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

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The transectional anatomy of photosynthetic flowering culms of *Arundinella berteroniana* (Schult.) Hitchc. & Chase and *A. hispida* (Willd.) Kunze 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 sheath 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.

INTRODUCTION

Some species of *Arundinella* Radii 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
(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

| Taxon                          | Terminology                                      | Reference         |
|-------------------------------|--------------------------------------------------|-------------------|
| *Arundinella nepalensis*      | Thick-walled cells resembling isolated bundle sheath cells | Vickery 1935      |
| *Arundinella hirta*           | Characteristic cells containing many chloroplasts | Tateoka 1956      |
| *Garnotia stricta*            | Distinctive cells                                | Tateoka 1956a     |
| *Arundinella decempedalis*    | Reduzierte tertiäre Bundel                        | Conert 1957       |
| *Trichopteryx fructiculosa*   |                                                   |                   |
| *Arundinella nepalensis*      | Distinctive cells                                | Tateoka 1958      |
| *A. holcoides*                |                                                   |                   |
| *A. birmanica*                |                                                   |                   |
| *A. bengalenisis*             |                                                   |                   |
| *A. leptochloa*               |                                                   |                   |
| *A. purpurea*                 |                                                   |                   |
| *Garnotia stricta*            |                                                   |                   |
| *G. tectorum*                 |                                                   |                   |
| *G. boninensis*               |                                                   |                   |
| *G. acutigluma*               |                                                   |                   |
| *G. fusca*                    |                                                   |                   |
| *G. drymeia*                  |                                                   |                   |
| *Arundinella berteroniana*    |                                                   |                   |
| *Arundinella metzii*          |                                                   |                   |
| *Arundinella ecklonii*        |                                                   |                   |
| *Arundinella scaber*          |                                                   |                   |
| *A. pipistachya*              |                                                   |                   |
| *Antheophora cristata*        |                                                   |                   |
| *Arundinella fuscata*         |                                                   |                   |
| *A. metzii*                   |                                                   |                   |
| *A. palmer*                   |                                                   |                   |
| *A. spicata*                  |                                                   |                   |
| *Garnotia spp.*               |                                                   |                   |
| *Arundinella montana*         |                                                   |                   |
| *A. berteroniana*             |                                                   |                   |
| *Arundinella nepalensis*      |                                                   |                   |
| *Garnotia spp.*               |                                                   |                   |
| *Arundinella stricta*         |                                                   |                   |
| *Arundinella spp.*            |                                                   |                   |
| *Trichopteryx spp.*           |                                                   |                   |
| *Garnotia spp.*               |                                                   |                   |
| *Garnotia stricta*            |                                                   |                   |
| *Antheophora spp.*            |                                                   |                   |
| *Arthropogon spp.*            |                                                   |                   |
| *Garnotia spp.*               |                                                   |                   |
| *Garnotia spp.*               |                                                   |                   |
| *Garnotia stricta*            |                                                   |                   |
| *Arundinella nepalensis*      |                                                   |                   |
| *Arundinella hirta*           |                                                   |                   |
| *Arundinella hirta*           |                                                   |                   |
| *Arundinella nepalensis*      |                                                   |                   |
| *Antheophora spp.*            |                                                   |                   |
| *Arthropogon spp.*            |                                                   |                   |
| *Garnotia spp.*               |                                                   |                   |
| *Garnotia spp.*               |                                                   |                   |
| *Garnotia spp.*               |                                                   |                   |
| *Garnotia stricta*            |                                                   |                   |
| *Arundinella nepalensis*      |                                                   |                   |
| *Arundinella hirta*           |                                                   |                   |
| *Arundinella hirta*           |                                                   |                   |
| *Arundinella nepalensis*      |                                                   |                   |
| *Antheophora spp.*            |                                                   |                   |
| *Arthropogon spp.*            |                                                   |                   |
| *Garnotia spp.*               |                                                   |                   |
| *Garnotia spp.*               |                                                   |                   |
| *Garnotia stricta*            |                                                   |                   |
| *Arundinella nepalensis*      |                                                   |                   |
| *Arundinella hirta*           |                                                   |                   |
| *Arundinella hirta*           |                                                   |                   |
| *Arundinella nepalensis*      |                                                   |                   |
| *Garnotia stricta*            |                                                   |                   |
| *Antheophora spp.*            |                                                   |                   |
| *Arthropogon spp.*            |                                                   |                   |
| *Garnotia spp.*               |                                                   |                   |
| *Garnotia spp.*               |                                                   |                   |
| *Garnotia stricta*            |                                                   |                   |
| *Arundinella nepalensis*      |                                                   |                   |
| *Arundinella hirta*           |                                                   |                   |
| *Arundinella hirta*           |                                                   |                   |
| *Arundinella nepalensis*      |                                                   |                   |
| *Antheophora spp.*            |                                                   |                   |
| *Arthropogon spp.*            |                                                   |                   |
| *Garnotia spp.*               |                                                   |                   |
| *Garnotia spp.*               |                                                   |                   |
| *Garnotia stricta*            |                                                   |                   |
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 Arundinellinae (Tateoka 1956a, 1958); Garnotia of the Garnotiae (Tateoka 1956b, 1958); Arthropogon of the Arthropogoneae (Tateoka 1963) and Anthephora 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 Arundinellinae (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 Anthephora is required. We have examined leaves of 25 specimens of four species of Anthephora, 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 Arundinellinae 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 Arundinellinae. De Wet (1960) describes the peripheral 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. bertoniania (Schult.) Hitchc. & Chase and A. hispida (Wild.) 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. bertoniania**
  - BA 27/2263; BA 18993; Giusti 1214 (BA); Parodi 1781 (BA); Vervoorst & Curezzo 7751 (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 61726)*; 3558 (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 transsections was

