

Kranz distinctive cells in the culm of *Arundinella* (Arundinelleae; Panicoideae; Poaceae)

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Keywords: anatomy, *Arundinella*, C₄, culm, distinctive cells, double bundle sheath, NADP-me

ABSTRACT

The transectional anatomy of photosynthetic flowering culms of *Arundinella berteroniana* (Schult.) Hitchc. & Chase and *A. hispida* (Willd.) Kuntze from South America and *A. nepalensis* Trin. from Africa is described and illustrated. The vascular bundles are arranged in three distinct rings, the outermost being external to a continuous sclerenchymatous band. Each of these peripheral bundles is surrounded by two bundle sheaths, a complete mestome sheath and an incomplete, outer, parenchymatous Kranz sheath, the cells of which contain large, specialized chloroplasts. Kranz bundle sheath extensions are also present. The chlorenchyma tissue is also located in this narrow peripheral zone and is interrupted by the vascular bundles and their associated sclerenchyma. Dispersed throughout the chlorenchyma are small groups of Kranz distinctive cells, identical in structure to the outer bundle sheath cells. No chlorenchyma cell is, therefore, more than two cells distant from a Kranz cell. The structure of the chlorenchyma and bundle sheaths indicates that the C₄ photosynthetic pathway is operative in these culms.

This study clearly demonstrates the presence of the peculiar distinctive cells in the culms as well as in the leaves of *Arundinella*. Also of interest is the presence of an inner bundle sheath in the vascular bundles of the culm whereas the bundles of the leaves possess only a single sheath. It has already been shown that *Arundinella* is a NADP-me C₄ type and the anatomical predictor of a single Kranz sheath for NADP-me species, therefore, either does not hold in the culms of this genus or the culms are not NADP-me. This is only the second reported breakdown of this association between MS anatomy and the NADP-me biochemical C₄ type.

UITTREKSEL

Die anatomie van dwarssneë van fotosintetiese bloeiwysehalms van *Arundinella berteroniana* (Schult.) Hitchc. & Chase en *A. hispida* (Willd.) Kuntze vanaf Suid-Amerika en *A. nepalensis* Trin. van Afrika word beskryf en geïllustreer. Die vaatbondels is in drie duidelike ringe gerangskik, met die buitenste vaatbondels aan die buitekant van 'n aaneenlopende sklerenchiemband. Hierdie periferele vaatbondels word elk omring deur twee vaatbondelskedes, 'n volledige mestoomskede en 'n onvolledige, buitenste parenchiematische Kranz-skede waarvan die selle groot, gespesialiseerde chloroplaste bevat. Kranz-verlengings van die bondelskede is ook teenwoordig. Chlorenchiemweefsel is ook teenwoordig in hierdie smal periferele sone en word onderbreek deur die vaatbondels en hul meegaande sklerenchiem. Klein groepies Kranz-kenmerkende selle wat struktureel identies is aan die buitenste vaatbondelskedeselle is deur die chlorenchiem versprei. Geen chlorenchiemselle is dus meer as twee selle van 'n Kranz-sel verwyder nie. Die struktuur van die chlorenchiem en die vaatbondelskede dui aan dat die C₄-fotosintetiese weg in die halms gevolg word.

Hierdie studie toon duidelik die teenwoordigheid van die unieke kenmerkende selle in beide die halms en blare van *Arundinella*. Ook opvallend was die teenwoordigheid van 'n binneste vaatbondelskede in die vaatbondels van die halm, terwyl die vaatbondels van die blare slegs 'n enkele skede besit. Daar is reeds getoon dat *Arundinella* 'n NADP-me C₄- tipe is, en die anatomiese aanwyser van 'n enkele Kranz-skede vir NADP-me-spesie is dus of nie van toepassing op die halms van hierdie genus nie of die halms is nie NADP-me nie. Hierdie is slegs die tweede bevestiging van 'n NADP-me biochemiese C₄- tipe sonder MS anatomie.

INTRODUCTION

Some species of *Arundinella* Raddii are characterized by the presence of Kranz distinctive cells in the mesophyll of the leaf blades. *Arundinella* is a C₄ genus which possesses the Kranz syndrome (Brown 1977) and these distinctive cells are very similar to those of the Kranz mestome sheath which surrounds the vascular bundles (Brown 1975). The distinctive cells have thicker walls than those of the radially arranged chlorenchyma cells between which they are embedded (Carolin *et al.* 1973) and these walls also stain heavily. They contain abundant specialized chloroplasts which store starch (Brown 1975; Renvoize 1982a). In transection they occur either

singly between the vascular bundles or are found in groups of two to six cells without accompanying vascular tissue.

Some authors are of the opinion that the distinctive cell files connect with the parenchyma sheath cells (Carolin *et al.* 1973; Ellis 1977). However, in paradermal view it is evident that they are not continuous with the vascular tissue but are contiguous isolated Kranz cell strands that lie parallel to the vascular bundles and are not in contact with them (Crookston & Moss 1973). They are presumably functionally linked to the vascular bundles at intervals by cross veins (Crookston & Moss 1973; Crookston 1980; Renvoize 1982a). Where the cross veins traverse strands of distinctive cells some of these Kranz cells become appressed to the cross vein, so forming a functional link with the vascular tissue.

