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Anatomy of the genus *Kyllinga* in South Africa

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ABSTRACT

The anatomy of underground and aerial parts of South African species of the genus *Kyllinga* Rottb. is described. SEM micrographs of stomata and of silica bodies are provided. Two new records for South Africa: *K. polyphylla* Willd. ex Kunth and *K. nemoralis* (Forst.) Dandy are included.

RÉSUMÉ

ANATOMIE DU GENRE KYLLINGA *D'AFRIQUE DU SUD*

L'anatomie des parties souterraines et aériennes d'espèces Sud-Africaines du genre Kyllinga *Rottb. est décrite. Des photographies au MEB des stomates et des corps siliceux sont présentées. Deux espèces nouvelles pour l'Afrique du Sud,* K. polyphylla *Willd. ex Kunth et* K. nemoralis *(Forst.) Dandy, sont comprises dans cette étude.*

INTRODUCTION

Interest in the anatomy of Cyperaceae as a source of taxonomic data has been stimulated by the review by Metcalfe (1971) of the family, the discovery of the Kranz syndrome in the family and speculation that it has evolved twice in the Cyperaceae (Raynal, 1973), and with two anatomical manifestations (Laetsch, 1971; Carolin 1977).

Kyllinga has been included in two accounts of general anatomical features (Metcalfe *l.c.* and Govindarajalu, 1969) and mentioned in discussions of the Kranz syndrome by Brown (1975). Not all the South African species have, however, been surveyed.

MATERIALS AND METHODS

At least one example of each species represented in Natal was examined and, where possible, comparisons of other populations were made. A selected list of specimens is provided in Appendix 1.

Hand sections of aerial parts were cleared in saturated solution of chloral hydrate, washed and stained in Delafield's Haematoxylin before mounting in safranin jelly. Leaves, sheaths, culms and bracts were sectioned in the upper portion of the lower third of the organ where maximum size and maturity occurred.

Roots were sectioned 4–6 mm behind the growing points and rhizomes at an internode near the growing tip. Stolons were sectioned midway between plants. Underground portions were embedded in paraffin wax and sectioned with a rotary microtome; stained in safranin and fast green and mounted in Canada Balsam. Preliminary studies of the epidermis at light microscope level were made by stripping the epidermis using Metcalfe's method (1960) of scraping away underlying tissues. Silica bodies were studied by mounting epidermal strips in a saturated aqueous phenol solution.

For SEM studies, the epidermides were prepared by the method recommended by Stant (1973). Preparations of silica from vegetative parts were made by digesting the organic material in hydrogen peroxide and perchloric acid (Breveden & Hodges, 1973), after washing, the silica remnants were mounted on stubs and coated with gold palladium for viewing on a JS100 microscope.

RESULTS

Underground organs

Neither Metcalfe (1971) nor Govindarajalu (1969) distinguished between the rhizome of species such as *K. melanosperma* Nees and the stolon of *K. pulchella* Kunth or *K. nemoralis* (Forst.) Dandy. Both authors, however, drew attention to two anatomical patterns which correlate with this distinction.

Rhizome

Though morphologically variable in that internodes may be short (*K. melanosperma*) or long (*K. intricata* Nees and *K. colorata* (L.) Druce), anatomically there was a common pattern (Fig. 1).

In transverse section, the rhizome was found to consist of a prominent central stele separated from the cortex by a well defined endodermoid layer of radially elongated cells conspicuously lignified (Fig. 2B).

Amphivasal bundles were closely scattered within the parenchymatous ground tissue of the stele and concentrated particularly towards the periphery. Occasional cells of the ground tissue were filled with tannin.

Each vascular bundle consisted of a small central mass of sieve tubes and companion cells (particularly clear in *K. polyphylla*) surrounded by a single ring of xylem vessels and tracheids. The vessels were small in diameter (Fig. 2C). This amphivasal structure of the bundle is characteristic of the groups of Cyperaceae assigned to the Amphivasae by Plowman (1906).

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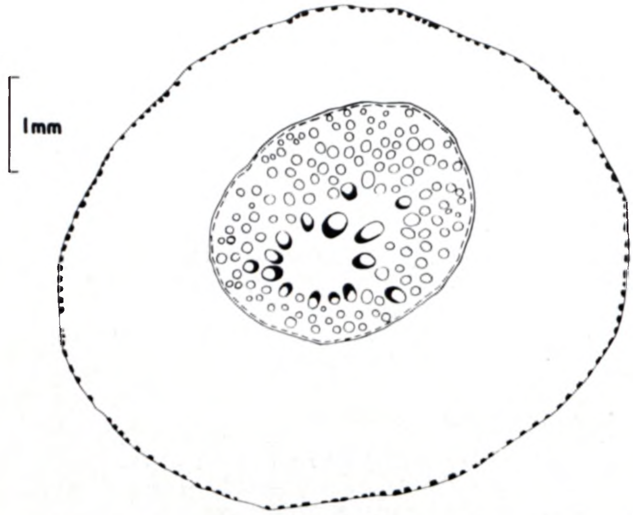

FIG. 1.—Plan of distribution of tissues in transverse section of rhizome of *Kyllinga polyphylla* Willd. ex Kunth.

A sheath of sclerenchyma cells which Plowman (*l.c.*) called the bundle periderm, surrounded most vascular bundles. Occasionally this was not clearly defined, whereas the bundle periderm of the more central bundles was often exaggerated centripetally, e.g. *K. polyphylla.*

Between the vascular bundles and endodermoid layer was a layer of thickened cells which varied from species to species. In *K. erecta* Schum. it consisted of 1–2 layers of sclerenchyma often merging into the bundle periderm of the peripheral bundles while in the majority of species investigated, it consisted of a single outer layer of sclerenchyma associated with 2 or 3 inner layers of small parenchyma cells which may later become lignified (Fig. 2B).

