

Leaf anatomy of the South African Danthonieae (Poaceae). XV. The genus *Elytrophorus*

R. P. ELLIS*

Keywords: Danthonieae, *Elytrophorus*, leaf anatomy, Poaceae

ABSTRACT

The leaf anatomy of *Elytrophorus globularis* Hack. and *E. spicatus* (Willd.) A. Camus is described and illustrated from freshly fixed material from SWA/Namibia and Botswana. It is shown that these two species are anatomically indistinguishable. It is suggested that they are conspecific, and that *E. spicatus* possibly represents juvenile plants with immature inflorescences. The anatomical evidence strongly refutes a chloridoid relationship for *Elytrophorus* but appears to support arundinoid affinities for the genus. Striking anatomical and ecological similarities exist between *Elytrophorus* and *Sacciolepis huillensis* (Rendle) Stapf. No significant leaf anatomical differences separate *Elytrophorus* from *S. huillensis* and some of the other C_3 panicoid taxa and, consequently, *Elytrophorus* may represent a link between the Arundinoideae and the Panicoideae.

UITTREKSEL

Die blaaranatomie van *Elytrophorus globularis* Hack. en *E. spicatus* (Willd.) A. Camus word beskryf en geïllustreer deur middel van gefikseerde materiaal afkomstig vanaf SWA/Namibië en Botswana. Daar word getoon dat hierdie twee spesies anatomies ononderskeibaar is. Daar word voorgestel dat hulle konspesifiek mag wees en dat *E. spicatus* net jong plante met onvolwasse bloeiwyse mag verteenwoordig. Die anatomiese bewyse weerlê verwantskappe met Chloridoideae vir *Elytrophorus* maar verwantskappe met Arundinoideae word ondersteun. Duidelike anatomiese en ekologiese ooreenkomste tussen *Elytrophorus* en *Sacciolepis huillensis* (Rendle) Stapf is waargeneem. Geen betekenisvolle anatomiese verskille skei *Elytrophorus* van *S. huillensis* en sommige van die ander C_3 taksa van die Panicoideae en *Elytrophorus* mag dus 'n skakel tussen die Arundinoideae en die Panicoideae verteenwoordig.

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INTRODUCTION

Elytrophorus Beauv. is a genus of unusual little grasses found in tropical Africa, India to South China and Australia, with the centre of distribution apparently in tropical Africa. The genus is therefore

restricted to warm tropical areas of the Old World surrounding the Indian Ocean.

Some authors have distinguished four species in the genus (Loxton 1976; Schweickerdt 1942). Other workers uphold only two species: *E. globularis* Hack. and *E. spicatus* (Willd.) A. Camus (Chippindall 1955; Clayton 1970; Smook & Gibbs Russell 1985). Both these species occur in southern Africa where they are restricted to the tropical northernmost parts of the region. In SWA/Namibia, *Elytrophorus* is found in Ovamboland and the Grootfontein, Okavango and Caprivi Districts, and in Botswana it occurs in the Mababe Depression and the Okavango Delta of Ngamiland. *E. globularis* has also been collected at Mosdene along the Nyl River in the Naboomspruit District of the Transvaal.

Both species are water-loving and are found exclusively on the edges of rainwater pans, ponds, depressions and in rice fields, particularly on the periphery of these shallow water bodies when moist mud is exposed as the water evaporates and recedes. Damp hydromorphic clay soil is preferred and the plants even thrive in the cracking clay. *Elytrophorus* can withstand a certain degree of inundation and can survive in standing water up to 0.2 m deep and is considered to be a true hydrophyte (Schweickerdt 1942). In ideal situations *Elytrophorus* can form dense communities, the individual plants varying in height from 10 mm to 0.5 m, depending on the prevailing moisture conditions.

Elytrophorus exhibits an unusual combination of anatomical features which have been described by Schweickerdt (1942), Jacques Felix (1962), Clifford & Watson (1977) and Palmer & Tucker (1981). The

*Botanical Research Institute, Department of Agriculture and Water Supply, Private Bag X101, Pretoria 0001.

objective of this paper is to describe and illustrate the leaf blade anatomy of both species and to relate this to the anatomical diagnoses of the subfamilies of the Poaceae as defined by Clifford & Watson (1977) and Renvoize (1981). The natural relationships of *Elytrophorus* are not readily apparent and agrostologists differ as to which subfamily and tribe this genus should be assigned to. The anatomical evidence will be fully discussed in an attempt to resolve this question.

