharta* (Poaceae) in southern Africa

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Keywords: anatomy, *Ehrharta*, morphology, Poaceae, southern Africa, taxonomy

ABSTRACT

Ehrharta Thunb. is a genus of Gondwanaland distribution with its centre of diversity in the winter rainfall Fynbos Biome of southern Africa. In recent subfamily treatments *Ehrharta* has proved difficult to place satisfactorily, and during the past five years it has been moved between Bambusoideae and Arundinoideae. However, most previous systematic studies using cryptic characters have covered only four taxa out of about 35. The present study includes all African taxa, and demarcates seven species groups on the basis of both spikelet morphology and leaf blade anatomy. Parallelism and/or convergence in vegetative macromorphology within and between the species groups is widespread, and is similar, in some cases, to adaptations found in other plant families in the Fynbos Biome. However, these macromorphological trends are not reflected in the leaf anatomy. Leaf anatomy is generally consistent with the spikelet morphology. Some anatomical differences between the species groups in *Ehrharta* appear to be as great as differences between taxa of much higher ranks elsewhere in the Poaceae. This wide range of variability may be related to an early divergence of Ehrharteae from other grasses, as suggested by the Gondwanaland distribution, and may explain the difficulty of placing this fascinating yet baffling genus in a subfamily.

UITTREKSEL

Ehrharta is 'n genus van Gondwanaland-verspreiding met sy middelpunt van verskeidenheid in die winterreënval-Fynbosbioom van suidelike Afrika. In onlangse subfamilie-behandelings is dit moeilik gevind om *Ehrharta* bevredigend te plaas, en gedurende die afgelope vyf jaar is dit oor en weer in Bambusoideae en Arundinoideae geplaas. Die meeste vorige sistematiese ondersoeke waarin verskuilde kenmerke gebruik is, het slegs vier taksons uit ongeveer 35 gedek. Die onderhawige ondersoek sluit al die Afrika-taksons in, en baken sewe spesiegroepe af op grond van die morfologie van die blompakkie en die anatomie van die blaarskyf. Parallelisme en/of konvergensie in vegetatiewe makromorfologie binne en tussen spesiegroepe is wydverspreid en is in sommige gevalle soortgelyk aan aanpassings wat by ander plantfamilies in die Fynbosbioom aangetref word. Hierdie makromorfologiese neigings word nie in die blaaranatomie weerspieël nie. Blaaranatomie is oor die algemeen in ooreenstemming met die morfologie van die blompakkie. Sommige anatomiese verskille tussen die spesiegroepe in *Ehrharta* blyk net so groot te wees soos verskille tussen taksons van 'n veel hoër rang elders in die Poaceae. Hierdie wye verskeidenheid mag verband hou met 'n vroeë divergensie van Ehrharteae vanaf ander grasse, soos aangedui deur die Gondwanaland-verspreiding, en mag 'n verklaring bied waarom hierdie bekorende maar raaiselagtige genus moeilik in 'n subfamilie geplaas kan word.

CONTENTS

INTRODUCTION

In the most recent treatment (Willemse 1982), the tribe Ehrharteae Nevski (1937) consists of only a single genus, *Ehrharta* Thunb. (1779) which includes the genera *Microlaena* R. Br., *Petriella* Zotov and *Tetrarhena* R. Br. Its distribution area in southern Africa, southwestern, southern and eastern Australia, Tasmania, New Zealand and Malesia falls within the cool-temperate Gondwanaland region (Figure 1). The centre of diversity for the genus is the winter rainfall Cape Floristic Region (Goldblatt 1978) or Fynbos Biome (Rutherford & Westfall 1986) of southern Africa, with about 35 taxa, the other 10 taxa being distributed unevenly elsewhere in the range of the genus. In southern Africa, *Ehrharta* can be divided into seven species groups demarcated on the basis of both spikelet morphology and leaf blade anatomy.

An understanding of the variation within *Ehrharta* in southern Africa is necessary, not only to improve the classification of the local taxa, but also to show the relationships between the bulk of the genus in southern Africa and its representatives in other Gondwanaland

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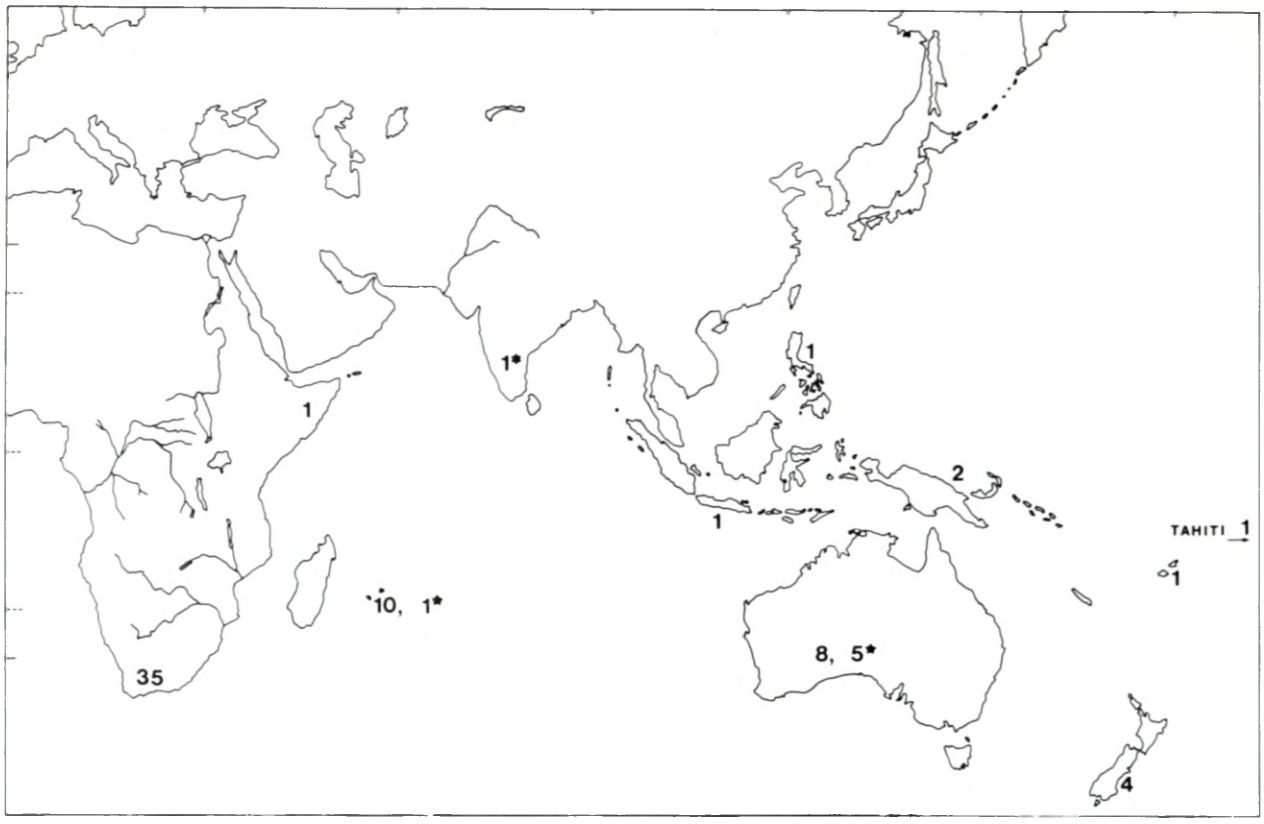


FIGURE 1.—Worldwide distribution of *Ehrharta*, showing the number of species and infraspecific taxa reported for various areas. The number of southern African species naturalized in India and Australia are indicated with an asterisk.

regions. *Ehrharta* may therefore serve as an additional plant group to indicate the floristic history of the Gondwanaland continents, and is the first representative of the Poaceae with this potential to be studied with this aim.

Additional information on *Ehrharta* is required because its position within the Poaceae is not yet settled. Since the time of Bentham & Hooker (1883), the group has been shuffled between the Phalarideae and the Oryzeae of the Pooideae (Festucoideae), the Ehrharteae and Arundineae of the Arundinoideae, the Ehrharteae of the Oryzoideae, and the Ehrharteae and the Oryzanae of the Bambusoideae. Modern studies based on cryptic characters such as leaf anatomy, chromosomes and embryo types have enabled most grass tribes to be clearly placed in one of about five subfamilies, but there is still no general agreement regarding the affinities of the Ehrharteae. Prat (1960) and Clifford & Watson (1977) place the tribe in an unclassified residue that does not fit neatly into any of the modern subfamilial concepts of the Poaceae. Most recently, Ehrharteae has been removed from the Arundinoideae (Renvoize 1981) to the Bambusoideae (Renvoize 1985; Watson *et al.* 1985).

The instability of the higher classification of the Ehrharteae may be partly a result of the high degree of variation in its anatomical characters. Differences between species and species groups in the southern African species appear to be as great as differences between taxa of much higher rank elsewhere in the Poaceae. Overseas workers who have examined only a few taxa may have erroneously concluded that they are representative of the entire genus or tribe. This wide range of variability may be a result of the early divergence of the Ehrharteae from other grasses, as suggested by the ancient Gondwanaland distribution pattern.