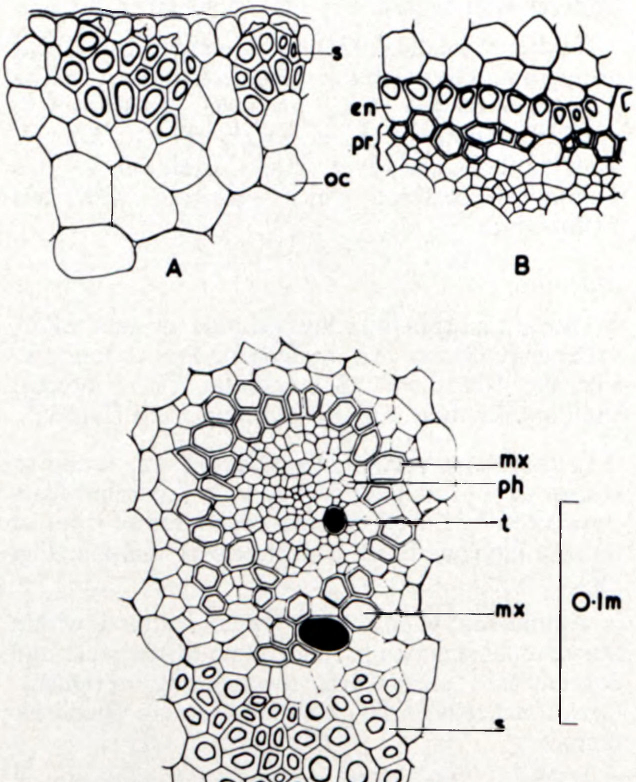

FIG. 2.—Details of portions of transverse sections of rhizome of *Kyllinga polyphylla* Willd. ex Kunth. A, epidermis and outer cortex (oc) with hypodermal strand (s); B, endodermoid layer (en); C, vascular bundle. (metaxylem, mx; phloem, ph; tannin cell, t; sclerenchyma, s.)

The cortex, too, varied. Probably, in all species, the cortex of the young rhizome is a simple starch-bearing parenchymatous zone which may change as the rhizome matures. In *K. polyphylla* and *K. erecta* the cortex retained this compact uniform form, but in *K. elatior* Kunth and *K. melanosperma,* the outer zone of the cortex became slightly lignified. Three collections of *K. pauciflora* Ridl. (*Getliffe* 174, 224, 265) and one of *K. colorata* (*Getliffe* 191) possessed an aerenchymatous inner cortex which was particularly noticeable in the ventral portion of the rhizome adpressed to the soil. All these plants grew in damp situations. Two other populations of *K. colorata (Getliffe* 23, *Ross* 993*)* growing in less damp habitats, did not develop this aerenchyma.

An irregular ring of groups of small sclerenchyma cells formed a type of hypodermis or series of hypodermal ribs within the epidermis of *K. erecta* and *K. polyphylla* and the epidermal cells of these two species contained small 'pegs' of lignin. A single tooth-like peg of lignin protruded from the inner tangential wall of each cell and extended about halfway into the cell (see Fig. 2A). A single epidermis of thickwalled cells surrounded other rhizomes examined.

Stolon

The stolons of *K. pulchella* and *K. nemoralis* consisted of a narrow stele and an aerenchymatous cortex (Fig. 3A).

The bundles of the stele were closely packed peripherally making it difficult to distinguish individual bundles. Centrally, they became more widely separated. Bundles were frequently U-shaped as the xylem did not completely surround the phloem (see Fig. 3C). True amphivasal bundles were rare even in the older portions of the more robust stolons of *K. nemoralis.*

In *K. pulchella* the endodermoid layer comprised a few layers of fairly large hexagonal, slightly lignified cells, whereas in *K. nemoralis* it was difficult to distinguish the thickened endodermoid layer from the thickened inner cortical layers.

In both species, an aerenchymatous inner cortex was differentiated from a narrow parenchymatous outer cortex. The aerenchyma was particularly well developed in *K. nemoralis* collected from a damp sandy river bed. Hypodermal ribs similar to those found in rhizomes were present and a simple epidermis enclosed the stolons.

Fresh material of *K. albiceps* (Ridl.) Rendle was not available for study.

Root

The young root consisted of a very narrow polyarch stele and a broad cortex of radially

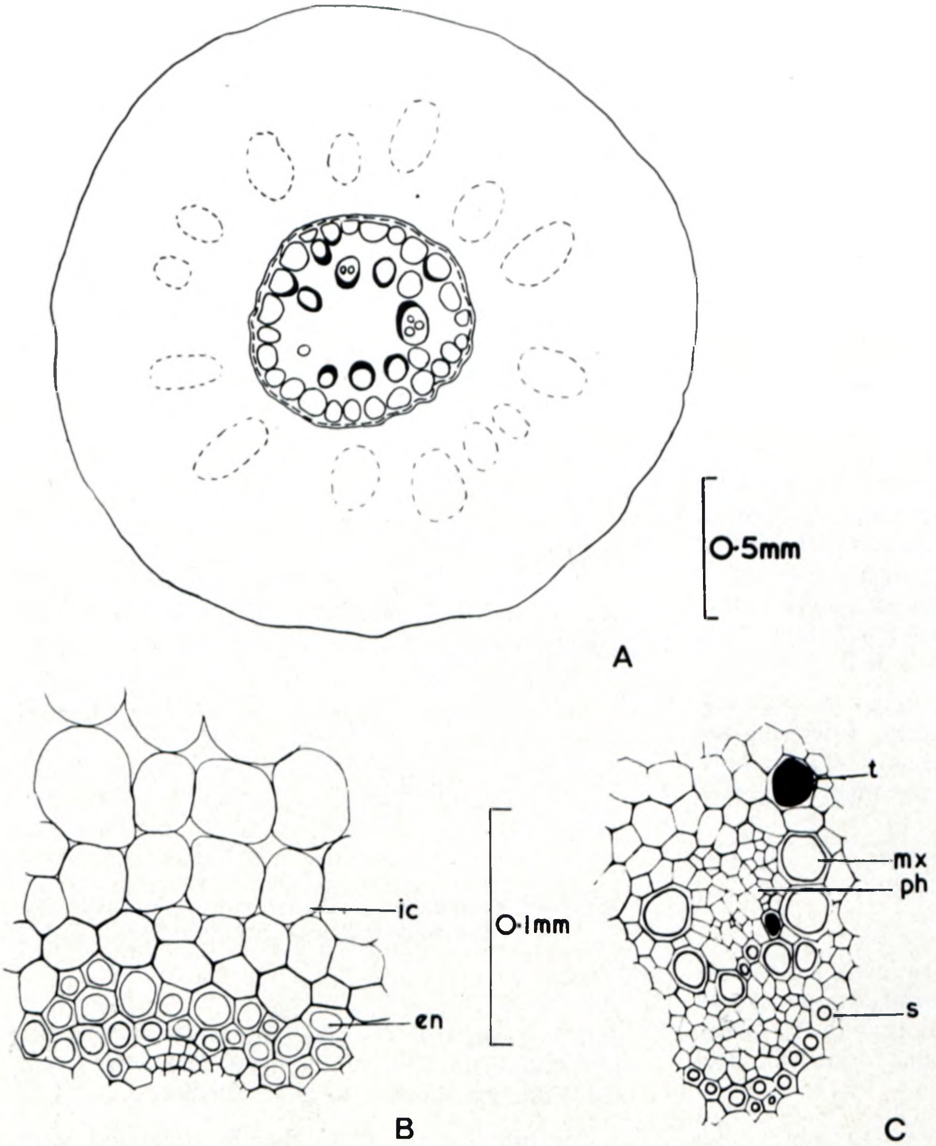

FIG. 3.—Stolon of *Kyllinga nemoralis* (Forst.) Dandy in transverse section. A, plan of distribution of tissues; B, inner cortex (ic), endodermoid layer (en); C, vascular bundle in detail. (tannin cell, t; metaxylem vessel, mx; phloem sieve tube, ph; sclerenchyma, s.)