These cells were first reported by Vickery (1935) in the leaf blade transection of *A. nepalensis* Trin. Tateoka

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MS. received: 1988.06.22.

TABLE 1.—Historical review of the study of Kranz distinctive cells in grass leaf blades

Taxon	Terminology	Reference
<i>Arundinella nepalensis</i>	Thick-walled cells resembling isolated bundle sheath cells	Vickery 1935
<i>Arundinella hirta</i>	Characteristic cells containing many chloroplasts	Tateoka 1956
<i>Garnotia stricta</i>	Distinctive cells	Tateoka 1956a
<i>Arundinella decempedalis</i> <i>Trichopteryx fructiculosa</i>	Reduzierte tertiäre Bündel	Conert 1957
<i>Arundinella nepalensis</i> , <i>A. holcoides</i> , <i>A. birmanica</i> , <i>A. decempedalis</i> , <i>A. bengalensis</i> , <i>A. leptochloa</i> , <i>A. purpurea</i> , <i>Garnotia stricta</i> , <i>G. tectorum</i> , <i>G. boninensis</i> , <i>G. acutigluma</i> , <i>G. fuscata</i> , <i>G. drymeia</i>	Distinctive cells	Tateoka 1958
<i>Arundinella berteroniana</i>	Similar to parenchyma sheath cells	Brown 1958
<i>Arundinella metzii</i>	Circular cells	Metcalfe 1960
<i>Arundinella ecklonii</i>	—	Jacques-Félix 1962
<i>Arthropogon scaber</i> , <i>A. piptostachya</i>	Distinctive cells	Tateoka 1963
<i>Antheophora cristata</i>	Distinctive cells	Johnson 1964
<i>Arundinella fuscata</i> , <i>A. metzii</i> , <i>A. palmeri</i> , <i>A. spicata</i>	Células redondeadas algo incoloras de estructura semejante a la de las células de la vaina parenquimática	Türpe 1970
<i>Garnotia</i> spp.	Cells similar to bundle sheath cells	Gould 1972
<i>Arundinella montana</i> , <i>A. berteroniana</i>	Distinctive cells	Li & Phipps 1973
<i>Arundinella nepalensis</i>	Isolated parenchyma sheath cells	Carolin <i>et al.</i> 1973
<i>Antheophora cristata</i>	Distinctive cells	Johnson & Brown 1973
<i>Arundinella hirta</i>	Specialized parenchyma cells	Crookston & Moss 1973
<i>Arundinella</i> spp. <i>Arthropogon</i> spp. <i>Antheophora</i> spp. <i>Garnotia</i> spp.	Distinctive cells	Brown 1975
<i>Arundinella nepalensis</i> <i>Garnotia stricta</i>	Interveinal circular cells	Hattersley & Watson 1975
<i>Antheophora</i> spp. <i>Arthropogon</i> spp. <i>Arundinella</i> spp. <i>Loudetia</i> spp. <i>Trichopteryx</i> spp. <i>Garnotia</i> spp.	Distinctive cells	Brown 1977
<i>Garnotia stricta</i>	Circular cells	Clifford & Watson 1977
<i>Arundinella nepalensis</i>	Distinctive cells	Ellis 1977
<i>Arundinella hirta</i>	Specialized parenchyma cells	Reger & Yates 1979
<i>Arundinella hirta</i>	Isolated Kranz cells	Crookston 1980
<i>Arundinella nepalensis</i>	Distinctive cells	Hattersley & Browning 1981
<i>Arundinella nepalensis</i>	Auxillary bundle cells	Renvoize 1982
<i>Garnotia stricta</i>	Auxillary bundle cells	Renvoize 1982
<i>Antheophora</i> spp. <i>Arthropogon</i> spp. <i>Arundinella</i> spp. <i>Loudetia</i> spp. <i>Trichopteryx</i> spp. <i>Garnotia</i> spp.	Circular cells	Watson, Dallwitz & Johnston 1986
<i>Arundinella</i> spp. <i>Garnotia</i> spp.	Auxillary bundle cells	Clayton & Renvoize 1986

(1956b) was the first to designate these cells calling them distinctive cells. Subsequently various authors have used differing terminology and a historical review of the study and terminology of these cells is given in Table 1.

This tabulated summary (Table 1) shows that the term distinctive cells appears to be the most widely accepted

for these structures and it will be used in this paper. However, the term distinctive cell does not convey the structure or function of these cells and the proposal of the term auxiliary bundle cells (Renvoize 1982a; Clayton & Renvoize 1986) has some merit since these cells undoubtedly are part of the photosynthetic system, being auxiliary photosynthetic strands. Hattersley *et al.* (1977) have

demonstrated that these cells are isolated photosynthetic carbon reduction (PCR, Kranz) strands embedded in the primary carbon assimilation (PCA) chlorenchyma tissue; and they exhibit NADP-me activity (Reger & Yates 1979). Ultrastructurally they are also seen to be similar to the Kranz mestome sheath cells. Both have large agranal chloroplasts containing numerous starch grains (Crookston & Moss 1973; Crookston 1980) and a suberized lamella is located in the cell walls (Hattersley & Browning 1981). The chloroplasts of the chlorenchyma cells, on the other hand, are free of starch and have well developed grana and the cell walls lack a suberized lamella. The distinctive cells are, therefore, undoubtedly Kranz cells and will be designated as such.