The representatives of *Ehrharta* in southern Africa may help to provide a better understanding both of the history of the flowering plants and of the early evolution of the Poaceae. They will therefore be treated in some detail. We propose to set out the species groups informally in this introductory paper, and thereafter to publish a parallel series of papers covering the taxonomy and anatomy of each species group. A concluding paper will present a formal generic and infrageneric classification and will develop hypotheses about the phylogeny of the species groups, and their phytogeographical significance.

MATERIALS AND METHODS

For the morphological investigations, herbarium specimens were examined from BOL, JF, K, NBG, PRE, SAM and STE. The PRE material includes the anatomical voucher specimens of Ellis, described below. Field observations were made for about 30 of the taxa. Spikelets were dissected without special preparation, and were observed with a dissecting microscope.

For the anatomical investigations, specimens of *Ehrharta* plants were collected in the field throughout South Africa during the period 1974 to 1984. A total of 160 specimens were collected representing most of the taxa recognized in this genus. This sample was designed to incorporate considerable morphological and geographical variation in many taxa. Herbarium voucher specimens were prepared for identification by the National Herbarium (PRE) after segments of leaf blade material had been removed and fixed in FAA (Johansen 1940).

Transverse sections, 10 μm thick, were prepared after desilicification in 30% hydrofluoric acid (Breakwell

1914), dehydration using the method of Feder & O'Brien (1968) and infiltration and embedding in Tissue Prep (Fisher Scientific). The sections were stained in safranin and fast green (Johansen 1940). The manual scraping method of Metcalfe (1960) was used to prepare scrapes of the abaxial epidermis. These were either double-stained in methylene blue and ruthenium red or only in safranin. The anatomical detail was recorded photographically using a Reicherdt Univar microscope and Ilford Pan F film (ASA 50).

The material fixed in FAA was also used for ultrastructural studies with a scanning electron microscope. The leaf blade segments were dehydrated in 2,2-dimethoxypropane (Merck) for 2 hours and then placed in 100% acetone for 5 minutes following the method described by Neumann, Rushing & Mueller (1982). The material was critical point dried with liquid CO_2 at 85 atmospheres at 40° C after which it was mounted on aluminium stubs with double sided tape. It was then glow discharge coated with a thin (± 400 A°) layer of metallic gold in a sputter coater. Preparations were either stored in a dessicator with silica gel or observed directly with an ISI SX-25 scanning electron microscope operated at 25 Kv accelerating voltage. Cuticular structure was photographed with a 6 × 7 cm camera on Ilford FP4 120 film at varying magnification.

HISTORICAL BACKGROUND

The classification of Ehrharta *within the Poaceae*

The placement of *Ehrharta* in the grass family has varied at both the tribal and subfamilial level (Table 1). Most older systems, based only on spikelet morphology, place *Ehrharta* in Phalarideae because of the two sterile florets below the single fertile floret. Modern treatments based on a number of cryptic characters place the genus in a tribe of its own, Ehrharteae. Although first distinguished as an entity by Link (1827), his authorship of the name cannot be accepted for nomenclatural reasons (Willemse 1982). Thus, Nevski (1937) is the recognized author for Ehrharteae, which was also described in error as new by Tateoka (1957). Nees (1841), in the earliest treatment of southern African grasses that adopted a suprageneric classification, placed *Ehrharta* in the Oryzeae, although Trinius (1839), working in co-operation with Nees, had earlier placed it in the Phalarideae, where it remained until the modern system of Stebbins & Crampton (1961), who placed the tribe back into the Oryzoideae.

Although there is now agreement on tribal composition, the question of subfamily classification is not yet settled. The most recent treatments include Ehrharteae in Bambusoideae (Renvoize 1985; Watson *et al.* 1985), but both discuss the difficulty of including Ehrharteae in the subfamily as they constitute it. Renvoize (1985) states that there is no clear correlation between anatomical and other characters, such as embryo type and lodicules, and Watson *et al.* (1985) indicate that, although they decided to treat the group as bambusoid, other numerical analyses either place it as arundinoid or lose it altogether. Soderstrom & Ellis (in prep.), who classify bambusoid genera and allies, place the Ehrharteae outside the Bambusoideae, closer to Arundinoideae.

This confused situation may be explained partly because, as Table 1 indicates, the modern subfamily classifications are based on a very small set of data derived from only a few species. In this century, only Tateoka (1963) has examined more than three taxa, and only four taxa in all have been examined either for chromosomes, embryos or leaf blade anatomy. The detailed study of the southern African taxa of *Ehrharta* presented in this and following papers should provide the breadth of information needed to indicate the natural affinities of this fascinating but baffling genus.

The southern African species of Ehrharta

The study of African *Ehrharta* falls into three phases, which correspond roughly to the 18th, 19th and 20th centuries. The earliest phase was characterized by the description of species in four different genera. L. C. M. Richard (1779) described *Trochera striata*, and a few months later Thunberg (1779) described *Ehrharta capensis*. These names were based on different types but represent the same taxon. Soon after, Linnaeus (1791) described two more species, but placed them in the genus *Aira*. Lamarck (1786), J. E. Smith (1789, 1790) and J. F. Gmelin (1791) each described species in Thunberg's genus *Ehrharta*. However, Thunberg himself (1794) accounted for his specimens collected from the Cape in *Melica*, so that his *Prodromus plantarum capensium* treatment comprised two genuine *Melica* species and four species of *Ehrharta*.

The second phase, one of consolidation, began in the next century with Swartz's (1802) thorough and beautifully illustrated study of the genus, in which he recognized nine species, each with synonyms. He described no new taxa, but moved Thunberg's 'Melicas' to *Ehrharta*. He was aware of, but did not take up, *Trochera* as the name for the genus. He also did not always follow priority of publication in applying the specific epithets, although his synonymy within each species is otherwise sound. Palisot de Beauvois (1812) alone took up the name *Trochera*, to which he attributed two species.

Schrader (1821) covered 17 species, including all those in Swartz's (1802) treatment as well as eight new species that were based on the specimens of Hesse. He was the first to divide the genus into sections, distinguishing two entities on the character of bulbous *versus* fibrous 'roots'. Although published two years later, Thunberg's (1823) *Flora capensis* treatment was merely a summary of Swartz (1802), and did not include Schrader's species. During this period of consolidation, a few new species were described by Kunth (1829), by Schultes (1830) and by Steudel (1853).

Most ambitious of the nineteenth-century studies of *Ehrharta* were those of Nees ab Esenbeck (1832, 1839, 1841). His *Florae Africae Australioris* (1841) recognized 25 species, of which nine were described by him, using collections of Drège and Ecklon. Nees also put forward a multitude of varieties (nine in *E. calycina* alone), which, however were not validly published because he did not consistently apply Articles 24–27 of the *ICBN* (Linder 1985). He adopted Schrader's basic division of the genus by 'root' type, and in addition subdivided the fibrous-rooted species according to size and hairiness of the sterile lemmas. These subdivisions are

TABLE 1.—Subfamily and tribal classifications of *Ehrharta* by various authors

Treatment	Subfamily or series	Tribe	Characters emphasized	Taxa examined
Nees (1841) also Steudel (1855)		Oryzeae	Spikelet 1-flowered; Stamens 6	25 species
Bentham (1883) also Stapf (1900, 1917) Hackel (1887) Hubbard (1973)	Poaceae	Phalarideae	Spikelet deciduous above glumes; bisexual flower 1, terminal	*E. longiflora*
Avdulov (1931)	Series B (= Festucoid)	Oryzeae	Chromosomes	*E. erecta*
Pilger (1954)	Festucoideae	Phalarideae	Numerous spikelet and cryptic characters	Not stated
Reeder (1957)	'Oryzoid-Olyroid type'		Embryos	1 species, not named
Tateoka (1957, 1963)	Arundinoideae	Ehrharteae	Leaf blade anatomy	19 species
Prat (1960)	'*Genre a position discutée*'			
Metcalfe (1960)	'Intermediate between panicoid and festucoid'		Leaf blade anatomy	*E. erecta* *E. villosa* var. *maxima*
Stebbins & Crampton (1961)	Oryzoideae	Ehrharteae	Not stated	Not stated
Jacques-Felix (1962)	Ehrhartoideae	Ehrharteae	Spikelets, chromosomes, leaf blade anatomy	*E. erecta* *E. calycina*
Clayton (1970)	(Bambusoid)	Ehrharteae	Embryo	*E. erecta*
Clifford & Watson (1977)	Undefined residue		300 spikelet, morphological and cryptic characters	Not stated
Renvoize (1981)	Arundinoideae	Ehrharteae	Leaf blade anatomy	Not stated
Renvoize (1985)	Bambusoideae	Ehrharteae	Leaf blade anatomy	*E. calycina* *E. erecta* *E. dura*
Watson *et al.* (1985)	Bambusoideae (Oryzanae)		300 spikelet, morphological and cryptic characters	Not stated

still recognized, although a number of the species have been re-aligned.