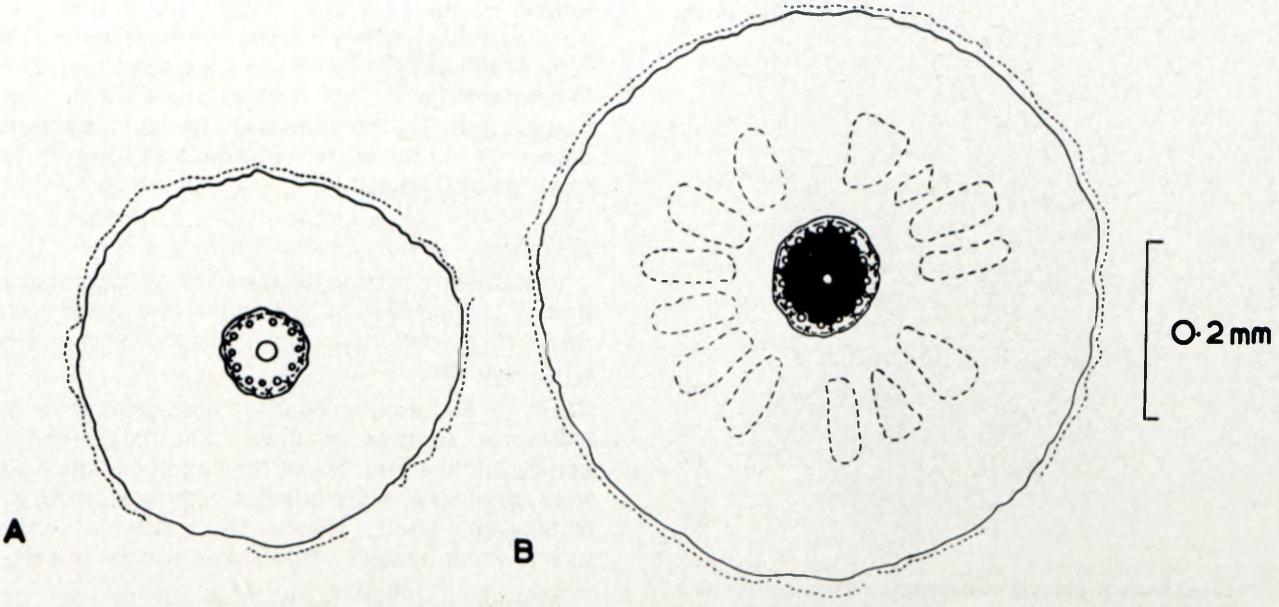

FIG. 4.—Plan of distribution of tissues in roots. A, young root of *Kyllinga nemoralis* (Forst.) Dandy; B, older root of *K. pauciflora* Ridl. with aerenchymatous cortex.

arranged, starch-filled parenchyma cells. The cortex was frequently differentiated into an inner slightly thickened cortex and an outer cortex of which the outer layers were also slightly thickened and closely packed forming an exodermis beneath the piliferous layer (Fig. 4).

In older roots, aerenchymatous tissue developed in the inner cortex due to partial breakdown of radial rows of cortical parenchyma. This aerenchyma was frequently very extensive and made sectioning difficult as the complete cortex became detached from the stele, or the piliferous layer and exodermis from the remainder of the cortex.

Centrally placed in the stele were from 1–5 large metaxylem vessels in a ground tissue of tracheids and sclerenchyma. With age, this packing tissue became heavily lignified. Alternating groups of phloem and protoxylem were arranged peripherally. From 8–22 groups of phloem, each composed of 1–4 sieve tubes with companion cells were found. Protoxylem groups usually consisted of a single small vessel associated with, perhaps, 1 or 2 tracheids.

The protoxylem vessels interrupted the pericycle of hexagonal slightly lignified cells. Enclosing the stele was a well defined endodermis of large, radially elongate elements lignified on the inner tangential and radial walls (Fig. 5).

Aerial parts

Leaf sheath

In transverse sections, the sheath was a complete triangle (Fig. 6B). Two sides were better developed than the third, and were continuous with the blade. The intersection of these two sides formed the keel with a prominent vascular bundle which extended into the main vein of the leaf. The leaves, and therefore the sheaths, have 1/3 phyllotaxy.

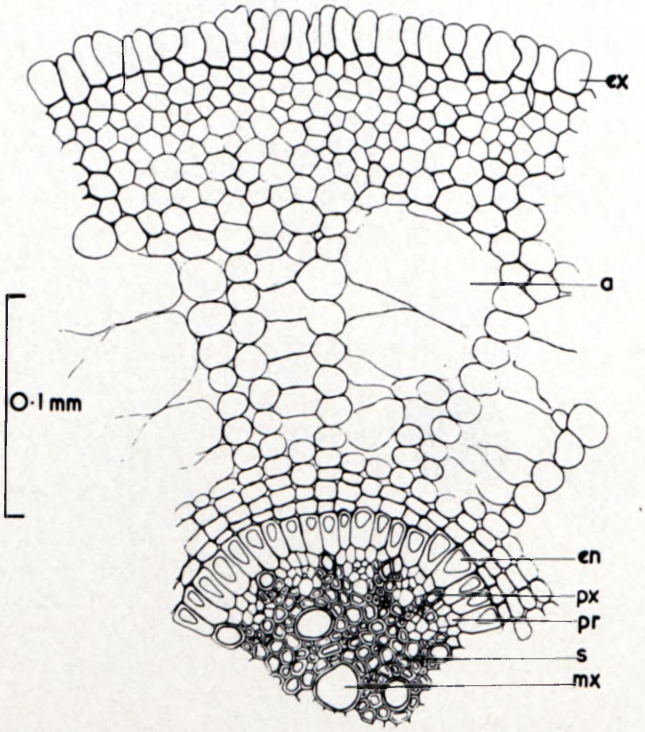

FIG. 5.—Detail of portion of transverse section older root of *Kyllinga pauciflora* Ridl. (ex = exodermis; a= airspace; en = endodermis; pr = pericycle; px = protoxylem; mx = metaxylem vessel; s = sclerenchyma.).