From Table 1 it can also be seen that distinctive cells have only been reliably reported in four genera belonging to four small tribes of the Panicoideae: *Arundinella* of the Arundinelleae (Tateoka 1956a, 1958); *Garnotia* of the Garnotieae (Tateoka 1956b, 1958); *Arthropogon* of the Arthropogoneae (Tateoka 1963) and *Antheophora* of the Anthephoreae (Johnson & Brown 1973). Watson *et al.* (1986) record 'circular cells' in nine genera of the Panicoideae. The reports of distinctive cells in *Trichopteryx* and *Loudetia* of the Arundinelleae (Brown 1977) appear to be misleading and probably refer to the very reduced vascular bundles surrounded by only three or four Kranz sheath cells which are known from these genera which also lack cross veins (Renvoize 1982a). Many authors have confirmed the occurrence of distinctive cells in *Arundinella* and *Garnotia* (Table 1) and *Arthropogon xerachne* (Sánchez & Arriaga 1988) but verification of their reported presence in *Antheophora* is required. We have examined leaves of 25 specimens of four species of *Antheophora*, all of which have very small minor vascular bundles consisting of only three or four bundle sheath cells surrounding a minute vascular strand. Consequently we query the reported presence of distinctive cells in this genus. We have also examined leaves of *Tristachya lejostachya* and *Loudetia flammida* (Sánchez & Arriaga 1988), *L. pedicellata* and *L. simplex* (Ellis 1977) without detecting the presence of distinctive cells. In all these cases a few xylem vessels were detected in association with the Kranz cells but these are not considered to be distinctive cells.

Nevertheless, as presently known, distinctive cells are characteristic of and unique to these four small tribes of the Panicoideae and may indicate phylogenetic relationships between them. Johnson & Brown (1973) consider the possession of distinctive cells to be sufficient grounds for considering these four tribes as constituting one tribe or even a supertribe. *Garnotia* and *Arundinella*, in particular, are very closely related (Renvoize 1982b) and appear to constitute a distinct and related group of genera sharing this interesting anatomical feature, as well as spikelet characteristics. Distinctive cells are not a characteristic of the tribe Arundinelleae but are only a feature of some species of *Arundinella* (Renvoize 1982a).

The culms (aerial stems) of grasses display considerable anatomical variation but, in contrast to the leaf blade, have been poorly documented (Sabnis 1921; Canfield 1933; De Wet 1960; Metcalfe 1960; Auquier & Somers 1967). Some of these studies include members of the Arundinelleae. De Wet (1960) describes the peri-

pheral vascular bundles of the culm of *Arundinella* as being surrounded by a parenchymatous bundle sheath composed of small cells. Auquier & Somers (1967) consider the anatomical structure of the culm of *Arundinella* as belonging to the 'panicoid type' with the peripheral bundles surrounded by a well developed parenchymatous sheath. None of these authors refer to the presence of Kranz anatomy in the cortical zone of the culm. Sánchez (1979, 1981a, 1981b, 1983a, 1983b, 1984) is the first worker to report the presence and development of Kranz anatomy in flowering and stoloniferous culms. Kranz anatomy is only developed in the upper exposed parts of flowering culms and not the basal parts which are covered by the leaf sheath (Sánchez 1981a); it is therefore essential to examine comparative material.

The objective of this study is to determine whether *Arundinella* exhibits Kranz structure in the flowering culm. If this is so then it will also be of interest to see whether distinctive Kranz cells are also present. This paper describes the structure and arrangement of these cells in the culms of three species of *Arundinella*: *A. berteroniana* (Schult.) Hitchc. & Chase and *A. hispida* (Willd.) Kuntze from Argentina and *A. nepalensis* from South Africa. *A. hispida* from the New World and *A. nepalensis* from the Old World appear to be closely related and Phipps (1967) included them both in the Nepalenses series which he considered to be central to the genus.

MATERIALS AND METHODS

Transverse and longitudinal sections of flowering culms were made from segments taken from the centre of the first internode below the inflorescence. Both herbarium and field collected material fixed in FAA was used. Sections were either free-hand or the material was desiccated, embedded in wax and sectioned on a rotary microtome. These sections were stained with Alcian Blue and Safranin (Cutler 1978) or Fast Green and Safranin (Johansen 1940). Uncleared sections were soaked in 5% NaOH for 5–10 minutes to restore turgidity and were then used to observe chloroplast position in the Kranz cells.