The last of the comprehensive nineteenth-century accounts of *Ehrharta* was that of Steudel (1853). He compiled the species known at that time, 32 in all for southern Africa. Of greatest significance is his basic division of these species into two groups, not by the possession of a bulbous base, as previously, but by the separation of *E. setacea* and *E. rupestris* into a group ('Racemosae') distinct from the rest of the species ('Paniculatae'). It is unfortunate that he did not elaborate on the characters on which he based his decision, because this fundamental division in *Ehrharta* is supported by the present study. After 1855, no further work was done in the genus except that Kuntze (1891), rediscovering the priority of the genus name *Trochera*, transferred all the then-accepted taxa to *Trochera*.

The third phase in the taxonomic study of *Ehrharta* has been dominated by Stapf's (1900) *Flora capensis* treatment, which is the most recent critical study of the southern African taxa. He also recognized 25 species, of which six were newly described by him, and he placed a number of previously recognized species into synonymy. Chippindall (1955) adopted Stapf's concepts, only making changes in the keys and stressing close relationships between some of Stapf's taxa. She included a new species of C. E. Hubbard (1933), but omitted that of Mez (1921). Since 1955, new taxa have been described by Launert (1961) and Gibbs Russell (1984a, 1984b).

Stapf did not follow Kuntze (1891) in taking up the name *Trochera*, and soon after the conservation of generic names was permitted, *Ehrharta* of Thunberg was conserved over *Trochera* of L. C. M. Richard, which was rejected in ICBN (Voss *et al.* 1983).

TAXONOMIC CHARACTERS

The taxa described by previous workers can be grouped into seven easily recognizable groups on the basis of morphological and anatomical characters as shown in Table 2. A brief discussion of those characters found to be useful in this regard follows.

Morphological characters

1. Macromorphological characters

For a genus of moderate size, *Ehrharta* has a wide range of macromorphological characters, a selection of which are shown in Table 2. They are reasonably well known, from the detailed descriptions of Stapf (1900) and the briefer but more image-creating descriptions of Chippindall (1955). However, unless the species are placed in groups based on spikelet morphology and leaf blade anatomy, the diversity of vegetative characters is confusing. With these groupings, it can be seen that

TABLE 2.—Morphological and anatomical characters used to differentiate species groups in *Ehrharta*. Each group is referred to by the name of a widespread species that exhibits the characters of the group

	Setacea							Capensis							Erecta					Calycina							Villosa			Ramosa				Dura	
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35
MORPHOLOGY																																			
1. HABIT:																																			
Annual (A)															A	(A)	(A)	(A)	A		A	A	A		A										
Perennial (P)	P	P	P	P	P	P	P	P	P	P	P	P	P	P		P	P	P		P				P		P	P	P	P	P	P	P	P	P	P
2. CULMS:																																			
Suffrutescent (S)	S		S	S		S	S							S													S	S	S	S					
Herbaceous (H)		H	(H)		H			H	H	H	H	H	H		H	H	H	H	H	H	H	H	H	H	H	H					H	H	H	H	H
3. INTERNODES BULBOUS (B)								B	B	B	B	B	B														(B)			(B)			(B)		
4. LEAF LIGULES:																																			
Glabrous (G), Ciliate (H)	H	H	H	H	H	H	H	H	H	H	H	H	H	H	G	G	G	G	G	H	G	G	G	H	G	G	H	H	H	H	H	H	H	G	G
5. LEAF BLADES:																																			
Setaceous, rolled, folded (S)	S		S	S		S	S	S																			S	S	S	S	S	S	S		S
Reduced or absent (R)														(R)													R	R	R	R					
6. SPIKELET NUMBER	4–8	1–2	5–9	5–15	1–4	5–17	1–2	∞	∞	∞	∞	∞	<35	<40	∞	∞	∞	∞	∞	∞	∞	∞	∞	∞	∞	∞	∞	∞	∞	<40	<40	<20	1–5	∞	∞
7. SPIKELET LENGTH (mm)	4–6	4–5	4–6	6–8	4–7	7–8	4–5	10–12	8–10	7–12	7–10	7–10	9–13	10–13	4–12	3–4	4–5	5–8	2–4	3–5	2–3	3–5	2–3	4–9	5–9	3–4	10–14	11–14	14–18	6–9	6–8	7–8	5–7	13–15	9–17
8. GLUME/SPIKELET LENGTH	⅓	⅓	⅓	⅔–≅[7]	≅	⅔–¾	≅	½–⅔	½–⅔	⅓–½	½	½	⅓	⅔–¾	⅓	½–⅔	½–⅔	½–⅔	½	>	⅔–¾	≅	≅	⅔–≅	≅	≅	½–¾	¾	≅	≅	⅔–≅	≅	>	⅓–½	⅓–½
9. 1st STERILE LEMMA:																																			
Reduced (R), ≅ 2nd st. lemma (2)	R	R	R	R	R	R	R	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2
10. 2nd STERILE BASE:																																			
Constricted (C)										C	C	C			C	C	C	C	C		C	C			C										
Stipitate (S)								S	S	(S)	S	S	S	(S)	S											S	S	S	S							
Appendages (A)																				A	A	A	A	A	A	A				A	A	A	A		
11. STERILE LEMMA TEXTURE:																																			
Smooth (S)															(S)	S				S		S	S	S	S	S	S	S	S						
Rough (R)	R	R	R	R	R	R	R	R	R	R	R	R	R	R	R		R	R	R		R									R	R	R	R	R	R
12. STERILE LEMMA SIDES:																																			
Glabrous (G)	G	G	G	G	G	G	G	G	G	G	G	G	G	G	G	G	G	G	G	G	G					G				G	G	G	G	G	G
Hairy (H)																						H	H	H	H		H	H	H		(H)				
13. STERILE LEMMA BASES:																																			
Glabrous (G), Bearded (B)	G	G	G	G	G	G	G	B	B	B	B	B	B	B	B	G	B	B	G	G	G	?	?	?	?	G	B	B	B	B	B	B	B	B	B
14. STERILE LEMMA TIPS:																																			
Mucronate (M), Awned (A)								M		M	M	M	M	M	A				A		M	M		M	A		M	M	M				A	A
LEAF ANATOMY								Longi-folia		Capensis																									
1. MIDRIB AND KEEL:																																			
Keel absent (A)	A	A	A	A	A	A	*	*	A					A						A		A	A	A	A	A	A	A	A	A	A	A	A	A	*
Keel present (P)										P	P	*	*		P	P	P	*	P		P			P											
2. ADAXIAL RIBS:																																			
Absent (A)										A	A	*	*	A		(A)														A	A	A	A		
Slight (S), Large (L), Massive (M)	L	L	L	L	L	L	*	*	M						S	S	S	*	S	S		A	(S)	S	(A) S,L	S	S,L	S,L	S,L	S,L	(S)	(S)	(S)	L	*
3. MESOPHYLL:																																			
Arm cells (A)	A	A	A		A	A	*																												
Compact isodiametric (B)				B																										(B)	B	(B)	B		
Compact angular (C)								*	C	C	C	*	*	C						C		C	C	C	C	C	C	C	C		C		C	C	*
Diffuse irregular (I)															I	I	I	*	I		I														
4. EPIDERMAL ZONATION:																																			
Differentiated (D)					(D)		(D)			D	D	*	*	D	D	D	D	*	D	D	D	D	D	D	D	D	D	D	D	D	D	D	D	D	D
Undifferentiated (U)	U	U	U	U	U	U	U	*	U																										
5. INTERCOSTAL LONG CELLS:																																			
Hexagonal length (μ)	<10	<10	<10	<10	<10	<10	<10	*	<10	10–20	10–20	*	10–20	10–20	>20	>20	>20	*	>20	10–20	>20	>20	>20	>20	>20	>20				10–20					
Rectangular (R)																											R	R	R	R	R	R	R	R	R
Sinuous walls (S)	S	S	S	S	S	S	S	*	S	S	S	*	S	S										(S)			S	S	S	S	S	S	S	S	S
Straight walls (W)													(W)	(W)	W	W	W	*	W	W	W	W	W	W	W	W									
6. STOMATA:																																			
Absent (A)	A	A	A	A		A		*	A																										
Wax bodies present (P), absent (X)					X		X			P	P	*	*	*	P	P	P	*	*	*	P	P	P	P	*	P	X	X	X	X	*	X	X	P	*
Epidermal flanges (E)																											E	E	E						
7. SILICA BODIES:																																			
Paired (P), Short rows (S)	P	P	P	P	P	P	P	*	P	P	P	*	P	P	S	S	S	*	S	S	S	S	S	S	S	S	P	P	P	P	P	P	P	P	*
Rounded (R) Dumbell (D)	R	R	R	R	R	R	R	*	R	D	D	*	D	D	D	D	D	*	D	D	D	D	D	D	D	D	R	R	R	R	D	D	R	R	*
8. PRICKLES:																																			
Hook-like (H), Macrohair-like (M)	H	H	H	H	H	H	H	*		H	H	*	M	M	M	M	M	*	H,M	M	H,M	H,M	H,M	H,M	H	M	H			H	H	H	H	H	*
9. MICROHAIRS:																																			
Distal cell truncated (X), not tapering (Y), tapering (Z)	X	X	X	X	Y	X	X	*		Z	Z	*	*	Z	Z	Z	Z	*	Z	*	Z	Z	Z	Z	*	Z	Z	*	*	Y	Y	Y	Y	Y	*
10. EPICUTICULAR WAX:																																			
Present (P), Absent (A)	P	P	P	A	P	A	*	*	A	P	P	*	*	P	P	P	P	*	P	*	P	P	P	P	*	P	P	*	*	P	P	P	P	P	*