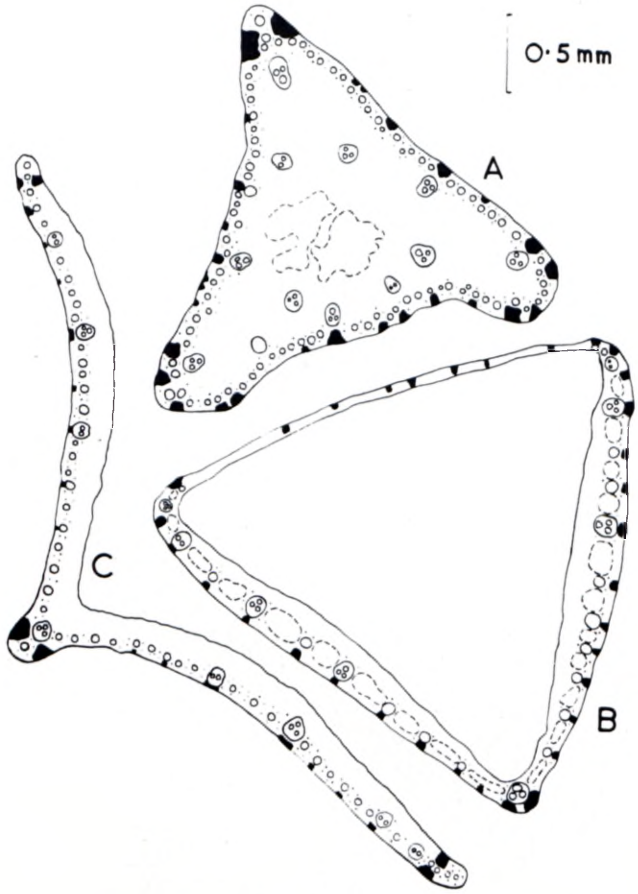

FIG. 6.—Plan of distribution of tissues in transverse section of leaf culm and leaf sheath of *Kyllinga nemoralis* (Forst.) Dandy.

The broad arms of the sheaths contained many vascular bundles alternating with well developed airspaces (Fig. 6B), whereas the third side was 2–3 cells thick, without vascular strands but with small hypodermal strands of sclerenchyma. The vascular bundle of the keel was solitary, but a first order bundle of the type found in the midrib of the leaf and subtended by two pulviniform sclerenchyma strands. Similar smaller strands were associated with minor vascular bundles. Stomata were found on the outer epidermis and the inner epidermis was composed of small thinwalled cells.

Leaf

In transverse section the leaves of *Kyllinga* species were V-shaped (Fig. 6C) or, in the case of the broad leaves of *K. elatior,* flanged V-shaped (terminology after Metcalfe, 1971).

Up to 88 vascular bundles were present in the transverse sections of these. The larger midrib bundle and two or three of the bundles of the blade were large first order bundles with two prominent metaxylem vessels, whereas the rest were smaller second order bundles without conspicuous vessels.

Metcalfe (1971) drew attention to the two superimposed bundles of the midrib of *Kyllinga* and *Pycreus* species as distinct from other members of the Cypereae. His material of *K. erecta* was an exception, but in the material of *K. erecta* examined in this study, two bundles were found in the midrib but *K. pulchella* leaves had one. This may, however, not be a consistent feature of *K. pulchella* which may vary as does *K. erecta*.

The upper vascular bundle of a double bundle midrib is a large first order bundle with two prominent metaxylem vessels. The lower vascular bundle is very much smaller. Associated with the midrib vascular tissue is the pair of pulviniform sclerenchyma girders characteristic of the Cypereae (Metcalfe, 1971) (Fig. 7A).

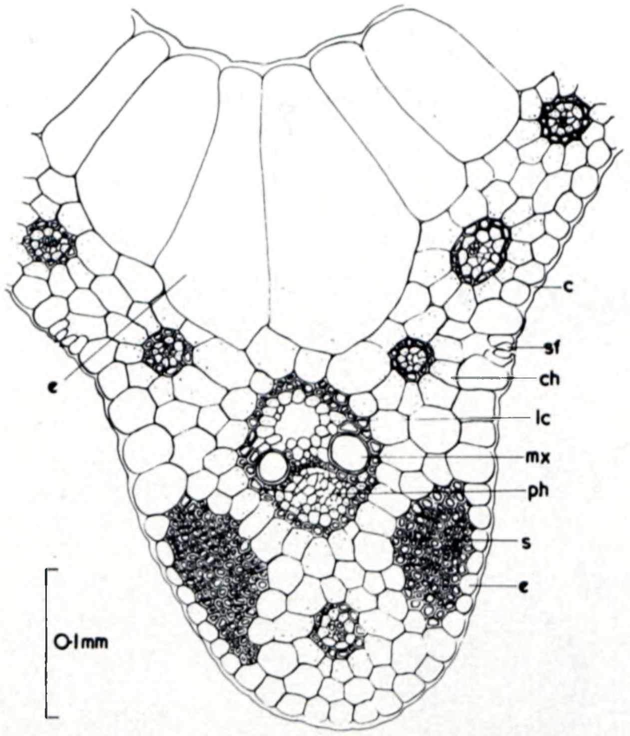

FIG. 7.—Detail of transverse section of midrib of *Kyllinga nemoralis* (Forst.) Dandy. (e = epidermis; c = cuticle; st = stoma; ch = chlorenchyma; lc = lysigenous cavity; mx =metaxylem vessel; ph = phloem; s = sclerenchyma.).

The vascular bundles of *Kyllinga* are surrounded by a conspicuous inner sheath, the Kranz sheath, and an outer sclerenchymatous sheath. Radiating chlorenchyma of the mesophyll is particularly conspicuous around the smaller bundles (Fig. 8). In the larger bundles, the inner Kranz sheath is interrupted by the two metaxylem vessels but in smaller bundles is a complete ring in transverse section. The inner sheath cells have been shown to have the modified chloroplasts of the Kranz syndrome (Carolin, 1977; Gordon-Gray & Gilliland, 1978) in contrast to the Calvin type chloroplasts of the radiating mesophyll cells (Laetsch, 1969).