* only leaf blade material examined.
found to be ± 2 mm in *A. berteroniana* and *A. hispida* and ± 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 unicylindrical sclerenchymatous ring encloses the parenchymatous pith, the centre of which may be hollow (Figures 2A; 4A) or not (Figures 2C; 3A).

The peripheral 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 crossveins 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
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.—Transectional culm anatomy of *Arundinella bertero­niana*, Giusti 1214. A, outline of culm with solid pith (p), × 100; B, detail of peripheral zone with internal vascular bundles, sclerenchymatous ring (s) and outermost Kranz zone, × 250; C, outer, peripheral zone showing darkly stained, thickened lignified tissue of the mestome sheaths, sclerenchyma girders and the sclerenchyma ring, × 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, × 100; B, peripheral zone showing inner vascular bundles, sclerenchyma ring and chlorenchyma tissue (c) interrupted by outer ring of Kranz vascular bundles, × 250; C, detail of chlorenchyma, distinctive cells (d), Kranz outer bundle sheath and sheath extensions, inner mestome sheath and sclerenchyma ring, × 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, × 100; B, anatomical detail of distinctive cells (d) and single, Kranz vascular bundle sheath (m), Ellis 1617, × 400. C, *A. bertero­niana* with distinctive cell groups dispersed in the chlorenchyma tissue, Davidsen 32217, × 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 mesophyll 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 C₄ 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.

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REFERENCES

AUQUIER, P. & SOMERS, Y. 1967. Recherches histotaxonomiques sur le chaume des Poaceae. Bulletin de la Société Royale Botanique de Belgique 100: 95–140.

BROWN, W. V. 1958. Leaf anatomy in grass systematics. Botanical Gazette 119: 170–178.

BROWN, W. V. 1975. Variations in anatomy, associations, and origins of Kranz tissue. American Journal of Botany 62: 395–402.

BROWN, W. V. 1977. The Kranz syndrome and its subtypes in grass systematics. Memoirs of the Torrey Botanical Club 23: 1–97.

CANFIELD, R. H. 1933. Stem structure of grasses in the Jomadas region. Audio 77: 226–354.

CAROLIN, R. C., JACOBS, S. W. L. & VESK, M. 1973. The structure of the cells of the mesophyll and parenchymatous bundle sheath of the Gramineae. Botanical Journal of the Linnean Society 66: 259–275.

CLAYTON, W. D. & RENVOIZE, S. A. 1986. Genera graminum: grasses of the world. Kew Bulletin Additional Series 13: 1–389.

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

CONERT, H. J. 1957. Beiträge zur Monograph der Arundinelleae. Botanische Jahrbacher 77: 226–354.

CROOKSTON, R. K. 1980. The structure and function of C₄ vascular tissue—some unanswered questions. Berichte der Deutschen Botanischen Gesellschaft 93: 71–78.

CROOKSTON, R. K. & MOSS, D. N. 1973. A variation of C₄ leaf anatomy in Arundinella hirta (Gramineae). Plant Physiology 52: 397–402.

CUTLER, D. 1978. Applied plant anatomy. Academic Press, London.

DE WET, J. M. J. 1960. Culm anatomy in relation to taxonomy. Bothalia 7: 311–316.

ELLIS, R. P. 1977. Distribution of the Kranz syndrome in the southern African Eragrostidoideae and Panicoidae according to bundle sheath anatomy and cytology. Agroplantae 9: 73–110.

GOULD, F. W. 1972. A systematic treatment of Garnotia (Gramineae). Kew Bulletin 27: 515–562.

HATTERSLEY, P. W. 1987. Variations in photosynthetic pathway. In T. R. Soderstrom et al., Grass systematics and evolution. Smithsonian Institution Press, Washington D.C.

HATTERSLEY, P. W. & BROWNING, A. J. 1981. Occurrence of the suberized lamella in leaves of grasses of different photosynthetic types. 1. In parenchymatous bundle sheaths and PCR (Kranz) sheaths. Protoplasma 109: 371–401.

HATTERSLEY, P. W. & WATSON, L. 1975. Anatomical parameters for predicting photosynthetic pathways of grass leaves: the 'maximum lateral cell count' and the 'maximum cells distant count'. Photosymomorphology 25: 325–333.