The species and infraspecific taxa in each group are indicated by number, as follows: 1, *E. rupestris* subsp. *rupestris*; 2, *E. rupestris* subsp. *dodii*; 3, *E. rupestris* subsp. *tricostata*; 4, *E. setacea* subsp. *setacea*; 5, *E. setacea* subsp. *uniflora*; 6, *E. setacea* subsp. *scabra*; 7, *E. setacea* subsp. *disticha*; 8, *E. longifolia*; 9, *E. ottonis*; 10, *E. capensis* var. *capensis*; 11, *E. capensis* var. *intermedia*; 12, *E. bulbosa*; 13, *E. eburnea*; 14, *E. barbinodis*; 15, *E. longiflora*; 16, *E. erecta* var. *erecta*; 17, *E. erecta* var. *natalensis*; 18, *E. erecta* var. *abyssinica*; 19, *E. triandra*; 20, *E. longigluma*; 21, *E. delicatula*; 22, *E. brevifolia* var. *cuspidata*; 23, *E. brevifolia* var. *brevifolia*; 24, *E. calycina*; 25, *E. pusilla*; 26, *E. melicoides*; 27, *E. gigantea*; 28, *E. villosa* var. *villosa*; 29, *E. villosa* var. *maxima*; 30, *E. ramosa*; 31, *E. rehmannii* var. *rehmannii*; 32, *E. subspicata*; 33, *E. rehmannii* var. *filiformis*; 34, *E. microlaena*; 35, *E. dura*.

* anatomical preparations not available.

there are a few parallel trends that occur in several species groups, and that a number of differences in structure are associated with each trend. For example, suffrutescence occurs in four of the species groups (Setacea, Capensis, Gigantea and Ramosa), and involves, in each group, long branched rhizomes, much branched culms that serve as the main photosynthetic organ, and reduction of leaf blades.

a. *Habit* in the majority of *Ehrharta* species is perennial, but several are annual. The annual habit seems related to unpredictable moisture availability. All the annual species, except one, occur in the drier northwestern part of the range of the genus, centred on the Succulent Karoo, from about Clanwilliam north to southern SWA/Namibia. These species fall only in the Erecta and Calycina groups, and each has closely related perennial species in the more mesic central part of the distribution of the genus. The other annual species, *E. longiflora*, grows in seasonally wet places, and it has, for an *Ehrharta*, a wide distribution, occurring not only in arid areas to the northwest, but as far east as Port Alfred. It is the only species in which the spikelet morphology is not consistent with the leaf blade anatomy.

b. *Rhizomes* occur in all perennial species, but the form of the rhizome varies widely, and is correlated with the substrate. Species that grow between rocks have tough, branched, naked rhizomes that are hardly different from the lower part of the culm. These rhizomes can creep for several meters in deep cracks, so that the plant forms a dense linear cushion. Species that occur in sand have long branching rhizomes that run 0,3 m or more below the soil surface and send up culms at the tips, so that a single plant can appear to be a loose colony several meters across. These rhizomes may be naked or densely clothed by hairy cataphylls. Species that grow in clay or loam soils usually have short knotted rhizomes that do not spread far away from the base of the individual plant, although in a few species unbranched rhizomes a few centimeters long and with papery cataphylls may occur.

c. *Culm* characteristics are the most important in determining the overall appearance of a grass plant, and in *Ehrharta* the culms are very diverse. In different taxa the culms vary from solitary to numerous, from herbaceous to wiry or woody, from erect to procumbent, from unbranched to simply or verticillately branched. Length varies between taxa from less than 100 mm to over 1,5 m in flowering individuals.

Taxa in the Capensis groups have the lowest (sometimes the two lowest) internodes modified into an extremely hard cylindrical or globose bulb-like structure. The occurrence of this 'bulb' may be associated with the periodic fires in the fynbos. 'Bulbous' species are much in evidence for a year or two after a fire, but apparently do not occur in long-unburned situations. However, immediately following the next burn, flowering plants may be found with many old dead 'bulbs' hidden underground, indicating that the plant is several years old, having survived the fireless period in this form.

Stolons are known only in a local limestone variant of the widespread species *E. calycina*.

d. *Leaves*, as in other grasses, are composed of sheath, ligule and blade. The sheaths are split to the base and usually cylindrical, or rarely keeled. In some species the upper sheaths may be longer than the internodes, so the leaves are closely imbricate. In suffrutescent species with reduced leaf blades the sheaths may be persistent around the culm, or be held outward at an angle, or they may be lost. The basal sheaths may be persistent, densely clothing the base of the culm, or they may slip away from the culm with age, leaving it exposed. A few taxa may be distinguished by a characteristic colour of the basal sheaths.

The ligules are short, usually less than 3 mm long, and take the form of a ciliate rim in all species groups except the Erecta and Calycina groups, in which most taxa have glabrous ligules.

The leaf blades vary from broad and flat, often with one or both margins with a heavy undulate marginal vein, to folded, rolled, setaceous or absent. Length varies between taxa, from less than 100 mm to over 1 m. Loss or reduction of leaf blades is correlated with suffrutescence. In these taxa, the phenology of leaf blade development should be studied in the field, because it is possible that striking differences in appearance may be due to the age of a plant rather than to genetic differences.

e. *Inflorescences* are most commonly paniculate, but in some taxa may be reduced to a raceme with few spikelets, and there is often a tendency for the narrower inflorescences to be secund. Generally the inflorescence is exserted far above the highest leaf sheath, but in a few taxa (especially annuals) it is closely subtended or even enveloped below by an inflated leaf sheath. In some taxa with racemose inflorescences the main axis curves sinuously around the appressed spikelets.

2. Spikelet morphology

The spikelets are usually laterally compressed, although in some taxa the sides are rounded. At maturity, the spikelet is shed as a unit above the glumes, which are persistent on the pedicel. A spikelet consists of a pair of glumes, two empty sterile lemmas, and, at the tip of the rachis, a fertile floret composed of lemma, palea and bisexual flower. Each species group has a characteristic range of spikelet sizes.

a. *Glumes* are subequal, and may be shorter than, equal to or longer than the whole spikelet, and relative glume length is a useful character for distinguishing between species in a group. The glumes are more papery in texture than the lemmas, and are unornamented.

b. *Sterile lemmas* are the single most striking spikelet feature of *Ehrharta*. Their curious sculpturing in some species is unknown elsewhere in the grass family, and renders a detached spikelet immediately recognizable. Shape, relative size and ornamentation of the sterile lemmas are the most useful characters in separating the species groups. In three of the species groups, Erecta, Calycina and Dura, the tips of the sterile lemmas can have long awns, and in the Capensis and Villosa groups the bases are shortly stipitate. In most Ehrhartas the sterile lemmas are of similar size and the smaller fertile lemma differs from them, but in the Setacea group the first sterile lemma is short and glume-like and the fertile lemma is similar to the second sterile lemma.

The lemma surfaces may be dull or shining, scaberulous or smooth. The sides and margins may be glabrous or have hairs of various lengths, and the bases may be glabrous or bearded. The bases of the second sterile lemma and the fertile lemma come together in a hinge-like joint that resembles an earlobe, and which may have a membranous appendage. All these characteristics are used in separating the species groups. Differences in transverse and longitudinal ribs and veins distinguish species within the groups.

c. *Fertile florets* have a lemma that is smaller and more laterally compressed than the sterile lemmas, and is unornamented. The palea is sickle-shaped or straight, is much smaller then the lemma and is usually hidden within it. The fertile florets of most species are similar, and are not useful for distinguishing species or groups.

d. *Flower* structure is remarkable in *Ehrharta* because of the presence of six stamens in most species, although some of the taxa with small spikelets may have five, four, three or one stamens. The two lodicules are relatively large and flat, and are usually ovate or 2-lobed.

e. *Caryopsis* information for comparison is lacking because of the small number of spikelets that are found to have mature fruits. It appears that the spikelet is shed as soon as the fruit is mature. The lack of this information, as well as data about embryos, is a serious defect in our knowledge of the genus.

Anatomical characters

A suite of leaf blade anatomical characters separate and define the various species groups in *Ehrharta*. These cryptic features are manifested in the leaf blade as seen in transverse section, in the abaxial epidermis in surface view and ultrastructurally (Table 2). Some of these characters distinguishing the species groups recognized in *Ehrharta* are generally considered to be features of high taxonomic value, important at the subfamily level in the Poaceae. In *Ehrharta*, however, they separate taxa below the generic level. Examples are differences in mesophyll structure and microhair shape.