Material examined

A. berteroniana

BA 27/2263; BA 18993; Giusti 1214 (BA); Parodi 1781 (BA); Vervoorst & Cuezso 7731 (CTES).

A. hispida

BA 11258; BA 16098; Schinini & Tressens 24545 (BA); Schinini *et al.* 17348 (CTES); Quarin 409 (CTES); Schulz 3469 (CTES); Royo 238 (CTES).

A. nepalensis

BAA 19752; Ellis 479 (PRE 61722)*, 1218 (PRE 61723)*, 1368 (PRE 61724)*, 1436 (PRE 61725)*, 1481 (PRE 61726)*, 1617 (PRE 61727)*, 2116 (PRE 61728)*, 3358 (PRE 622413)*, 4977.

ANATOMICAL DESCRIPTION OF THE CULM

The general shape of the sections is circular (Figures 1A; 2A, C & E; 3A; 4A) with a smooth or slightly undulating outline. The diameter of the transections was

* only leaf blade material examined.

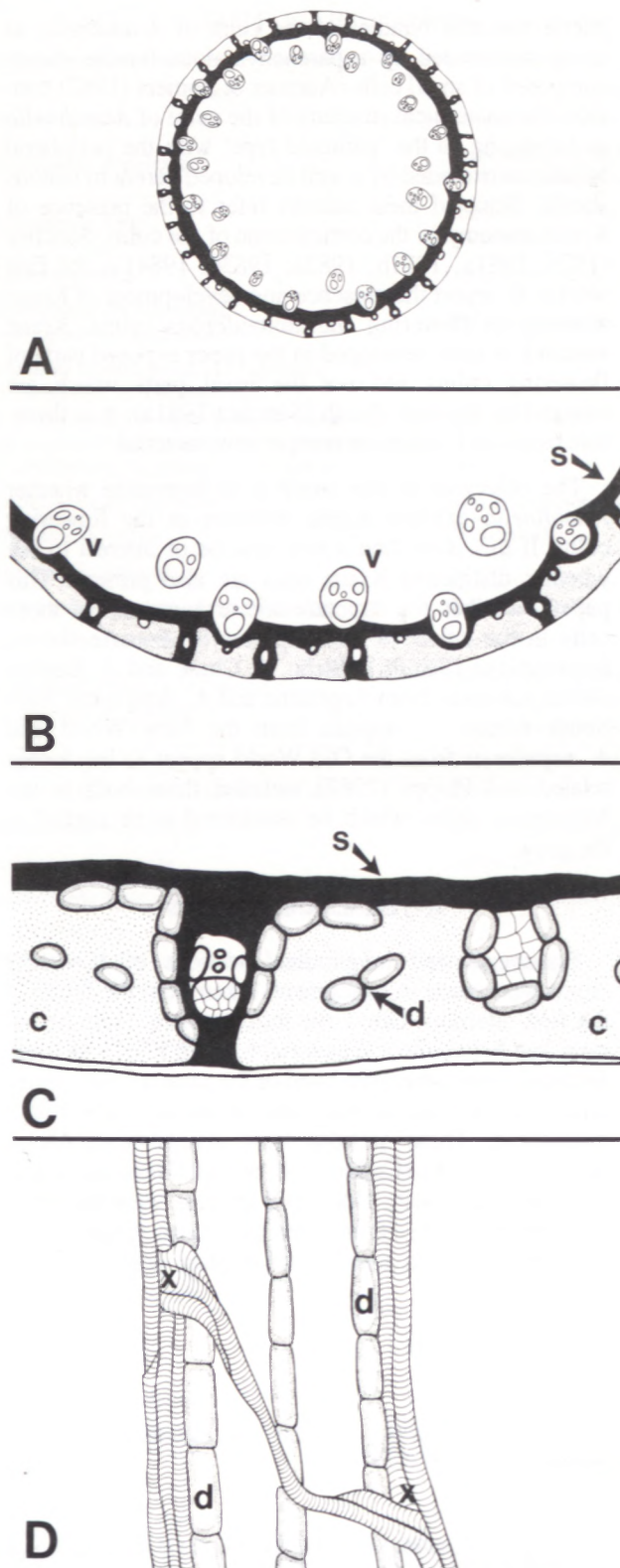


FIGURE 1.—Schematic diagrams of the culm anatomy of *Arundinella*. A, transsection of the first internode of a flowering culm; B, transsectional detail showing arrangement of vascular bundles (v) and the location of the sclerenchymatous ring (s); C, detail of the peripheral zone showing distinctive cells (d) in the chlorenchyma (c); D, paradermal longitudinal view of Kranz distinctive cells (d) with a transverse connection of xylem (x).

found to be ± 2 mm in *A. berteroniana* and *A. hispida* and $\pm 1,5$ mm in *A. nepalensis*.

The epidermis is simple. Stomata were observed adjacent to the chlorenchyma zones and the subsidiary cells

are at the same level as the epidermal cells (Figures 2D; 4C). No prickle hairs or hooks were observed.