MATERIALS AND METHODS

Plants of *Elytrophorus* were collected in SWA/Namibia and Botswana during the late summers (April or May) of 1977, 1981 and 1983. Herbarium voucher specimens were prepared for verification by the National Herbarium (PRE). Segments of leaf blade material were removed in the field and immediately fixed in FAA (Johansen 1940).

Transverse sections, 10 μ thick, were prepared after desilicification in 30% hydrofluoric acid (Breakwell 1914), dehydration following the method of Feder & O'Brien (1968) and infiltration and embedding in Tissue Prep (Fisher Scientific). These

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 leaf epidermis. These were either stained in safranin or double-stained in methylene blue and ruthenium red. The anatomical structure was recorded photographically using a Reicherdt Univar microscope and Ilford Pan F film (50 ASA).

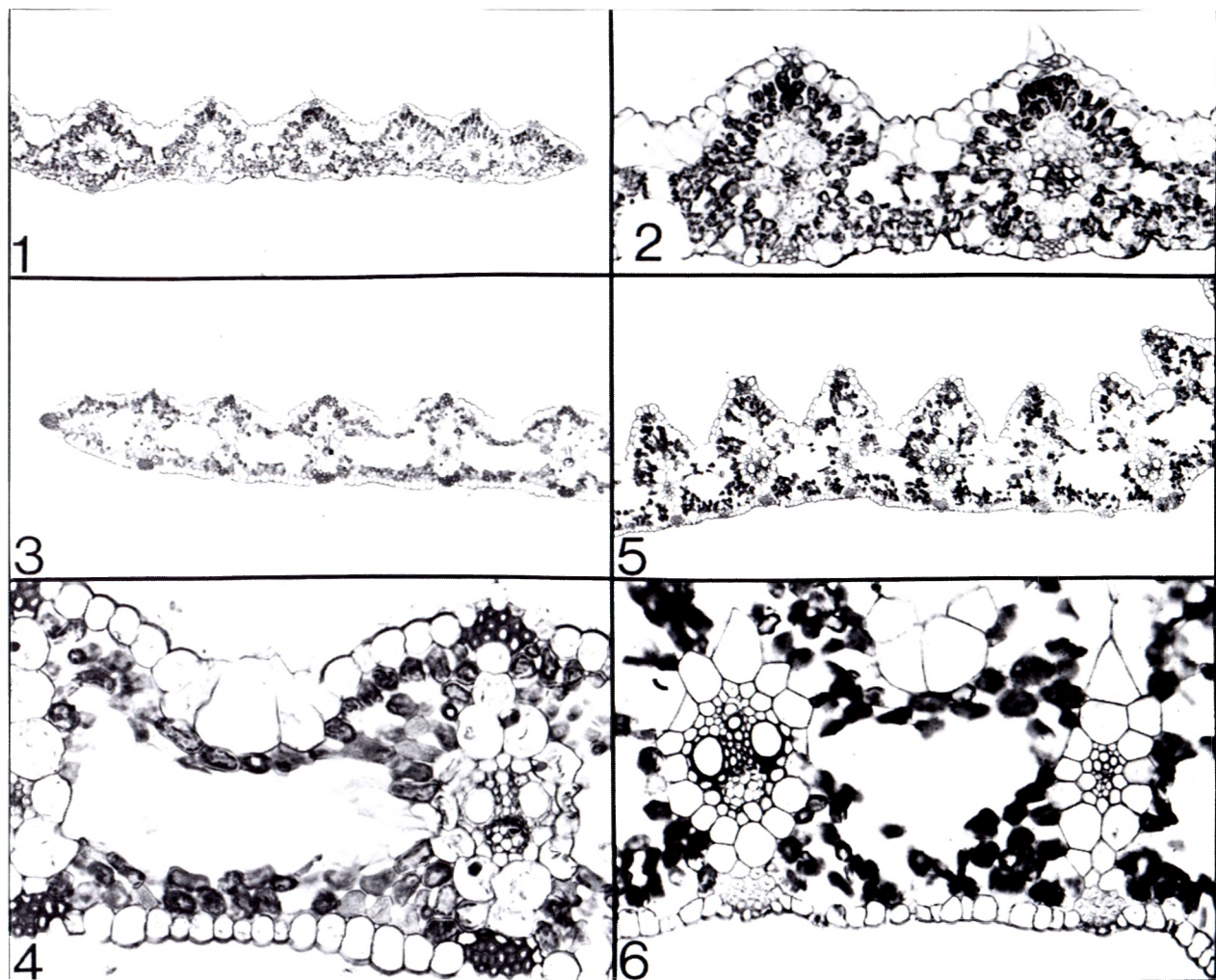
In the anatomical descriptions which follow, the standardized terminology of Ellis (1976, 1979) will be used, together with the following abbreviations:

- vb/s – vascular bundle/s
- 1'vb/s – first order vascular bundle/s
- 3'vb/s – third order vascular bundle/s
- ibs – inner bundle sheath; mestome sheath
- obs – outer bundle sheath; parenchyma bundle sheath

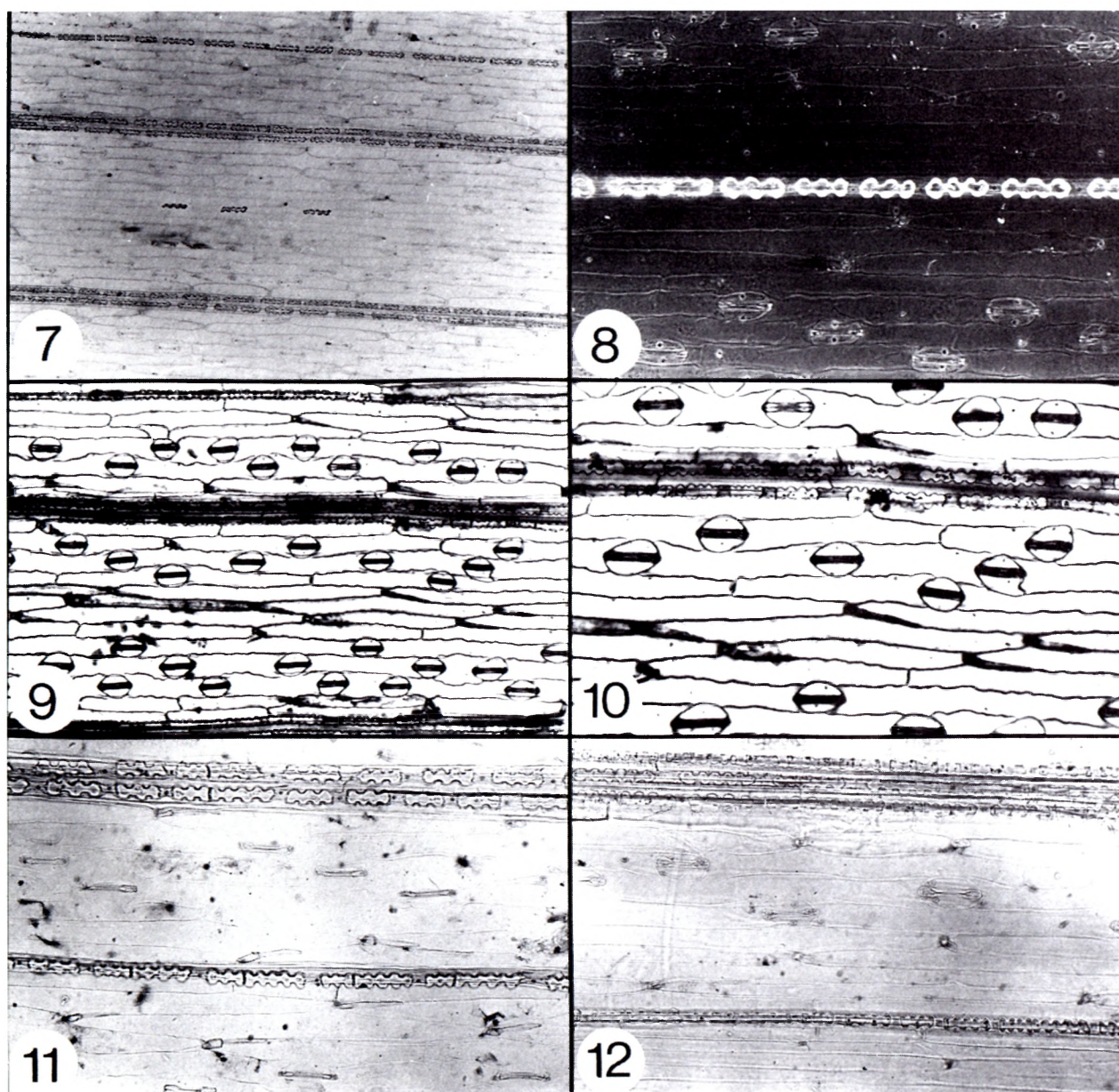
Specimens examined:

Elytrophorus globularis

SWA/NAMIBIA. — 1714 (Ruacana Falls): Ovamboland, Eunda (–DA), *Ellis* 2586, 1723 (Singalamwe): eastern Caprivi, Sachona (–CD), *Ellis* 3705, 1724 (Katima Mulilo): eastern Caprivi, Chaka turnoff on Bukalo-Muyako road (–CB), *Ellis* 3714, 2116 (Okahandja): 32 km N of Okahandja on road to Otjiwarongo (–DB), *Gibbs Russell & Smook* 5330.



FIGURES 1–6.—Leaf blade anatomy of *Elytrophorus globularis* as seen in transverse section. 1–2, *Ellis* 2586: 1, leaf margin, $\times 100$; 2, detail of diffuse, semi-radiate chlorenchyma and non-Kranz outer bundle sheath cells, $\times 250$. 3–4, *Ellis* 2899: 3, lateral part of lamina with lacunae between all vascular bundles, $\times 100$; 4, detail of lacuna, chlorenchyma and first order vascular bundle, $\times 400$. 5–6, *Gibbs Russell & Smook* 5330: 5, outline with triangular adaxial ribs, $\times 100$; 6, diffuse chlorenchyma, lacuna and colourless bundle sheath cells, $\times 400$.



FIGURES 7-12.—Abaxial epidermis of *Elytrophorus globularis*. 7, *Ellis* 2904 showing costal and intercostal zones, $\times 160$. 8, *Ellis* 2900, phase contrast with nodular silica bodies, stomata, microhairs and intercostal long cells, $\times 400$. 9-10, *Ellis* 2586: 9, costal and intercostal zones and stomatal distribution, $\times 250$; 10, note silica bodies, stomata, microhairs and long cells, $\times 400$. 11, *Ellis* 3705, nodular silica bodies and microhairs, $\times 400$. 12, *Ellis* 3714, detail of epidermal cells, $\times 400$.

BOTSWANA. — 1824 (Kachikau): Chobe National Park, Goha Hills (–AC), *Ellis* 2914. 1924 (Joverega): 100 km N of Maun on road to Moremi (–AC), *Ellis* 2904. 2023 (Kwebe Hills): Samedupe Drift over Botletle River (–BA), *Ellis* 2899, 2900.

Elytrophorus spicatus

SWA/NAMIBIA. — 1724 (Katima Mulilo): eastern Caprivi, Salambala between Bukalo and Ibbu (–DA), *Ellis* 3718.

BOTSWANA. — 1824 (Kachikau): Chobe National Park, Goha Hills (–AC), *Ellis* 2913.

ANATOMICAL DESCRIPTION OF THE GENUS *ELYTROPHORUS*

Leaf in transverse section

Outline: expanded, broadly V-shaped. **Ribs and furrows:** rounded adaxial ribs present over all vbs (Figures 1-3; 13-14); sometimes somewhat triangular (Figure 5); all ribs of similar size. Shallow, wide

furrows between all vbs (Figures 1-5; 13-14). Abaxial surface without undulations. **Median vascular bundle:** no structurally distinct midrib present (Figures 5 & 13). **Vascular bundle arrangement:** 5 1'vbs in leaf section; 1 3'vb between consecutive 1'vbs; no 2'vbs. All vbs situated in centre of blade (Figures 2, 4 & 14) except in specimen with triangular ribs (Figure 5). **Vascular bundle description:** 3'vbs elliptical and angular; 1'vbs elliptical to round; phloem adjoins ibs; metaxylem vessels narrow and round. **Vascular bundle sheaths:** obs round, entire; sometimes with slight adaxial extensions (Figures 2, 4, 6 & 14). Obs cells round, irregular in size, with thin walls and containing few or no chloroplasts. Ibs entire without wall thickenings. **Sclerenchyma:** small adaxial and abaxial strands associated with all vbs; abaxial strand usually in contact with the obs (Figures 2, 4, 6 & 14). Small cap in margin (Figures 1, 3 & 13). **Mesophyll:**

diffuse chlorenchyma tending to radiate condition around vbs; lateral cell count greater than 4; central cells very diffuse and irregular tending to break down into lacunae (Figures 4 & 6) which are then located between all vbs. No colourless cells present. *Adaxial epidermal cells*: small groups of bulliform cells located at the bases of all furrows. Epidermal cells thin-walled and inflated; a few prickles associated with ribs. *Abaxial epidermal cells*: thin-walled, inflated with thin cuticle; no epidermal appendages.