The 10 characters which were scored for all the southern African *Ehrharta* taxa are diagramatically represented in Table 4. This suite of anatomical characters in combination serves to define and diagnose each of the seven species groups as well as two subgroups within one of the groups. The variation encountered in most of the characters in most of the groups will be fully described and discussed in subsequent papers. The character states used to define each of the groups here are, therefore, somewhat generalized and may vary within certain limits and intergrade between certain groups. In the cases where variation was observed, definite lines of development could be traced and the variation could usually be interpreted on this basis.

1. Midrib or keel

The vascular structure of the keel or midrib is an important character in grass taxonomy at the subfamily level. Complex vasculature of the keel would definitely support bambusoid affinities as suggested by many authors. This type of keel does not occur in any of the species groups from South Africa but the presence of only a median vascular bundle or the presence of a definite keel with additional parenchyma tissue differs between the species groups recognized, and only varies within the Calycina group.

2. Ribs and furrows

Adaxial ribs and furrows, particularly the massive ribs of the Longifolia group, distinguish certain groups. The raised, inflated abaxial epidermal cells in the mid-intercostal zones of the Calycina group are diagnostic and of considerable phylogenetic interest because this characteristic is shared with the Phalarideae with which the Ehrharteae has been linked by earlier authors. These epidermal cells are also evident in the epidermis as seen in surface view.

3. Mesophyll

The chlorenchyma cells of *Ehrharta* are surprisingly variable in structure and arrangement. In the Setacea group arm cells definitely are present in some taxa. This is a bambusoid characteristic but is also known in some taxa without bambusoid or oryzoid affinities (Watson *et al.* 1985). In some groups the chlorenchyma cells are compact and angular with minute air spaces but, in other groups this tissue is very diffuse, of irregular, rounded cells with air spaces clearly visible. In the Villosa group the abaxial layer of chlorenchyma is very regular and almost palisade-like.

4. Epidermal zonation

Some groups are distinguished by costal and intercostal zones on the abaxial surface. Zonation is not evident in the Setacea and Longifolia groups and this is associated with an absence of abaxial stomata as observed in these two groups. This lack of zonation appears to be associated with the ecological conditions of the Mountain Fynbos with very low soil nutrition and also occurs in many of the danthonoid grasses from the same habitats. Species from the Lowland Fynbos, on the other hand, have clear epidermal zonation and abaxial stomata. These characters tend to vary in groups which have a wide ecological tolerance and occur in both these two major habitat types.

5. Intercostal long cells

Hexagonal or inflated but rather short long cells with sinuous walls distinguish some groups, whereas others have elongate, fusiform, hexagonal intercostal long cells with straight walls. In the Calycina group with this latter type of long cell, the mid-intercostal cells are much longer than the lateral ones and these cells are also the raised, inflated cells as seen in transverse section. In other groups the intercostal long cells are rectangular with sinuous walls.

6. Abaxial stomata

The stomata of the various species groups of *Ehrharta* are also of taxonomic interest. They may be absent on the abaxial surface, as in the Longifolia group and in many taxa of the Setacea group. In the Capensis group the guard cells are clearly visible but the subsidiary cells are covered with wax platelets, as seen with the scanning electron microscope. In the Erecta group the stomata are often obscured by large, solid wax plugs, whereas, in the Calycina group cubical wax granules often overlie the stomata. In the Villosa group the stomata are sunken and overarched by four characteristic papilla-like flanges from the adjoining long cells. In the Ramosa group the

stomata have no associated wax deposits whereas in the Dura group the pores are obscured by dense accumulations of wax platelets. Stomatal structure, and associated epicuticular wax, therefore, serves to distinguish all but two of the species groups in *Ehrharta* and provides useful characters at the species level. The low dome-shaped subsidiary cells, which are present throughout *Ehrharta*, are typical of, but not exclusive to, the Arundinoideae (Renvoize 1981).

7. Costal silica bodies

The silica bodies of *Ehrharta* are somewhat variable and rather difficult to use as diagnostic characters. Single, rounded, or paired bodies characterize some groups whereas in others this type of body is more dumbbell-shaped. In the Erecta and Calycina groups the costal silica bodies are in short chains and of the dumbbell type but this shape can only be determined by varying the focus. Silica body shape and arrangement is often a character differentiating taxa at higher taxonomic levels than that of genus.

8. Prickles

The costal macrohair-like type of prickle hair is only found in the Erecta and Calycina groups. This type of hair is common in the pooid and bambusoid grasses but is much rarer in the arundinoids. In the other species groups of *Ehrharta*, only shortly barbed prickles occur, except in the Longifolia subgroup of the Capensis group where prickle hairs are absent.

9. Microhairs

Microhairs in *Ehrharta* are very small and difficult to observe with the light microscope. However, they are clearly visible with the SEM and clear differences between the species groups are visible. The hairs may have short, truncated distal cells or this cell may taper to an acute apex. The length of the hairs also differs between the species groups. The Longifolia subgroup is the only grouping that does not possess abaxial microhairs. Microhair shape is a very important character separating the subfamilies of the Poaceae and the degree of variation observed in *Ehrharta* is most unusual.

10. Epicuticular wax

The occurrence and nature of the epicuticular wax deposits also appears to be a useful taxonomic character in *Ehrharta*, serving to distinguish between the species groups. The wax may be absent or present either as fine rods or as heavier platelets. The significance of this wax as a feature of higher taxonomic application is unknown.

The suite of leaf anatomical characters used to distinguish the species groups in *Ehrharta*, therefore, includes a wide spectrum of attributes and, in combination, these features serve to assign any given specimen to a particular group. However, it is not easy to identify to the species level using leaf anatomical criteria because the species are not so distinct anatomically. Nevertheless, the recognition and definition of the seven groups of species in this very difficult genus will definitely help in providing new insights into the phylogenetic relationships of the genus, until such time as sufficient embryo and chromosome data are available.

OUTLINE OF SPECIES GROUPS

Each of the species groups in *Ehrharta* can be described on the basis of a set of morphological and anatomical characters as summarized in Tables 3 & 4 respectively. A brief synopsis of characters and diagnosis is then given for the constituent taxa of each group.

SETACEA GROUP

Included taxa (Gibbs Russell 1984)

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

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

Morphological description

1. Perennial.
2. Culms herbaceous or suffrutescent.
3. No parts bulbous.
4. Leaf ligules ciliate.
5. Leaf blades expanded in herbaceous taxa, either setaceous or folded in suffrutescent taxa.
6. Spikelets fewer than 20.
7. Spikelets 4–8 mm long.
8. Glumes one third to almost equalling lemma length.
9. First sterile lemma reduced and glume-like, with veins.
10. Second sterile lemma base not stipitate, lacking appendages.
11. Sterile lemma surface rough.
12. Sterile lemma sides glabrous.
13. Sterile lemma bases not bearded.
14. Sterile lemma tips awnless, not mucronate.

Anatomical description

1. No keel developed; only median vascular bundle present.
2. Adaxial ribs and furrows present; ribs rounded and well developed (except in *E. setacea* subsp. *disticha* and subsp. *uniflora*).
3. Mesophyll compact, of small rounded or isodiametric cells; tendency for arm cell-like invaginations in all taxa; *E. setacea* subsp. *scabra* with typical bambusoid-like arm cells.
4. Costal and intercostal zones not differentiated (except in those species with abaxial stomata — *E. setacea* subsp. *disticha* and subsp. *uniflora*).
5. Intercostal long cells inflated to hexagonal; short, less than 20 μm long (usually less than 10 μm long); with sinuous walls.
6. Abaxial stomata absent (except in *E. setacea* subsp. *disticha* and subsp. *uniflora* and then without wax platelets).
7. Costal silica bodies single or paired or absent; rounded.
8. Costal and intercostal prickles present; either hooks or asperites with very short barbs; absent in *E. setacea* subsp. *disticha* and subsp. *uniflora*.
9. Microhairs with short, truncated distal cell; longer in *E. setacea* subsp. *disticha* and subsp. *uniflora*.
10. Epicuticular wax either absent or as fine rods.

Distinguished by:

First sterile lemma reduced, glume-like. Spikelets fewer than 20. Arm cells present.