A discontinuous ring of chlorenchyma is present below the epidermis. This ring consists of 1–6 layers of rachymorph cells none of which are more than two cells distant from a Kranz cell. This tissue is interrupted at regular intervals by the sclerenchyma girders of the peripheral vascular bundles (Figures 1B; 2B, D & F; 3C; 4B). This peripheral zone is narrow, occupying $1/10$ – $1/12$ of the total diameter of the culm transection.

This peripheral chlorenchymatous zone is bounded internally by a continuous ring of sclerenchyma consisting of 1–3(–4) layers of lignified, fibrous cells (Figures 1B; 2B, D & F; 3C; 4B). This unicylindrical sclerenchymatous ring encloses the parenchymatous pith, the centre of which may be hollow (Figures 2A; 4A) or not (Figures 2C; 3A).

The vascular bundles are arranged in 3(–6) distinct circles or rings and are alternately spaced (Figures 1A; 2A, C & E; 3A; 4A), although rarely 4 or 5 circles of bundles are present. The bundles can be divided into two types: peripheral bundles and non-peripheral bundles.

The peripheral vascular bundles are external to the sclerenchymatous ring and occur in two distinct size classes. The larger first or second order bundles with metaxylem vessels are partially attached to the sclerenchyma ring and are linked to the epidermis by sclerenchyma girders (Figures 1C; 2B, D & F; 3C; 4B). These bundles are surrounded by two bundle sheaths, a complete mestome sheath and an incomplete Kranz parenchyma sheath (Figures 1C; 2B & D; 4C). Bundle sheath extensions of the latter sheath may extend along the outer surface of the sclerenchymatous ring for a distance of from 2–3 cells (Figures 1C; 4C). Some of the larger bundles may exhibit a partial or complete periphloematic sheath (Caro 1961). The smaller third order peripheral bundles without metaxylem vessels do not have sclerenchyma girders attaching them to the epidermis (Figures 1C; 2F; 4C). These bundles are surrounded by only a single incomplete Kranz parenchyma sheath, interrupted where it adjoins the sclerenchymatous ring. These smaller bundles may also possess bundle sheath extensions.

Distinctive Kranz cells are present in the peripheral zone (Figures 1C; 2B; 4B & C). These cells are similar in structure to the Kranz parenchyma sheath cells of all the vascular bundles of this zone. They have thicker walls and larger, predominately centrifugally located chloroplasts than do the chlorenchyma cells and are found singly or in groups of 1–3(–4) without associated xylem or phloem cells.

In paradermal view the Kranz distinctive cells form long rows, 1 or 2 cells wide, that lie parallel to the vascular bundles but are not accompanied by vascular tissue (Figure 1D). They are connected by lateral cross-veins which traverse from one vascular bundle to another. These interconnections consist only of xylem elements and they are not accompanied by bundle sheath cells. No phloem cells were seen. Interconnections are relatively common in the chlorenchymatous zone in the culms of *Arundinella*.

A second and third (seldom a fourth or fifth) circle of collateral vascular bundles is situated on the inner side of