This pattern of inner Kranz sheath and outer sclerenchymatous sheath is characteristic of the Chlorocypereae and is contrasted with the fimbristyloid type in which an additional outer sheath later is present.

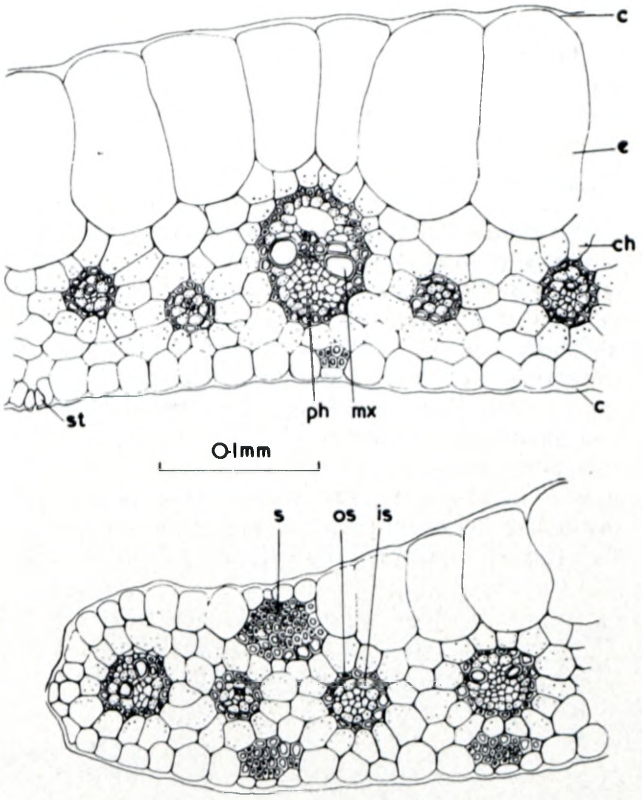

FIG. 8.—Detail of portions of transverse section of blade of leaf of *Kyllinga nemoralis* (Forst.) Dandy. A, median portion of blade (c = cuticle; e = epidermis; ch = chlorenchyma sheath; mx = metaxylem; ph = phloem; st = stoma.); B, lip of blade. (s = sclerenchyma; os = outer sclerenchymatous bundle sheath; is = inner sclerenchymatous bundle sheath.)

The most conspicuous feature of the leaves was the upper epidermis of large elongated cells occupying half the width of the leaf cross sections. In most leaves, the epidermis was a single layer of cells, but in some examples of *K. alba* (*Ross* 693) and *K. alata* Nees (*Ward* 4980, *Lennox* s.n.), it consisted of a double row of smaller cells. In several sections of *K. alata* (*Getliffe* 169, *Ward* 554) a double epidermis at the margins gave way to a single epidermis above the midrib. Further study of this feature is necessary to establish whether the number of rows of epidermal cells is arbitrary or governed by environmental factors, such as available moisture.

In every case, the upper epidermis was covered by a thick cuticle and was without stomata. Occasional hypodermal ribs of sclerenchyma occurred beneath this epidermis, but in none of the species examined was this very conspicuous except at tips of the leaf (Fig. 8B). The lower epidermis, which consisted of small rounded cells covered by a thin cuticle, was well provided with stomata. Beneath this layer, small hypodermal rib strands were frequent. In every case, silica bodies were restricted to epidermal cells adjacent to these strands. Air cavities between the vascular bundles were mentioned by Metcalfe (*l.c.*), but appear to be very rare in the genus and were seen only in *K. polyphylla* in this study.

Bracts

The anatomy of the bracts resembled that of the leaf in every respect except that they were smaller and graded in size from lowest to smallest upper bract.

Culms

The culms of all *Kyllinga* species investigated were basically triangular in transverse section (Fig. 9). Variation from the concave-sided, acute-angled triangle of *K. elatior* to the rounded triangle of *K. pulchella* and *K. alata* was found. The shape in transverse section was more or less constant for each species with slight variations in the number of ridges and furrows in *K. odorata* (Fig. 9H). In the extreme variations such as *K. elatior* (Fig. 9A) and *K. pauciflora* (Fig. 9I), the shapes were sufficiently distinctive to be considered as diagnostic characters. Culms of *K. nemoralis* (Fig. 9B), *K. polyphylla* (Fig. 9I), the shapes were sufficiently distinctive to be considered as diagnostic characters. Culms of *K. nemoralis* (Fig. 9B), *K. polyphylla* (Fig. 9F) and *K. melanosperma* (Fig. 9D), were all of similar shape and hardly distinguishable on this basis. Similarly, *K. colorata* (Fig. 9C) and *K. odorata* (Fig. 9H) were scarcely separable.

An epidermis of a single layer of cells with markedly cutinized outer tangential walls surrounded the culms. This epidermis was covered by a thick cuticle and contained stomata in the furrows within the epidermis, at regular intervals around the edge of the sections, and particularly at the ridges, was a hypodermis of pulviniform ribs of sclerenchyma. The ground tissue was differentiated into an outer assimilatory layer and an inner colourless parenchymatous zone.