CAPENSIS GROUP

Included taxa (Gibbs Russell 1984a; Smook & Gibbs Russell 1985)

E. longifolia Schrad.

E. ottonis Kunth ex Nees

TABLE 3.—Morphological characters diagnostic for the species groups in *Ehrharta*

	SETACEA	CAPENSIS		ERECTA	CALYCINA	VILLOSA	RAMOSA	DURA
		LONGIFOLIA	CAPENSIS					
HABIT	PERENNIAL	PERENNIAL	PERENNIAL	ANNUAL OR PERENNIAL	ANNUAL OR PERENNIAL	PERENNIAL	PERENNIAL	PERENNIAL
CULMS	SUFFRUTESCENT OR HERBACEOUS	HERBACEOUS	HERBACEOUS (r. suffrutescent)	HERBACEOUS	HERBACEOUS	SUFFRUTESCENT	HERBACEOUS (r. suffrutescent)	HERBACEOUS
INTERNODES	THIN	LOWEST BULBOUS	LOWEST BULBOUS (r. thin)	THIN	THIN	(rhizome subbulbous)	(upper with bulbous galls)	THIN
LEAF LIGULES	CILIATE	CILIATE	CILIATE	GLABROUS	GLABROUS	CILIATE	CILIATE	GLABROUS
LEAF BLADES	SETACEOUS OR EXPANDED	EXPANDED OR SETACEOUS	EXPANDED	EXPANDED	EXPANDED	REDUCED	REDUCED OR SETACEOUS	SETACEOUS OR EXPANDED
SPIKELET NUMBER	FEW	MANY	MANY	MANY	MANY	MANY	FEW	MANY
SPIKELET SIZE	SMALL	LARGE	LARGE	SMALL	SMALL	VERY LARGE	SMALL	VERY LARGE
GLUME LENGTH	SHORT OR LONG	SHORT	SHORT	SHORT	LONG	LONG	LONG	SHORT
FIRST STERILE LEMMA	REDUCED	EQUALLING 2nd	EQUALLING 2nd	EQUALLING 2nd	EQUALLING 2nd	EQUALLING 2nd	EQUALLING 2nd	EQUALLING 2nd
SECOND STERILE LEMMA BASE	STRAIGHT	STIPITATE	STIPITATE	CONSTRICTED	APPENDAGED	STIPITATE	APPENDAGED	STRAIGHT
STERILE LEMMA TEXTURE	ROUGH	ROUGH	ROUGH	ROUGH OR SMOOTH	SMOOTH	SMOOTH	ROUGH	ROUGH
STERILE LEMMA SIDES	GLABROUS	GLABROUS	GLABROUS	GLABROUS	HAIRY OR GLABROUS	HAIRY	GLABROUS	GLABROUS
STERILE LEMMA BASES	GLABROUS	BEARDED	BEARDED	BEARDED OR GLABROUS	GLABROUS OR ??	BEARDED	BEARDED	BEARDED
STERILE LEMMA TIPS	ROUNDED	MUCRONATE	MUCRONATE	ROUNDED OR AWNED	MUCRONATE OR AWNED	MUCRONATE	ROUNDED	AWNED

E. barbinodis Nees ex Trin.
E. capensis Thunb.
E. bulbosa J. E. Sm.
E. eburnea Gibbs Russell

Morphological description

1. Perennial.
2. Culms herbaceous (except *E. barbinodis* where they are suffrutescent).
3. Culm base bulbous at lowest internode (except *E. barbinodis*).
4. Leaf ligules ciliate.
5. Leaf blades expanded or rolled (but very short in *E. barbinodis*).
6. Spikelets many (but less than 35 in *E. eburnea*).
7. Spikelets 7–13 mm long.
8. Glumes ⅓–¾ lemma length.
9. First sterile lemma not reduced, lacking veins.
10. Second sterile lemma base stipitate, lacking appendages.
11. Sterile lemma surface rough.
12. Sterile lemma sides glabrous.
13. Sterile lemma bases bearded.
14. Sterile lemma tips awnless, mucronate.

Distinguished by:

Lowest culm node bulbous (except *E. barbinodis*). Second sterile lemma stipitate. Spikelets large, 7–13 mm long, hairy at margins.

Anatomical description

Anatomically this group cannot be defined satisfactorily as the taxa included vary greatly in anatomy. Nevertheless, two distinct and anatomically homogeneous subgroups can be distingushed and these will be dealt with separately.

LONGIFOLIA SUBGROUP

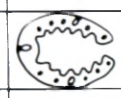
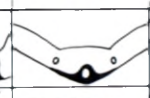
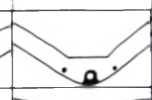
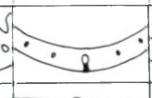
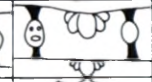
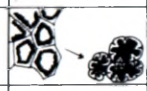
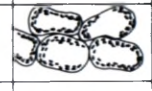
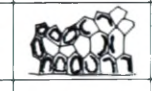
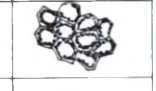
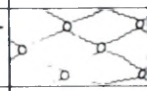
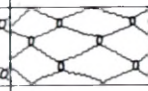
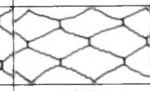
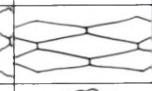
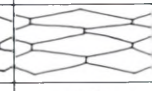
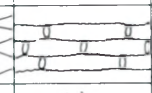
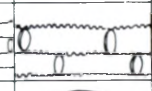
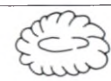
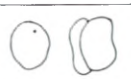
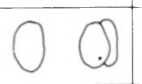
Included taxa (Smook & Gibbs Russell 1985)

E. longifolia Schrad.
E. ottonis Kunth. ex Nees

Anatomical description

1. Keels absent; median vascular bundle undifferentiated from lateral first order vascular bundles.
2. Massive adaxial ribs and deep, cleft-like furrows with interlocking prickles.
3. Mesophyll compact, of large angular cells; in U-shaped groups occupying the sides and bases of the furrows.

TABLE 4.—Anatomical characters diagnostic for the species groups in *Ehrharta*

SPECIES GROUPS	SETACEA	CAPENSIS		ERECTA	CALYCINA	VILLOSA	RAMOSA	DURA
		LONGIFOLIA	CAPENSIS					
KEEL AND MIDRIB								
RIBS AND FURROWS								
MESOPHYLL CELLS								
EPIDERMAL ZONATION	NOT PRESENT	NOT PRESENT	PRESENT	PRESENT	PRESENT	PRESENT	PRESENT	PRESENT
INTERCOSTAL LONG CELLS								
ABAXIAL STOMATA	ABSENT	ABSENT						
COSTAL SILICA BODIES								
COSTAL PRICKLES		ABSENT						
ABAXIAL MICROHAIRS		ABSENT						
EPI-CUTICULAR WAX	ABSENT OR PRESENT	ABSENT	PRESENT	PRESENT	PRESENT	PRESENT	ABSENT	ABSENT

4. Costal and intercostal zones only slightly differentiated.
5. Intercostal long cells inflated and short; less than 10 μm long; with sinuous walls.
6. Abaxial stomata absent.
7. Costal silica bodies paired or single; rounded.
8. Costal prickles absent.
9. Abaxial microhairs absent.
10. Epicuticular wax absent.

Distinguished by:

Setaceous leaves without arm cells.

CAPENSIS SUBGROUP

Included taxa (Gibbs Russell 1984a; Smook & Gibbs Russell 1985)

E. barbinodis Nees ex Trin.

E. capensis Thunb.

E. bulbosa J. E. Sm.

E. eburnea Gibbs Russell

Anatomical description

1. Keel present comprising 1 or 3 vascular bundles *(E. capensis)* or absent *(E.barbinodis)*; margin with conspicuous sclerenchyma cap.
2. Adaxial ribs and furrows absent.
3. Mesophyll semi-radiate; of compact but large, angular cells.
4. Costal and intercostal zones well differentiated.
5. Intercostal long cells elongate hexagonal, fusiform; between 10–20 μm long; with slightly sinuous walls.
6. Abaxial stomata present; subsidiary cells covered with wax platelets but pore visible.
7. Costal silica bodies single or paired; irregularly dumbbell-shaped.
8. Costal prickles with short barbs and intercostal prickles elongated, macrohair-like with bulbous bases.
9. Microhairs elongate, with tapering distal cell.
10. Epicuticular wax deposits as fine rods.

Distinguished by:

Presence of midrib and hexagonal long cells less than 20 μm long; stomata with wax platelets.

ERECTA GROUP

Included taxa (Smook & Gibbs Russell 1985)

E. erecta Lam.

var. *erecta*

var. *natalensis* Stapf

var. *abyssinica* (Hochst.) Pilg.

E. triandra Nees ex Trin.

E. longiflora J. E. Sm. (but spikelets similar to Capensis group)

Morphological description

1. Perennial or annual.
2. Culms herbaceous.
3. No parts bulbous.
4. Leaf ligules glabrous.
5. Leaf blades expanded.
6. Spikelets many.

7. Spikelets 3,0–7,5 mm long.
8. Glumes ½–⅔ lemma length.
9. First sterile lemma not reduced, veined.
10. Second sterile lemma base not stipitate, lacking appendages.
11. Sterile lemma surface rough (but smooth in some specimens of *E. erecta* subsp. *erecta).*
12. Sterile lemma sides glabrous.
13. Sterile lemma bases bearded (except in *E. erecta* subsp. *erecta* and *E. triandra*).
14. Sterile lemma tips not mucronate.

Anatomical description

1. Keel present; comprises one vascular bundle with ground parenchyma.
2. Very slight adaxial ribs and wide, shallow furrows present; may be absent.
3. Mesophyll rather diffuse of somewhat irregular, rounded cells; air spaces clearly visible.
4. Costal and intercostal zones clearly differentiated.
5. Mid-intercostal long cells hexagonal, fusiform in shape; elongate, more than 30 μm long; straight-walled.
6. Abaxial stomata present; subsidiary cells always with wax deposits, often in the form of a solid plug blocking the stomatal aperture.
7. Costal silica bodies in short chains; usually dumbbell-shaped with the central part only visibly by varying focus.
8. Costal and intercostal prickles present; all taxa with the macrohair-like type of prickle; asperites sometimes occur.
9. Microhairs elongate with markedly tapering distal cell.
10. Epicuticular wax always present.