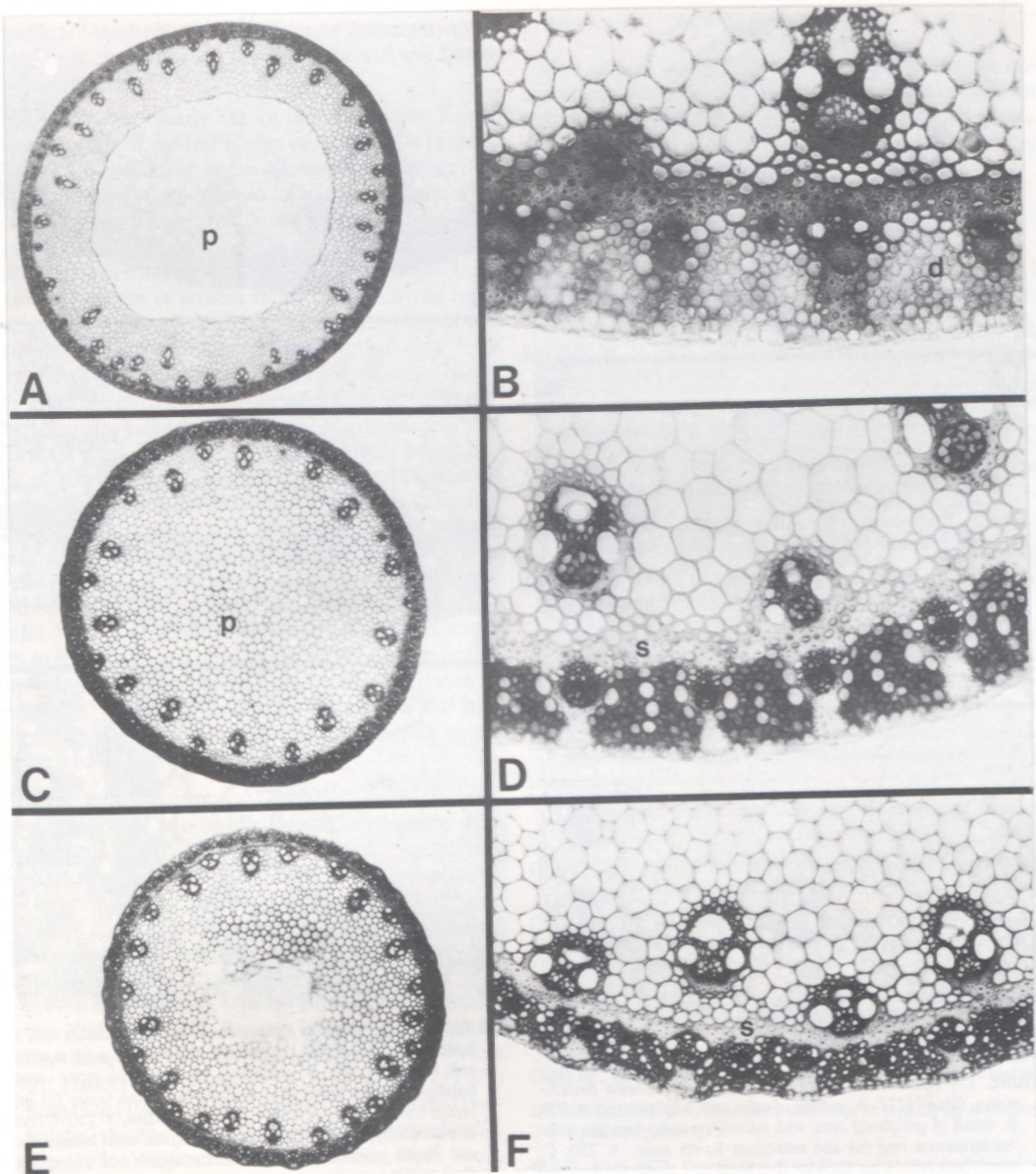


FIGURE 2.—Culm anatomy of *Arundinella hispida* as seen in transverse section. A–B, *Schinini & Tressens 24545*: A, culm outline with hollow pith (p), $\times 50$; B, peripheral zone with vascular bundles, chlorenchyma and distinctive cells (d) external to the continuous sclerenchyma ring (s), $\times 400$. C–D, *Schinini et al. 17348*: C, culm outline showing solid pith (p), $\times 50$; D, detail of peripheral Kranz tissue with distinctive cells in the chlorenchyma external to the sclerenchyma ring (s), $\times 400$. E–F, *BA 11258*: E, culm outline, $\times 50$; F, detail of peripheral zone with external vascular bundles, the sclerenchyma ring (s) and internal vascular bundles in the pith, $\times 250$.

the sclerenchymatous ring. The second circle is partially embedded in these fibres but the other circles are located in the parenchymatous ground tissue of the pith. These inner two circles of bundles consist only of larger, first order vascular bundles surrounded by a single mestome sheath (Figures 1B; 2B, D & F; 3B, C; 4B).

DISCUSSION AND CONCLUSIONS

The presence of these rare and specialized Kranz distinctive cells has previously been confirmed in only two genera, *Arundinella* and *Garnotia*. However, there has

been much confusion in the literature regarding the terminology for these cells (Table 1) and, although *Watson et al. (1986)* record circular cells in nine genera, it is not clear whether these are all homologous with the particular cells described here. This situation is confusing and unsatisfactory and it is proposed that the term Kranz distinctive cells should in future be employed only for isolated groups of, or single, Kranz cells in the mesophyll which are not associated with contiguous vascular tissue. The term distinctive cells enjoys historical precedent (*Tateoka 1956b*) and Kranz distinctive cells also gives an indication of their function. Furthermore this designation is explicit even when translated into other