Abaxial epidermis in surface view

Intercostal long cells: very elongate (Figures 8, 9 & 15), not rectangular but side walls slightly angled outwards and cell narrowing toward end walls; anticlinal walls unthickened and very slightly undulating (Figures 10 & 15); adjoin one another or separated by stomata or microhairs (Figures 8, 10 & 15). *Stomata*: low dome-shaped (Figures 8, 10 & 15); 4 or 6 files per intercostal zone but absent in centre of zones; rows of stomata adjacent to one another (Figure 10); usually 1, sometimes 2 interstomatal long cells between successive stomata in file. *Intercostal short cells*: absent. *Papillae*: absent. *Prickles*: not present on abaxial surface. *Microhairs*: bicellular; very short basal cell and long tapering distal cell (Figures 8, 10, 11, 12 & 15); hairs slightly longer than stomata; present on edges and centre of intercostal zones. *Macrohairs*: absent. *Silica bodies*: costal; elongated nodular (Figure 8) to almost sinuous and crenate (Figures 11, 12, 15 & 16); in pairs or separated by short cells; granules often present. *Costal zones*: 1, 3 or 5 cells wide; files with silica bodies alternating with files of costal long cells; these very narrow and long.

DISCUSSION AND CONCLUSIONS

Differences between the species of *Elytrophorus*

In his treatment, Schweickerdt (1942) considered the genus *Elytrophorus* to comprise four species: *E. globularis* and *E. spicatus* as well as *E. africanus* Schweick. and *E. interruptus* Pilg. The latter two species are now considered to be synonyms of *E. globularis* (Clayton 1970) and consequently, the present study includes the two species which represent all currently recognized members of the genus.

The anatomical details described by Schweickerdt (1942) agree closely with the observations of this study. The only significant departure concerns the mention of aerenchymatous cells traversing the lacunae. Schweickerdt considers this tissue to be a striking characteristic of the genus. In the present study, however, no aerenchyma or stellate cells were observed in any of the ten specimens examined. Most specimens had lacunae located between the vascular bundles (Figures 3–6) but these cavities were never seen to be traversed by colourless aerenchyma cells. In addition, in some specimens of both species, the lacunae were not even fully developed (Figures 1 & 2, 13 & 14) although the central mesophyll between the vascular bundles was more diffuse, with larger intercellular air spaces appearing to represent the in-

itial stages of cellular breakdown prior to the formation of the typical lacunae. If this is so, then the lacunae of *Elytrophorus* are lysigenous cavities arising by the dissolution of entire cells during the later ontogenetic stages of the leaf. The replacement of these broken down mesophyll cells by aerenchyma cells at this late stage of leaf differentiation appears unlikely.

Schweickerdt (1942) mentions aerenchyma tissue in all four species he studied although the cells are only illustrated in *E. spicatus*. The specimens examined by him were prepared from dried herbarium material and he remarks that tissue recovery was not satisfactory and this is reflected in his camera lucida drawings. His details and measurements of the softer tissues, in particular, may not necessarily be reliable and accurate.