HATTERSLEY, P. W. & WATSON, L. 1976. C₄ grasses: an anatomical criterion for distinguishing between NADP-malic enzyme species and PCR or NAD-malic enzyme species. Australian Journal of Botany 24: 297–308.

HATTERSLEY, P. W., WATSON, L. & OSMOND, C. B. 1977. In situ immunofluorescent labelling of Ribulose-1,5-biphosphate
carboxylase in leaves of C₃ and C₄ plants. *Australian Journal of Plant Physiology* 4: 523–539.

JACQUES-FELIX H. 1962. *Les graminées d’Afrique Tropicale. 1. Generalités, classification, description des genres.* Institut de Recherches Agronomiques Tropicales et des Cultures Vivieres, Paris.

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

JOHNSON, M. C. 1964. *An electron microscope study of the photosynthetic apparatus in plants with special reference to the Gramineae.* Ph.D. thesis, University of Texas, Austin.

JOHNSON, M. C. & BROWN, W. V. 1973. Grass leaf ultrastructural variations. *American Journal of Botany* 60: 727–735.

LI, Y.-H. C. & PHIPPS, J. B. 1973. Studies in the Arundinelleae. XV. Taximetrics of leaf anatomy. *Canadian Journal of Botany* 51: 657–680.

METCALFE, C. R. 1960. *Anatomy of the Monocotyledons. 1. Gramineae.* Clarendon Press, Oxford.

PHIPPS, J. B. 1967. Studies in the Arundinelleae (Gramineae). V. The series of the genus *Arundinella.* *Canadian Journal of Botany* 45: 1047–1057.

REGER, B. J. & YATES, I. E. 1979. Distribution of photosynthetic enzymes between mesophyll specialized chlorenchyma and bundle sheath cells of *Arundinella hirta.* *Plant Physiology* 63: 209–212.

RENOIZE, S. A. 1982a. A survey of leaf-blade anatomy in grasses. II. *Arundinelleae.* *Kew Bulletin* 37: 489–495.

RENOIZE, S. A. 1982b. A survey of leaf-blade anatomy in grasses. III. *Garnotideae.* *Kew Bulletin* 37: 497–500.

SABNIS, T. S. 1921. The physiological anatomy of the plants of the Indian desert. *Journal of Indian Botany* 2: 217–227.

SANCHEZ, E. 1979. Estructura Kranz en tallos de *Gramineae.* *Kurtziana* 12–13: 113–118.

SANCHEZ, E. 1981a. Desarrollo de la estructura Kranz en tallos de *Gramineae.* *Lilloa* 35: 37–40.

SANCHEZ, E. 1981b. Variación de la estructura Kranz en el tallo de *Diandrosclaria glomerata.* *Lilloa* 35: 41–46.

SANCHEZ, E. 1983a. Estudios anatómicos en *Blepharidachne Hackel* (Poaceae, Eragrostidoideae, Eragrostideae). *Revista de Museo Argentino de Ciencias Naturales. Botánica* 6: 73–87.

SANCHEZ, E. 1983b. *Dasyochloa Willdenow ex Rydberg (Poaceae), género monotípico de Norteamérica.* *Lilloa* 36: 130–138.

SANCHEZ, E. 1984. Estudios anatómicos en el género *Munroa* (Poaceae, Chloridoideae, Eragrostideae). *Darwiniana* 25: 43–57.

SANCHEZ, E. & ARRIAGA, M. 1988. El síndrome de Kranz en Arundinelleae (Panicoidaeae, Poaceae) de la Flora Sudamericana. *Parodiana* 6.

TATEOKA, T. 1956a. Re-examination of anatomical characteristics of the leaves of Eragrostidoideae and Panicoidaeae (Poaceae). *Journal of Japanese Botany* 31: 210–218.

TATEOKA, T. 1956b. Notes on some grasses. I. *Botanical Magazine, Tokyo* 69: 311–315.

TATEOKA, T. 1958. Notes on some grasses. VIII. On leaf structure of *Arundinella* and *Garnota.* *Botanical Gazette* 110: 101–109.

TATEOKA, T. 1963. Notes on some grasses. XV. Affinities and species relationships of *Arthropogon* and relatives, with reference to leaf structure. *Botanical Magazine, Tokyo* 76: 286–291.

TÜRPE, A. M. 1970. Sobre la anatomia foliar de *Jansenella griffithiana* (Poaceae, Arundinelleae). *Senckenbergiana Biologica* 51: 277–285.

VICKERY, J. W. 1935. Leaf anatomy and vegetative characters of the indigenous grasses of New South Wales. *Proceedings of the Linnean Society of New South Wales* 60: 340–373.

WATSON, L., DALLWITZ, M. J. & JOHNSTON, C. R. 1986. Grass genera of the world: 728 detailed descriptions from an automated database. *Australian Journal of Botany* 34: 223–230.