Distinguished by:

Spikelets small, and first sterile lemma well developed, and glumes short, and sterile lemmas constricted at base, lacking appendages, and lemma sides glabrous. Raised abaxial epidermal long cells absent and stomata with wax plugs.

CALYCINA GROUP

Included taxa (Smook & Gibbs Russell 1985)

E. brevifolia Schrad.

var. *brevifolia*

var. *cuspidata* Nees

E. calycina J. E. Sm.

E. delicatula (Nees) Stapf

E. longigluma C. E. Hubb.

E. melicoides Thunb.

E. pusilla Nees ex Trin.

Morphogical description

1. Perennial or annual.
2. Culms herbaceous.
3. No parts bulbous.
4. Leaf ligules glabrous or ciliate.
5. Leaf blades expanded.
6. Spikelets many.
7. Spikelets 3,2–8,5 mm long.
8. Glumes two thirds longer than lemma length.
9. First sterile lemma not reduced, veined.
10. Second sterile lemma base not stipitate, with ear-like appendages.
11. Sterile lemma surface smooth.
12. Sterile lemma sides glabrous or hairy.
13. Sterile lemma bases hairy (but not conspicuously bearded) in hairy taxa, but glabrous taxa not bearded.
14. Sterile lemma tips mucronate or rounded.

Anatomical description

1. Keel absent, except in some specimens of *E. calycina* and *E. brevifolia* var. *cuspidata*.
2. Slight adaxial ribs and furrows; may be well developed in *E. calycina* and *E. melicoides* and may be absent in *E. calycina* and *E. brevifolia* var. *cuspidata;* raised, inflated abaxial epidermal cells always present in mid-intercostal zones.
3. Mesophyll generally compact of irregular (usually quite large), straight-walled cells; air spaces small; chlorenchyma cells often striated and refractive, possibly silicified.
4. Costal and intercostal zones clearly differentiated.
5. Mid-intercostal long cells elongated, fusiform (more than 25 μm long); raised; with straight walls; shorter in *E. longigluma;* these cells often stain in *E. calycina* and *E. melicoides*.
6. Abaxial stomata always present; pore aperture often obscured by cubical wax granules.
7. Costal silica bodies in short chains; variably dumbbell-shaped of the type which varies in shape with differing focus.
8. Costal and intercostal prickles present; sometimes with short barbs only *(E. pusilla)* but otherwise all taxa with macrohair type of prickle.
9. Microhairs finger-like with tapering distal cell.
10. Epicuticular wax always developed.

Distinguished by:

Spikelets small, and glumes long, and first sterile lemma well developed, and second sterile lemma base not stipitate, with ear-like appendages. Raised mid-intercostal long cells and cubical wax granules associated with stomata.

VILLOSA GROUP

Included taxa (Smook & Gibbs Russell 1985)

E. gigantea Thunb.

E. villosa Schult. f.

var. *maxima* Stapf

var. *villosa*

Morphological description

1. Perennial.
2. Suffrutescent.
3. Rhizome internodes sub-bulbous *(E. gigantea).*
4. Leaf ligules ciliate.
5. Leaf blades reduced, rolled.
6. Spikelets many.
7. Spikelets 10–18 mm long.
8. Glumes one half to longer than lemma length.
9. First sterile lemma not reduced, veined.
10. Second sterile lemma base stipitate, lacking appendages.
11. Sterile lemma surface smooth.

12. Sterile lemma sides profusely hairy.
13. Sterile lemma bases conspicuously bearded.
14. Sterile lemma tips mucronate.

Anatomical description

1. Keel absent; median vascular bundle identical to lateral first order bundles.
2. Adaxial ribs and furrows present; well developed; rounded ribs of medium size.
3. Mesophyll semi-radiate of large, angular cells; abaxial layer of chlorenchyma regular and somewhat palisade-like in arrangement.
4. Costal and intercostal zones differentiated.
5. Intercostal long cells rectangular in shape; sinuous walls; sometimes mid-intercostal long cells tend to be hexagonal.
6. Abaxial stomata present; sunken and overarched by four papilla-like flanges from the adjacent epidermal cells.
7. Costal silica bodies absent or irregular in occurrence; single or paired; round in shape.
8. Prickles absent *(E. villosa)* or costal and intercostal prickles present *(E. gigantea)*; hairs not macrohair-like.
9. Microhairs rather short but with tapering distal cell.
10. Epicuticular wax present but variable.

Distinguished by:

Culms over 1 m long, suffrutescent. Leaf blades reduced, rolled. Spikelets very large, lemmas profusely hairy and conspicuously bearded, stipitate, mucronate. Stomata with four epidermal flanges.

RAMOSA GROUP

Included taxa (Smook & Gibbs Russell 1985)

E. ramosa (Thunb.) Thunb.

E. rehmannii Stapf

var. *rehmannii*

var. *filiformis* Stapf

E. *subspicata* Stapf

Morphological description

1. Perennial.
2. Herbaceous or suffrutescent.
3. Upper internodes sometimes form bulbous galls in *E. ramosa* and *E. rehmannii* var. *filiformis*.
4. Leaf ligules ciliate.
5. Leaf blades expanded to rolled in herbaceous taxa, absent or very reduced in suffrutescent *E. ramosa*.
6. Spikelets few.
7. Spikelets 5,5–8,8 mm long.
8. Glumes two thirds longer than lemma length.
9. First sterile lemma not reduced, veined.
10. Second sterile lemma not stipitate.
11. Sterile lemma surface rough.
12. Sterile lemma sides glabrous (few short hairs in *E. rehmannii* var. *rehmannii)*.
13. Sterile lemma bases bearded.
14. Sterile lemma tips truncate, not mucronate.

Anatomical description

1. No keel; median vascular bundle only.
2. Ribs and furrows either absent or very slight ribs only present.
3. Mesophyll compact of small to medium, angular, isodiametric chlorenchyma cells.
4. Costal and intercostal zones differentiated.
5. Intercostal long cells rectangular but tending to hexagonal shape in mid-intercostal files in a few specimens; walls always sinuous.
6. Abaxial stomata present; no associated wax deposits; with distinct stomatal rims.
7. Costal silica bodies single or paired; irregular in shape being short dumbbell-shaped to rounded.
8. Costal and intercostal prickles present; with short to long barbs but not of the macrohair-like type.
9. Microhairs with distal cell not tapering.
10. Epicuticular wax absent.

Distinguished by:

Spikelets small, and sterile lemmas well developed, with tips rounded, sides rough and glabrous, bases glabrous and with basal appendages. Stomata with distinct rims and no wax deposits.

DURA GROUP

Included taxa (Smook & Gibbs Russell 1985)

E. dura Nees ex Trin.

E. microlaena Nees ex Trin.

Morphological description

1. Perennial.
2. Herbaceous.
3. No parts bulbous.
4. Leaf ligules glabrous.
5. Leaf blades well developed (setaceous in *E. dura)*.
6. Spikelets many.
7. Spikelets 9–17 mm long.
8. Glumes ⅓–½ lemma length.
9. First sterile lemma not reduced, veined.
10. Second sterile lemma base not stipitate, lacking appendages.
11. Sterile lemma surface rough.
12. Sterile lemma sides glabrous.
13. Sterile lemma bases bearded.
14. Sterile lemma tips long awned.

Anatomical description

1. No keel or midrib present.
2. Well developed adaxial ribs and furrows; ribs flat-topped and furrows cleft-like.
3. Mesophyll compact, of large angular cells; air spaces not visible.
4. Costal and intercostal zones differentiated.
5. Intercostal long cells rectangular with slightly sinuous walls; tanniniferous cells.
6. Abaxial stomata present; pore obscured by dense accumulation of wax platelets.
7. Costal silica bodies single or paired; irregularly dumbbell-shaped.
8. Costal prickles only; with very short barbs.

9. Microhairs very variable; with sharply tapering point or distal cell blunt; distal cell apparently not dehiscent.

10. Epicuticular wax absent except in association with the stomata.

Distinguished by:

Spikelets very large, lemmas glabrous. Plants perennial and spikelets awned. Tanniniferous cells present and stomatal pores obscured by wax platelets.

CONCLUSIONS

A better understanding of the taxonomy and systematics of *Ehrharta* is needed because its morphological and anatomical variation and its geographic distribution indicate that the genus may provide important clues towards understanding the natural relationships of the Poaceae. The southern African species fall into seven groups based on both spikelet morphology and vegetative anatomy, while the vegetative macromorphology exhibits parallelism and/or convergence between the groups. The series of papers to follow will relate the details of morphological and anatomical structure of each species group to the interpretation of relationships within *Ehrharta*, as it is presently circumscribed and within the rest of the grass family.