From 20 to 100 small vascular bundles were

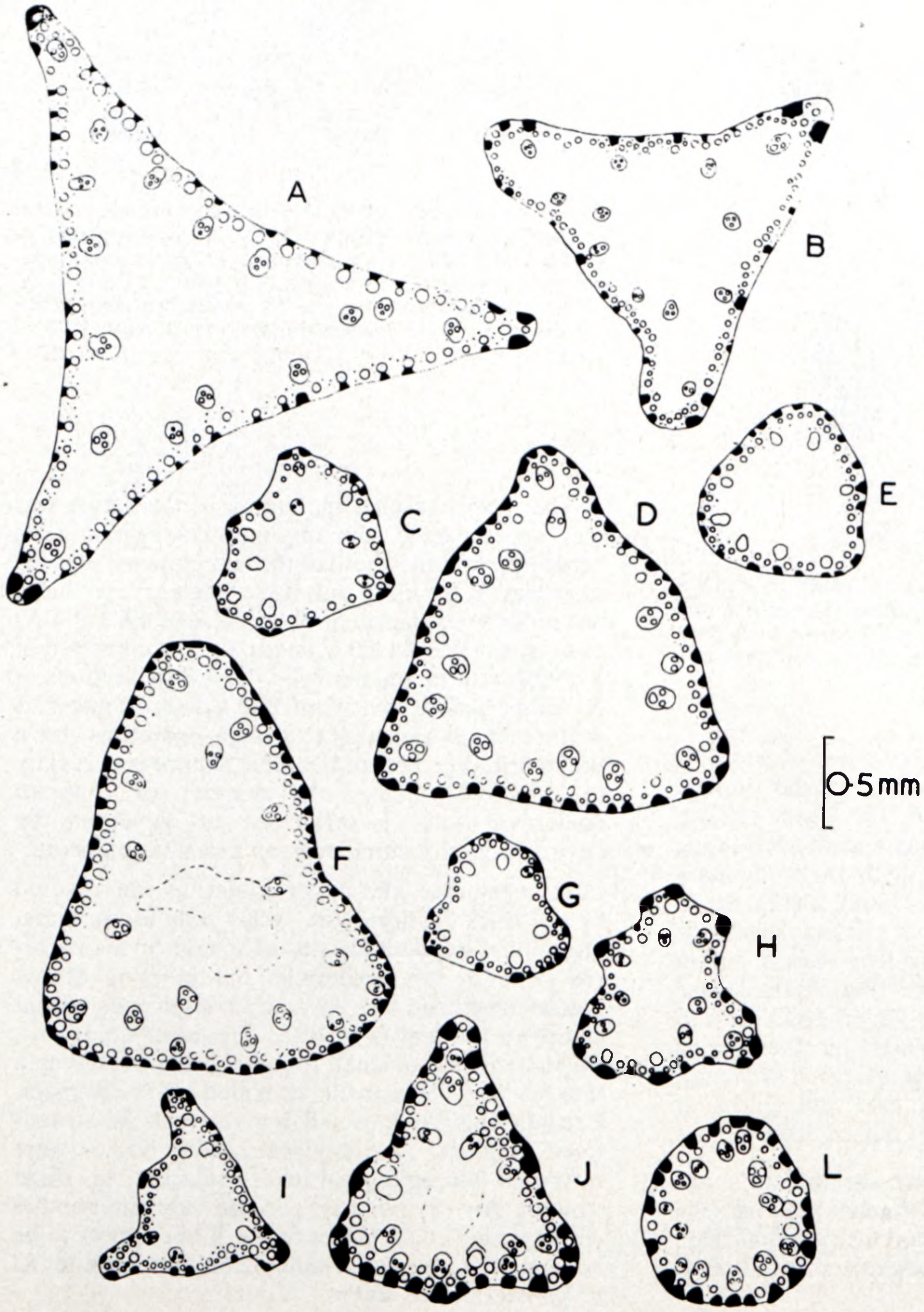

FIG. 9.—Plans of transverse sections of culms of *Kyllinga* species. A, *K. elatior* Kunth; B, *K. nemoralis* (Forst.) Dandy; C, *K. colorata* (L.) Druce; D, *K. melanosperma* Nees; E, *K. pulchella* Kunth. F, *K. polyphylla* Willd, ex Kunth., G, *K. erecta* Schum.; H, *K. odorata* Vahl; I, *K. pauciflora* Ridl.; J. *K. alba* Nees; L, *K. alata* Nees.

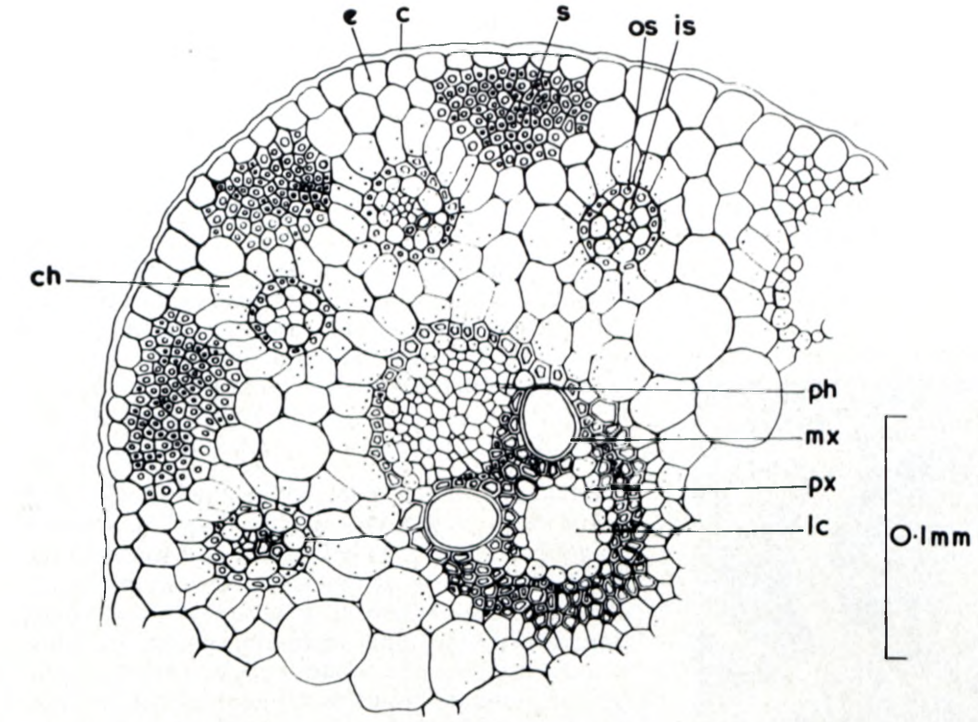

FIG. 10.—Detail of portion of transverse section of culm of *Kyllinga melanosperma* Nees. (e = epidermis; c = cuticle; s = sclerenchyma; os = outer bundle sheath; is = inner bundle sheath; chl = chlorenchymatous sheath; ph = phloem; mx = metaxylem vessel; px = protoxylem vessel; lc = lysigenous cavity.)

located in the outer regions of the ground tissue, and 12−18 larger bundles were situated nearer the centre. An extensive pith was present sometimes degenerating to form an airspace system (Fig. 9F & J).

The outer bundles, similar to the second order bundles of the leaf, had poorly defined vascular tissue surrounded by conspicuous inner chlorenchymatous and outer sclerenchymatous bundle sheaths and the characteristic radiating chlorenchyma which constituted outer assimilator-zone of the culm (Fig. 10).

Conspicuous first order bundles of the type found in the leaves were found towards the inner limits of the assimilatory zone and were associated with sclerenchyma sheaths which were better developed centripetally (Fig. 10).