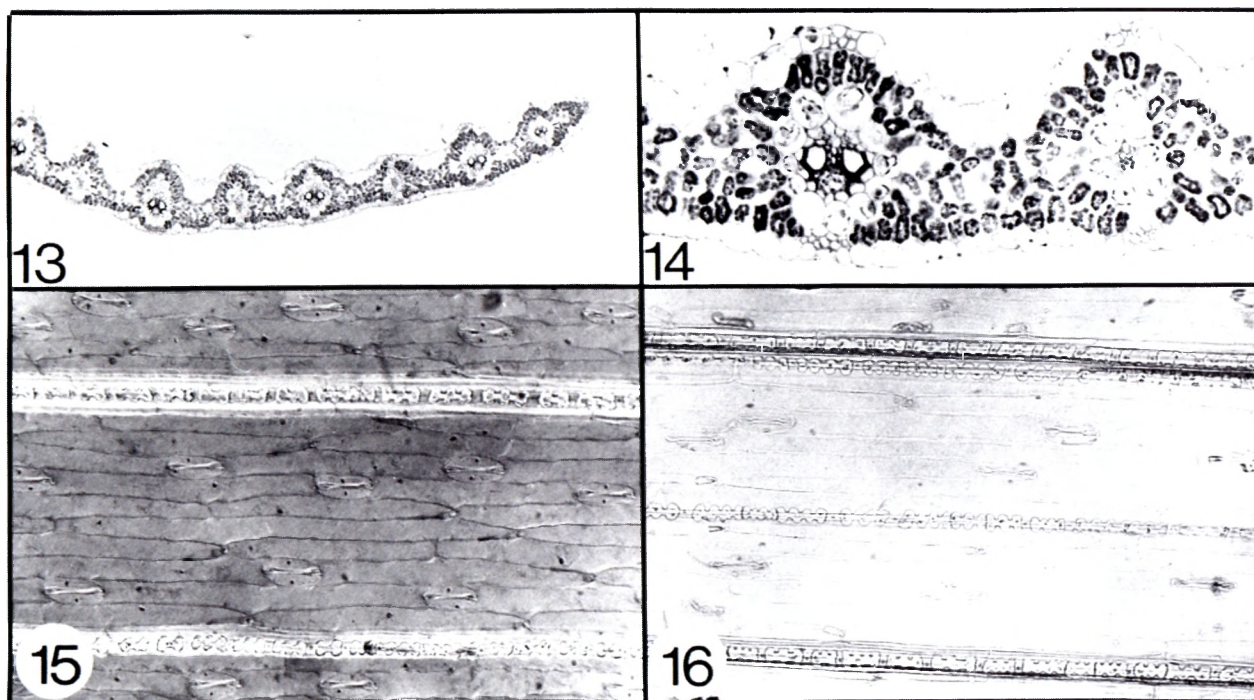
This may also explain another difference between the findings of this study and those of Schweickerdt (1942). In the latter study diagnostic anatomical differences were detected between *E. globularis* and *E. spicatus* whereas in the present study no differences were observed. According to Schweickerdt (1942), *E. spicatus* is characterized by having a leaf blade of 0.3–0.36 mm thick, with both adaxial and abaxial ribs and furrows and with bulliform cells between all bundles. *E. globularis* is said to differ in having a thinner blade (0.15–0.28 mm), neither surface being ridged, and well developed bulliform cells only occurring in the region of the midrib. This interspecific variation appears to be contradicted by the illustration of *E. globularis* (Jacques Felix 1962), which shows large triangular adaxial ribs as well as lacunae, whereas an illustration of *E. spicatus* (Clifford & Watson 1977) shows neither ribs nor lacunae. In the above studies only a single specimen from each species was examined and intraspecific variation could not be ascertained with much confidence. In the present study, however, variation has been shown to occur within each of the species and the sample of each species studied exhibited as much variation as that considered by Schweickerdt (1942) to justify separation of the two species. Examples are, as mentioned, the differences in adaxial rib and lacuna development in different specimens of *E. globularis* (Figures 3 & 5).

The present study shows that *E. globularis* and *E. spicatus* are indistinguishable on anatomical grounds. These results, and the observation that both species may occur at the same locality at the same time, throw doubt on the validity of upholding two separate species. *E. spicatus* may merely represent juvenile plants with younger or immature inflorescences. This hypothesis requires testing.

Subfamilial and tribal classification

General

The classification of *Elytrophorus* has been the subject of much debate in the literature. Some authors consider it to belong to the Chloridoideae, and Chippindall (1955) and Bor (1960) placed *Elytrophorus* in the Eragrostideae. Clifford & Watson (1977) place it in their chloridoid group although they do note that the leaf anatomy is atypical, dis-



FIGURES 13–16.—Leaf anatomy of *Elytrophorus spicatus*. 13–15, *Ellis 2913*: 13, leaf outline, $\times 100$; 14, detail of semi-radiate mesophyll and vascular bundles, $\times 400$; 15, abaxial epidermis with nodular silica bodies, stomata and long cells, $\times 400$. 16, *Ellis 3718*, abaxial epidermis, $\times 400$.

playing a curious mixture of festucoid and panicoid features as well. Prat (1960) and Decker (1964) placed *Elytrophorus* in their unplaced genera although Decker noted similarities with the Danthonieae. Jacques Felix (1962) isolated the genus in a separate tribe, the Elytrophoreae, belonging to his series the Arundinoideae. This classification has been upheld by most modern authors and *Elytrophorus* is usually assigned to the Arundinoideae in the tribe Danthonieae (Clayton 1970; Loxton 1976) or the tribe Arundineae (Renvoize 1981). Renvoize (1981) considers *Elytrophorus* to conform closely to the coherent arundinoid core group which is virtually synonymous with the Danthonieae.