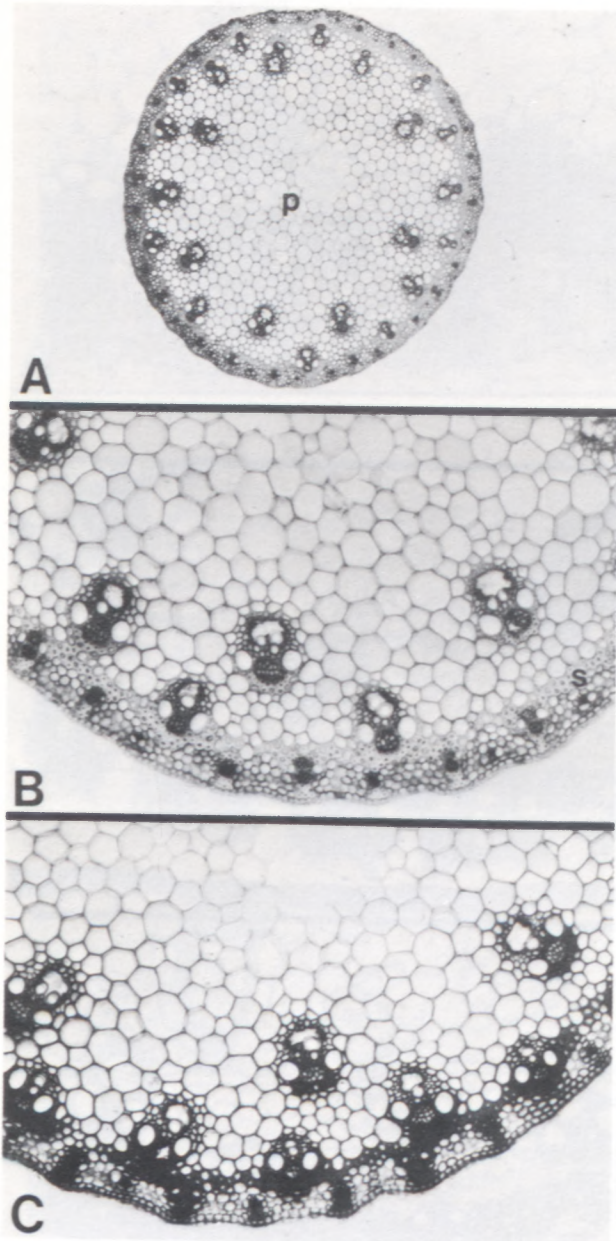


FIGURE 3.—Transsectional culm anatomy of *Arundinella berteroniana*, Giusti 1214. A, outline of culm with solid pith (p), $\times 100$; B, detail of peripheral zone with internal vascular bundles, sclerenchymatous ring (s) and outermost Kranz zone, $\times 250$; C, outer, peripheral zone showing darkly stained, thickened lignified tissue of the mestome sheaths, sclerenchyma girders and the sclerenchyma ring, $\times 250$.

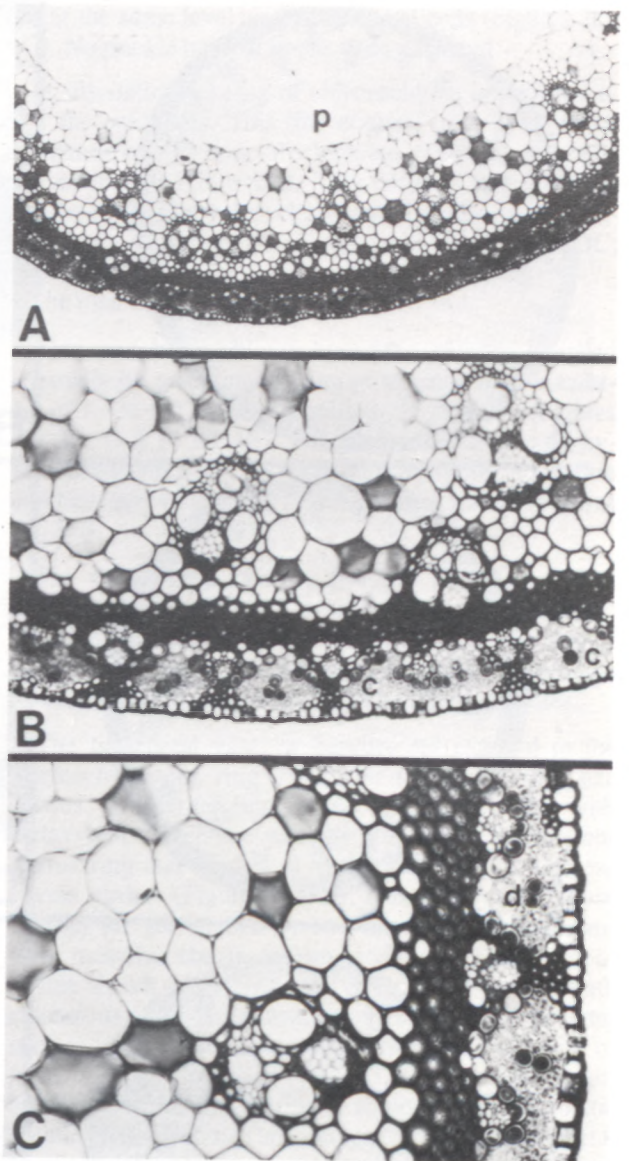


FIGURE 4.—Culm anatomy of *Arundinella nepalensis*, Ellis 4977. A, hollow pith (p) with two rings of vascular bundles in the outermost pith layers, $\times 100$; B, peripheral zone showing inner vascular bundles, sclerenchyma ring and chlorenchyma tissue (c) interrupted by outer ring of Kranz vascular bundles, $\times 250$; C, detail of chlorenchyma, distinctive cells (d), Kranz outer bundle sheath and sheath extensions, inner mestome sheath and sclerenchyma ring, $\times 400$.