Epidermal features

When describing the epidermis, Metcalfe (1960) recommended that the epidermal strip be visualized with the long axis of the leaf lying horizontally across the field. This had been done in the following description for the sake of uniformity.

The upper epidermis of the leaf consisted of horizontal parallel rows of ripple-walled cells which, in surface view, were rectangular. No stomata were seen and very little differentiation in size of epidermal cells occurred (Fig. 11).

The lower epidermis was divided into costal and intercostal regions. The cells of the intercostal zones resembled those of the upper epidermis, but were narrower. Occasionally some of the epidermal cells were shorter than neighbouring cells, but these cells were not 'short cells' of the type found in many Gramineae (Metcalfe, 1960) and they were not arranged in any definite pattern. the cells of the costal regions were long, narrow, ripple-walled cells arranged in parallel rows.

Stomata were found in horizontal bands in the intercostal regions. Narrow zones contained a single band of stomata, but up to three bands of stomata were found in wider zones. A band of stomata usually consisted of a single horizontal row of

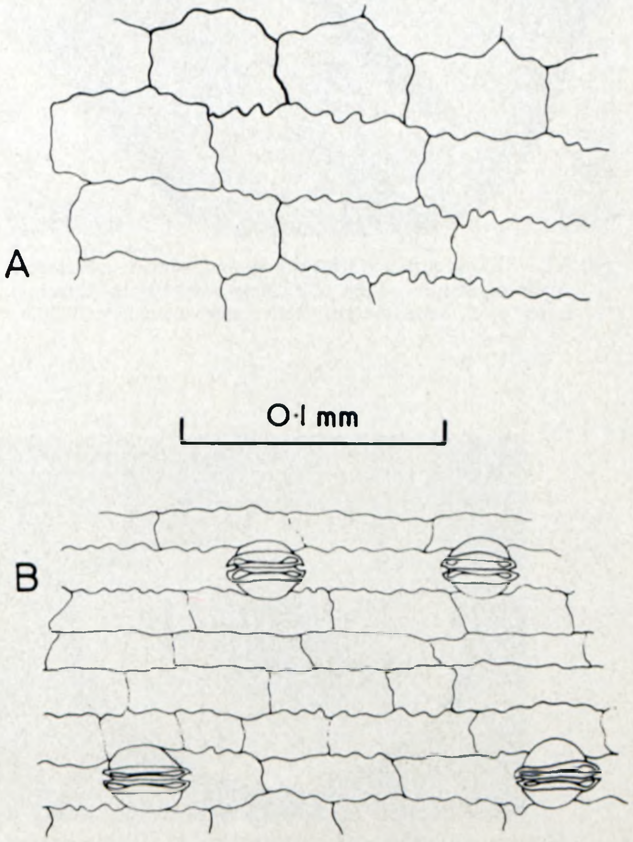

FIG. 11.—Epidermis of *Kyllinga polyphylla* Willd. ex Kunth. A, upper epidermis, B, lower epidermis intercostal zone.

alternating stomata and interstomal cells, but double rows of stomata also occurred, e.g. *K. nemoralis.*

Each stoma was bounded by two dumbbell-shaped guard cells each composed of a thickened central portion with thin-walled bulbous ends. The guard cells were flanked by subsidiary cells similar to those described by Metcalfe (1960) as 'low dome-shaped subsidiary cells' (Fig. 12).

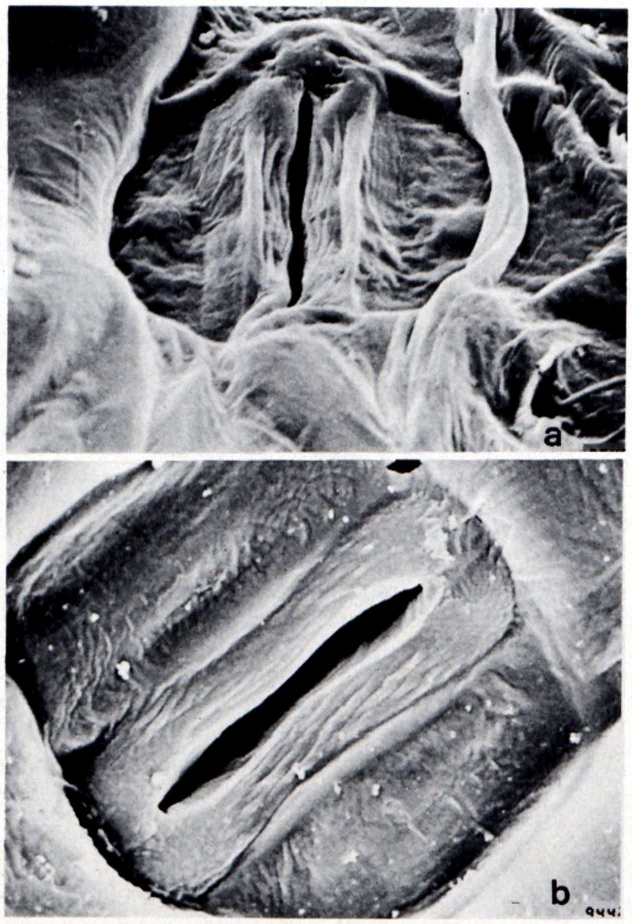

FIG. 12.—SEM of stomatal structure viewed from inner surface of epidermal strip. a, stoma of *Kyllinga colorata* (L.) Druce; b, stoma of *K. odorata* Vahl. Both approximately × 10 200.

Silica bodies were found only in epidermal cells associated with hypodermal strands of sclerenchyma. A single row of 3–8 conical silica bodies was found in each of these epidermal cells. The basic structure of the silica body is common amongst sedges.

Silica bodies when viewed at higher magnification appeared as low-domed platelets with a granular texture, the central dome surrounded by smaller satellites. The rim, unlike that of bodies described for *Rhynchospora* (Gordon-Gray *et al,* 1978) appears to be rough and irregular and not upturned (Fig. 13). Preparations also revealed the presence of silica 'skeletons' of epidermal cells suggesting that much of the epidermis was impregnated with silica.

Epidermal hairs occurred at the margins and below the keels of leaves and bracts and, in *K elatior* (*Getliffe* 12, 196, 201) hairs were also found in the intercostal regions of the leaf. Many culms of *K. alata* were also pubescent. In all species where hairs were found, the hairs were unicellular, bulbous-based and covered by a thick cuticle. The acuminate tip was orientated towards the apex of leaf or bract. The hairs of *K. alata* were visible to the naked eye and may be termed macrohairs but all others are probably better described as 'prickle-hairs' (Metcalfe, 1960). No multicellular hairs were seen (Fig. 14).