Affinities with the Chloridoideae

Evidence from leaf in transverse section

Elytrophorus has a double bundle sheath, as do the chloridoid grasses, but the outer sheath is thin-walled and non-Kranz, lacking specialized chloroplasts. It is therefore a C_3 genus, as is confirmed by $^{13}C/^{12}C$ ratios for *E. globularis* of -26.23% (Dinter 7390) and *E. spicatus* of -25.70% (Schweickhardt 2089). As far as is known, all chloridoid grasses are C_4 with only one possible exception (Ellis 1984) and therefore, have strongly radiate mesophyll and a maximum lateral cell count of less than four. In *Elytrophorus* this count is greater than 10 and, although the mesophyll displays a tendency to be radiate, it is of the *Isachne* type (Metcalf 1960) with several layers of elongated, diffuse cells with many air spaces all arranged in a somewhat radiate manner (Figures 2 & 14). This type of mesophyll is unknown in the Chloridoideae where a single layer of compact, tabular cells surrounds each bundle. In the chloridoid

type of anatomy the bulliform cells are usually associated with deeply penetrating fans of colourless cells, whereas in *Elytrophorus* none of these colourless cells occur. The evidence from leaf transections does not indicate a chloridoid connection for *Elytrophorus*.

Evidence from abaxial epidermis

Elongated microhairs with short basal cells, and much longer, tapering distal cells are common in *Elytrophorus* and were observed on all specimens examined in this study. The structure of these microhairs is illustrated in the accompanying photomicrographs (Figures 8, 10, 11, 12, 15 & 16) and even more clearly in the scanning electron micrographs of Palmer & Tucker (1981). This structure differs significantly from the chloridoid type which is always egg-shaped with shorter, inflated distal cells (Clifford & Watson 1977; Renvoize 1981). *Elytrophorus* also lacks long cells with sinuous walls which are typical of chloridoid grasses. The subsidiary cells of *Elytrophorus* are dome-shaped (Figure 10) or low dome-shaped (Figures 8, 12 & 15), whereas in the Chloridoideae they are predominantly triangular. Chloridoid grasses often have papillate epidermides whereas *Elytrophorus* does not, at least at the level of resolution of light microscopy. Palmer & Tucker (1981) illustrate tiny, warty papillae visible only at higher magnifications with the scanning electron microscope but these are, nevertheless, not of the chloridoid type. The horizontally elongated nodular to sinuous type of silica body found in *Elytrophorus* is unknown in the Chloridoideae where silica bodies are not elongated and are usually saddle-shaped, but may be cross-shaped, square or shortly dumbbell-shaped. In epidermal structure, therefore, *Elytro-*

phorus bears no resemblance whatsoever to the chloridoid condition.

Leaf anatomical evidence, therefore, does not support chloridoid phylogenetic affinities for *Elytrophorus* and the classification of this genus in the Chloridoideae cannot be supported.

Affinities with the Arundinoideae

Other workers place *Elytrophorus* in the rather ill-defined subfamily Arundinoideae (Jacques Felix 1962; Clayton 1970; Renvoize 1981). This subfamily cannot be defined as precisely as the other four subfamilies and lacks reliable diagnostic features. Nevertheless, a diagnosis of the Arundinoideae is possible (Clifford & Watson 1977; Renvoize 1981) and, in most respects *Elytrophorus* conforms very well to this definition.

Arundinoid microhairs are finger-like with tapering distal cells, the subsidiary cells are domed and the epidermis is not papillate — all characteristics of the epidermis of *Elytrophorus*. There are points of difference, however, where *Elytrophorus* does not conform to the arundinoid definition. The straight-walled long cells of *Elytrophorus* are an example, as are the nodular to sinuous or crenate silica bodies. These character states are more typical of the festuoid subfamily but they are not unknown in the Arundinoideae. The silica bodies of the arundinoid grasses are horizontally elongated and may be nodular, cross- or dumbbell-shaped and, consequently do not differ greatly from the *Elytrophorus* condition. In epidermal structure, therefore, *Elytrophorus* generally resembles the arundinoid type closely.