ACKNOWLEDGEMENTS

We thank L. Smook for support in field and herbarium; W. Roux and H. Ebertsohn for technical assistance; A. J. Romanowski for photography; and S. M. Perold for electron microscopy. We are especially grateful to J. F. Veldkamp and S. A. Renvoize for meticulous reviewing of the manuscript.

REFERENCES

AVDULOV, N. P. 1931. Karyo-systematische Untersuchung der Familie Gramineen. *Bulletin on Applied Botany, of Genetics and Plant Breeding*, Supplement 43.

BENTHAM, G. & HOOKER, J. D. 1883. *Genera plantarum*, Vol. 3, Part I. Reeve, London.

BREAKWELL, E. 1914. A study of the leaf anatomy of some native species of the genus *Andropogon* N.O. Gramineae. *Proceedings of the Linnean Society of New South Wales* 39: 385–394.

CHIPPINDALL, L. 1955. A guide to the identification of grasses in South Africa. In C. Meredith, *The grasses and pastures of South Africa*. Central News Agency, Cape Town.

CLAYTON, W. D. 1970. Gramineae. Part 1. In E. Milne-Redhead & R. M. Polhill, *Flora of tropical east Africa*. Crown Agents, London.

CLIFFORD, H. T. & WATSON, L. 1977. *Identifying grasses: data, methods and illustrations*. University of Queensland Press, St Lucia, Queensland.

FEDER, N. & O'BRIEN, O. P. 1968. Plant microtechnique: some principles and new methods. *American Journal of Botany* 55: 123–142.

GIBBS RUSSELL, G. E. 1984a. A new species of *Ehrharta* (Poaceae). *Bothalia* 15: 145–147.

GIBBS RUSSELL, G. E. 1984b. Notes on species of *Ehrharta* with a short first sterile lemma (Poaceae). *Bothalia* 15: 149–151.

GMELIN, J. F. 1791. *Caroli a Linne Systema Naturae*, edn 13, vol. 2. Beer, Leipzig.

GOLDBLATT, P. 1978. Analysis of the flora of southern Africa: its characteristics, relationships and origins. *Annals of the Missouri Botanical Garden* 65: 369–436.

HACKEL, E. 1887. Gramineen. In H. G. A. Engler & K. A. E. Prantl, *Die Natürlichen Pflanzenfamilien* 2,2.

HUBBARD, C. E. 1933. Notes on African grasses XIV. *Kew Bulletin* 1933: 498–502.

JACQUES-FÉLIX, H. 1962. *Les Graminées (Poaceae) d'Afrique Tropicale I*. Institut de Recherches Agronomiques Tropicales, Paris.

JOHANSEN, D. A. 1940. *Plant microtechnique*. McGraw-Hill, New York.

KUNTH, C. S. 1829. *Revision des Graminées*. J. Tatsu, Paris.

KUNTZE, C. E. O. 1891. *Revisio generum plantarum*. Felix, Leipzig.

LAMARCK, J. B. A. P. M. de. 1786. *Encyclopédie méthodique. Botanique*, vol. 2. Panckouke, Paris.

LAUNERT, E. 1961. Eine neue Art der Gattung *Ehrharta* Thunb. (Gramineae). *Mitteilungen aus der Botanischen Staatssammlung, München* 4: 161–163.

LINDER, H. P. 1985. Conspectus of the African species of Restionaceae. *Bothalia* 15: 387–503.

LINNAEUS, C. 1781. *Supplementum plantarum*. Impenfis Orphanotrophei, Brunsvigae.

LINNAEUS, C. 1830. *Systema vegetabilium* 7, 2. Ed. J. J. Roemer & J. A. Schultes. Cottae, Stuttgardt.

LINK, J. H. F. 1827. *Hortus regius botanicus berolinensis*, vol. 1. Reimer, Berlin.

METCALFE, C. R. 1960. *Anatomy of the Monocotyledons. I. Gramineae*. Clarendon Press, Oxford.

MEZ, C. 1921. Gramineae novae vel minus cognitae. IV. *Repertorium specierum novarum regni vegetabilis* 17: 291–303.

NEES AB ESENBECK, C. G. 1832. Plantae Ecklonianae. Gramineae. *Linnaea* 7: 273–356.

NEES AB ESENBECK, C. G. 1839. In C. B. Trinius, Phalarideae. *Zapiski Imperatorskoi akademii nauk*, ser. 6, 3: 59.

NEES AB ESENBECK, C. G. 1841. *Florae Africae Australioris*. Prausnitizianis, Cracow.

NEUMANN, A. J., RUSHING, A. E. & MUELLER, D. M. J. 1982. A modified, short protocol for preparation of Bryophytes for scanning electron microscopy. *The Bryologist* 85: 74–78.

NEVSKI, S. A. 1937. Beiträge zur Flora des Kuhitang-tau und seiner Vorgebirge. *Acta Instituti botanici Academiae scientiarum URSS*, ser. 1,4: 199–244.

PALISOT DE BEAUVOIS, A. M. F. J. 1812. *Essai d'une nouvelle agrostographie*. Imprimerie de Fain, Paris.

PILGER, R. 1955. Das System der Gramineae. *Botanische Jahrbücher* 76: 281–384.

PRAT, H. 1960. Vers une classification naturelle des Graminées. *Bulletin Societé botanique de France* 76: 32–79.

REEDER, J. R. 1957. The embryo in grass systematics. *American Journal of Botany* 44: 756–769.

RENVOIZE, S. A. 1981. The subfamily Arundinoideae and its position in relation to a general classification of the Gramineae. *Kew Bulletin* 36: 85–102.

RENVOIZE, S. A. 1985. A survey of leaf-blade anatomy in grasses. V. The bamboo allies. *Kew Bulletin* 40: 509–535.

RICHARD, L. C. M. 1799. *Journal de Physique* 13: 225.

RUTHERFORD, M. C. & WESTFALL, R. H. 1986. The biomes of southern African—an objective categorization. *Memoirs of the Botanical Survey of South Africa* No. 54.

SCHRADER, H. A. 1821. Analecta ad floram Capensem. Sect. II. Cyperaceae. Gramineae. *Göttingische gelehrte Anzeigen* 1821: 2065–2079.

SCHULTES, J. H. 1830. In C. Linnaeus, *Systema vegetabilium* 7, 2. Ed. J. J. Roemer & J. A. Schultes, Cottae, Stuttgart.

SMITH, J. E. 1789. *Plantarum icones hactenus ineditae* 1. J. Davis, London.

SMITH, J. E. 1790. *Plantarum icones hactenus ineditae* 2. J. Davis, London.

SMOOK, L. & GIBBS RUSSELL, G. E. 1985. Poaceae. In G. E. Gibbs Russell *et al.*, List of species of southern African plants, edn 2, part 1: 45–70. *Memoirs of the Botanical Survey of South Africa* No. 51.

SODERSTROM, T. R. & ELLIS, R. P. in prep. The position of bamboo genera and allies in a system of grass classification. *Smithsonian Contributions to Botany*.

STAPF, O. 1900. Gramineae. In W. T. Thiselton-Dyer, *Flora capensis* 8: 310–750.

STEBBINS, G. L. & CRAMPTON, B. 1961. A suggested revision of the grass genera of temperate North America. *Recent advances in botany*. University of Toronto Press, Toronto.

STEUDEL, E. G. 1829. Bemerkungen über einige Cyperaceen und Gramineen vom Vorgebirge der guten Hoffnung. *Flora (Jena)* 12: 491.

STEUDEL, E. G. 1853. *Synopsis plantarum graminearum*. Metzler, Stuttgart.

SWARTZ, O. 1802. The botanical history of the genus *Ehrharta*. *Trans-actions of the Linnean Society* 6: 40–64.

TATEOKA, T. 1957. A new phylogenetic system of Poaceae. *Journal of Japanese Botany* 32: 275–287.

TATEOKA, T. 1963. Notes on some grasses. XII. Relationships between Oryzeae and Ehrharteae, with special reference to leaf anatomy and histology. *The Botanical Gazette* 124: 264–270.

TAYLOR, H. C. 1978. Capensis. In M. J. A. Werger, *Biogeography and ecology of southern Africa* 1. Junk, The Hague.

THUNBERG, C. P. 1779. *Kungliga Svenska vetenskapsakademiens handlingar* 40: 217.

THUNBERG, C. P. 1794. *Prodromus plantarum capensium*. Edman, Uppsala.

THUNBERG, C. P. 1823. *Flora capensis*. Cottae, Stuttgart.

TRINIUS, C. B. 1839. Phalarideae. *Mémoires de l'Académie impérial des Sciences de St-Pétersbourg*, sér. 6. 5: 12–26.

VOSS, E. G. *et al.* 1983. *International code of botanical nomenclature*. In Regnum Vegetabile 111. Bohn, Scheltema & Holkema, Utrecht.

WATSON, L., CLIFFORD, H. T. & DALLWITZ, M. J. 1985. The classification of Poaceae: subfamilies and supertribes. *Australian Journal of Botany* 33: 433–484.

WILLEMSE, L. P. M. 1982. A discussion of the Ehrharteae (Gramineae) with special reference to the Malesian taxa formerly included in *Microlaena*. *Blumea* 28: 181–194.