CONCLUSION

The genus shows considerable uniformity in its anatomical features which limits the use of these as taxonomic characteristics at the species level. The close relationship between *Kyllinga* and *Pycreus* detected by Turrill (1922) and their unique midrib anatomy is interesting and worth further study.

ACKNOWLEDGEMENTS

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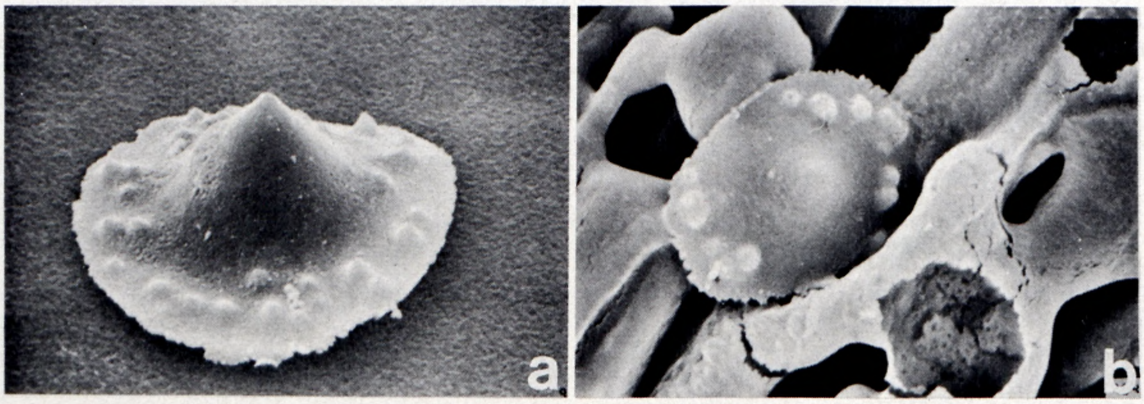

FIG. 13.—Silica remnants after digestion of leaves of *Kyllinga elatior* Kunth. showing low-domed silica body. a, silica body with conical centre and peripheral satellites. x × 13 500; b, silica body and silica outlines of epidermal cells, × 12 500.

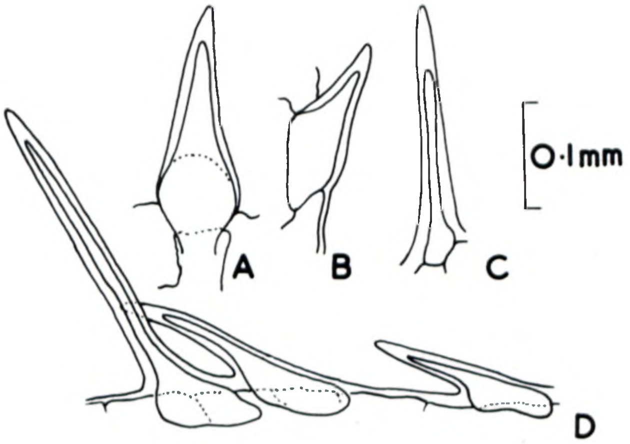

FIG. 14.—Epidermal hairs of *Kyllinga*. A + B, *K. elatior* Kunth; C + D, *K. alata* Nees.

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APPENDIX: CITATION OF SPECIMENS

K. alata *Nees*

2930 (Pietermaritzburg): The Dargle (–AC), *Getliffe 190* (NU); New Hanover, Fawn Leas (–BC), *Getliffe 169* (NU); Isipingo (–DD), *Ward 554* (NU). 2931 (Stanger): Wentworth District, Bluff (–CC), *Ward 4980* (NU); do. *Getliffe 1008* (J). 3029 (Kokstad): Bedford Farm Harding District (–DB), *Lennox s.n.* (NU).

K. alba *Nees*

2628 (Johannesburg): Benoni Golf Course (–AB), *Villet 3010* (J). 2632 (Bela Vista): Ndumu Game Reserve (–CD), *Ross 693* (NU). 2732 (Ubombo): Ubombo Village (–CA), *Getliffe 162* (NU).

K. colorata *(L) Druce*

2930 (Pietermaritzburg): Chase Valley (–CB), *Getliffe 23* (NU); University of Natal (–CB), *Getliffe 191* (NU); Botanic Gardens (–CB), *Ross 993* (NU); King Edward Avenue (–CB), *Getliffe 998, 999* (J).

K. elatior *Kunth.*

2830 (Dundee): Kranskop, Middledrift Road (–DD), *Getliffe 12* (NU). 2930 (Pietermaritzburg): Town Bush Valley, Cascade Falls (–CB), *Getliffe 196* (NU); Pinetown, B (–DD) *Getliffe 1005* (J); 2931 (Stanger): Inanda District, Mt. Edgecombe *Getliffe 201* (NU).

K. erecta *Schum.*

2930 (Pietermaritzburg): Thomas Moore School (–DD), *Getliffe 176* (NU); Pinetown (–DD), *Getliffe 1006.* (J).

K. melanosperma *Nees*

2429 (Zebediela): near Potgietersrus (–AA), *Edwards s.n.* (J).

K. nemoralis *(Forst.) Dandy*

2931 (Stanger): Durban Country Club Golf Course (–CC), *Getliffe 193* (NU); Durban Botanic Gardens (–CC), *Getliffe 996* (J).

K odorata *Vahl.*

2930 (Pietermaritzburg): Thomas Moore School, Pinetown, (–DD), *Getliffe 175;* do. *Getliffe 1004* (J).

K. pauciflora *Ridl.*

2930 (Pietermaritzburg): Lions River District, Rawdons Hotel (–AC), *Getliffe 224* (NU); Hermansburg District, vlei near school (–BB), *Getliffe 174* (NU); Impendhle Tillietudlem (–DB), *Getliffe 265* (NU).

K. polyphylla *Willd. ex Kunth*

2931 (Stanger): Durban, Windsor Park Golf Course (–CC), *Getliffe 28, 164, 292* (NU), do. *Getliffe 1010* (J).

K. pulchella *Kunth*

2930 (Pietermaritzburg): Lion's River District, Karkloof (–AC), *Getliffe 205B* (NU). 2629 (Bethal): 27 k from Standerton (–CC), *Getliffe 1011* (J).