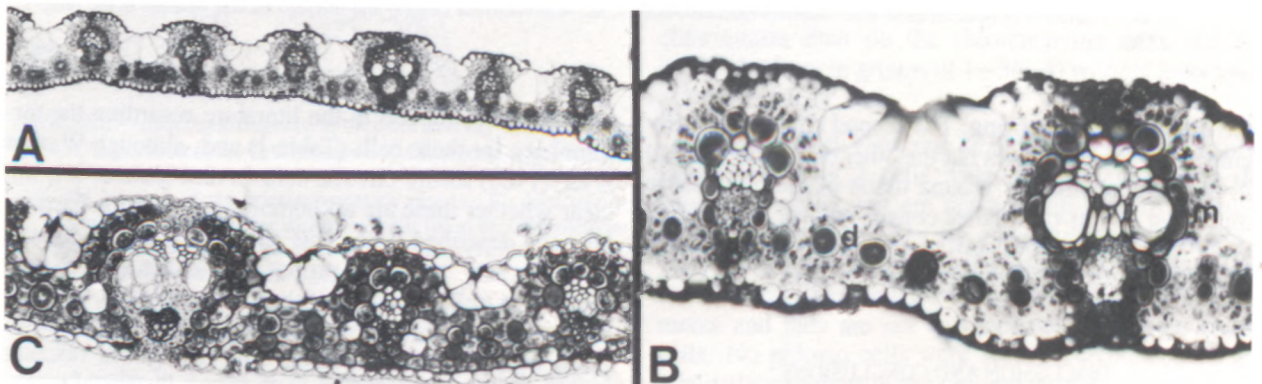


FIGURE 5.—Leaf blade anatomy of *Arundinella* in transverse section. A—B, *A. nepalensis*: A, distribution of distinctive cells in the chlorenchyma between all vascular bundles, Ellis 1481, $\times 100$; B, anatomical detail of distinctive cells (d) and single, Kranz vascular bundle sheath (m), Ellis 1617, $\times 400$. C, *A. berteroniana* with distinctive cell groups dispersed in the chlorenchyma tissue, Davids 32217, $\times 400$.

languages. Standardization on this most commonly used terminology should ensure the elimination of any future misunderstanding.

This study has clearly shown that the unique Kranz distinctive cells of the leaf blades of *Arundinella* (Figure 5A, B & C) also occur in the photosynthetic culms. In culm transections they are seen to be rounded cells with thickened walls which contain specialized chloroplasts. They are distinctly larger than the chlorenchyma cells in which they are embedded. These distinctive cells occur as isolated groups or strands in the chlorenchyma comprising one to three contiguous Kranz cells without accompanying vascular tissue. In paradermal view it is clear that they do not form part of the vascular tissue and, therefore cannot be considered as degenerate intercalary vascular bundles (Brown 1977). Instead they are seen to be long, isolated Kranz cell columns not physically connected to the vascular bundles but presumably functionally linked at regular intervals by vascular strands. This structure is virtually identical to that described for the distinctive cells of the leaf blades of several *Arundinella* species. There can be no doubt that these cells which are reported here in the culms of *Arundinella* for the first time, represent homologous structures in leaf blades and photosynthetic culms. The occurrence of Kranz anatomy in both culms and leaves is noteworthy, because grass species with Kranz leaf anatomy do not necessarily exhibit Kranz structure in the culm as well (Sánchez unpublished).

The fact that the peripheral first order vascular bundles are surrounded by two bundle sheaths, a complete mesotome sheath and an interrupted Kranz parenchyma sheath, is of considerable interest because this configuration (Figure 5) differs from the condition in the leaf blade as reported in the literature. Many authors record a single bundle sheath in the leaf of *Arundinella* species, which is referred to as the XyMS condition by Hattersley & Watson (1976) or as the MS type by Brown (1977). Examples are Vickery (1935), Brown (1958, 1977), Metcalfe (1960), Jacques-Félix (1962), Crookston & Moss (1973), Hattersley & Watson (1975, 1976), Ellis (1977) and Renvoize (1982a). Other workers have reported double bundle sheaths in the leaf blades of *Arundinella*. Tateoka (1956a) illustrates this PS condition for *A. hirta*, Conert (1957) for *A. decempedalis*, Tateoka (1958) for *A. leptochloa* and *A. villosa* and Li & Phipps (1973) for *A. bengalensis*. Some of these latter workers (Tateoka 1958; Li & Phipps 1973) studied *A. nepalensis* and *A. berteroniana*, which were also examined in the present study, and found them to have only a single bundle sheath. Eight specimens of *A. nepalensis* and one of *A. berteroniana* examined in this study were all observed to have only a single Kranz sheath in the leaf blade. It was, therefore, most unexpected to observe a definite, inner fibrous sheath in the first order bundles of the culm of all three species studied. This may reflect a general condition present in all NADP-me grasses or may be an exceptional condition limited to *Arundinella* and other taxa with distinctive cells. This interesting observation requires further study as it represents a rare exception to the XyMS character for predicting the NADP-me biochemical C₃ type (Hattersley 1987). This anatomical predictor for the NADP-me type may, therefore, apply to leaf blades only or leaves and culms of a given grass may have different photosynthetic pathways.

ACKNOWLEDGEMENTS

The authors are grateful to Aurelio Schinini for co-operation with collection of fresh material, A. Botha for technical assistance, A. Romanowski for the photography, G. Condy for the line drawings and M. van der Merwe for typing the manuscript.

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