In leaf transverse sections the same is true and *Elytrophorus* diverges little from the arundinoid type. Both are non-Kranz (with a few arundinoid exceptions), have double bundle sheaths and non-radiate or slightly radiate mesophyll and have a maximum lateral cell count greater than four. In addition the arundinoid grasses are also characterized by having adaxial ribs, as does *Elytrophorus*. Bulliform cells not associated with colourless cells is another characteristic common to both these groups. The leaf anatomy of *Elytrophorus*, as seen in transverse section, therefore, conforms very closely to the arundinoid type and there is no anatomical evidence for excluding *Elytrophorus* from this subfamily. The leaf anatomical data of this study support the classification of *Elytrophorus* in the Arundinoideae, as recommended by most modern authors.

Affinities with Sacciolepis and other C₃ Panicoideae

Although the above evidence may be convincing, other factors suggest caution in postulating arundinoid affinities for *Elytrophorus*. A similar distribution in hot, tropical areas is unknown in the other C_3 South African Danthonieae as discussed by Ellis *et al.* (1980). Apart from the ubiquitous *Phragmites*, *Elytrophorus* is the only C_3 arundinoid grass found in the northern tropical regions of southern Africa. In the hydrophytic habitats favoured by *Elytrophorus* the only other C_3 grasses belong either to the Oryzeae or the Paniceae. Little anatomical resemblance

exists between the oryzoid grasses and *Elytrophorus* but the C_3 type of panicoid anatomy of genera such as *Acroceras* and *Sacciolepis* and the leaf anatomy of *Elytrophorus* show striking similarities. *Sacciolepis huillensis* (Rendle) Stapf, in particular, is indistinguishable from *Elytrophorus* in leaf anatomy. These grasses share an identical habitat and physiognomy and the *S. huillensis* specimens examined in this study (Ellis 3716 & 3717) were collected together with *E. spicatus* (Ellis 3718) at the same locality at the same time. This observation may, or may not, be significant and deserves further discussion.

S. huillensis has nodular silica bodies, no intercostal short cells, long cells with straight or only slightly sinuous anticlinal walls and domed stomata. The microhairs are also elongated with a tapering distal cell, although the basal cell is slightly larger than that of *Elytrophorus*. In transection the anatomy of both species is virtually identical except, perhaps, that *S. huillensis* displays a tendency for the leaf to be somewhat thicker in the midrib. The work of Nixon (1953) confirms this anatomical structure for *S. huillensis*.

The anatomical resemblance between these two taxa, presently classified in two different subfamilies, may reflect convergent evolution in response to identical habitats, but the resemblance may also be phylogenetically significant. The leaf anatomy of *Elytrophorus* is strikingly similar to that of many of the C_3 panicoid taxa. This type of anatomy is fully described in Ellis (1986) and evaluated in relation to the panicoid grasses. The only anatomical differences between *Elytrophorus* and many of these panicoid species are the very sinuous long cells of the C_3 forest species in particular and the elongated but dumbbell-shaped silica bodies, although the nodular type may occur in some of these species.

Conclusions

The anatomical indications of this study are that *Elytrophorus* should possibly be assigned to the group of C_3 panicoid taxa rather than to the Danthonieae. The advisability of *Elytrophorus* being transferred to the Paniceae on morphological grounds needs to be carefully examined. It is of interest to note that the embryo of *Elytrophorus* is panicoid (Jacques Felix 1962) but the chromosome number of $x=13$ is most unusual for the Poaceae. In addition, the large group of C_3 panicoid grasses, including many species of *Panicum* as well as other genera, may warrant recognition at suprageneric level as they all share a similar basic leaf anatomy not found elsewhere in the Panicoideae. This group, together with *Elytrophorus*, may represent a primitive panicoid group forming a link between the Arundinoideae and the Panicoideae.

Elytrophorus is, therefore, a most interesting genus from a phylogenetic viewpoint and further studies on this genus may even help elucidate some aspects of evolution in the Poaceae as a whole. A better understanding of the systematics and taxonomy of *Elytrophorus* should help clarify our concepts of the grass subfamilies and their interrelationships.

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