STUDIES IN THE PANICEAE: GENERIC BOUNDARIES IN THE <u>BRACHIARIA</u> COMPLEX (POACEAE)

By

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STUDIES IN THE PANICEAE:

GENERIC BOUNDARIES IN THE <u>BRACHIARIA</u>

COMPLEX (POACEAE)

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PREFACE

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CHAPTER I

INTRODUCTION

Brachiaria Griseb. is a pantropical genus with approximately 100 species (Clayton and Renvoize, 1986) and its center of distribution in Africa. A member of the family Poaceae and tribe Paniceae, it is characterized by: (1) an inflorescence of racemes along a central axis; (2) an adaxial spikelet orientation; (3) the presence of both glumes; (4) a papillose to papillose-rugose fertile floret; and (5) an awnless or mucronate fertile lemma (Clayton and Renvoize, 1986; Thompson and Estes, 1986). Phenetic and phyologenetic affinites between Brachiaria and Urochloa Beauv., Panicum sect. Fasciculata Hitchc.,and Eriochloa H.B.K., and Acroceras Stapf, Alloteropsis Presl, Anthaenantiopsis Pilger, Axonopus Beauv., Chaetium Nees, Coridochloa Nees, Eccoptocarpha Launert, Entolasia Stapf, Leucophrys Rendle, Louisiella Hubbard & Leonard, Neurachne R. Br., Oryzidium Hubbard & Schweick, Pseudobrachiaria Launert, Psilochloa Launert, Remaria Flugge, Scutachne Hitchc. & Chase, Thuarea Pers., Yvesia A. Camus have been recognized and various interpretations of its generic boundaries and relationships have been offered for well over

150 years (Trinius, 1826; Chase, 1920; Stapf, 1934a, 1934b; Pilger, 1940; Hsu, 1965; Parodi, 1969; Blake, 1969, 1973; Butzin, 1970; Brown, 1977; Shaw and Smiens, 1980; Clayton and Renvoize, 1982, 1986; Thompson and Estes, 1986, Shaw and Webster, 1987; Webster, 1987).

Trinius (1826) originally recognized Brachiaria as a section of Panicum, however, the section was elevated to generic level by Grisebach (1853). Nash (1903) was the first to note the adaxial orientation of the spikelet in a treatment of the species in the southeastern United States. Chase (1920) and Stapf (1934a) then expanded the circumscription of Brachiaria by emphasizing this feature. They de-empahsized the morphology of the inflorescence as a generic trait. Parodi (1969) formally recognized the similarity between Brachiaria and Panicum sect. Fasciculata when he transferred P. adspersum and P. fasciculatum to Brachiaria on the basis of the adaxial orientation of the second and third spikelets below the apex of the inflorescence. Independently, Blake (1969) placed the entire section in Brachiaria on the basis of overall similarity. Hsu (1965) and Brown (1977) also believed that these two taxa should be combined. In contrast, Webster (1987) reduced Brachiaria to a monotypic genus with B. erucaeformis as the sole constituent. The remaining Australian species of Brachiaria, including those of section Fasciculata, he placed in Urochloa.

Shaw and Smiens (1980), Clayton and Renvoize, (1986), and Shaw and Webster(1987) noted a similar close relationship in morphology between Eriochloa and Brachiaria. The presence of a cup-shaped callus at the base of the spikelet in Eriochloa is traditionally used to separate the two taxa, but several species of Brachiaria possess a callus bead that Clayton (1975) hypothesized might be homologus up of Eriochloa.

Urochloa is also morphologically similar to Brachiaria. The former genus has a racemose inflorescence, both glumes, a rugose fertile floret, and a mucronate to awned fertile lemma, but differs in abaxial spikelet orientation (Burt et al., 1980; Clayton and Renvoize, 1986; Stapf, 1934b). Several species that have been included in Brachiaria fall within the circumscription of Urochloa, except for the orientation of the spikelet (Clayton and Renvoize, 1986). As a result of his extensive study of panicoid anthecial micromorphology, leaf epidermal anatomy, and lodicule morphology, Hsu (1965) questioned the emphasis placed on spikelet orientation. He noted that Brachiaria and Urochloa shared the same lemmatal surface pattern and that spikelet orientation seemed to be the only feature separating the two taxa. In their examination of Brachiaria's anthecial micromorphology and laminar epidermal micromorphology, Thompson and Estes (1986) found even more variation than had been discerned by Hsu. In addition to confirming similarities between Brachiaria and Urochloa, they discovered similarities between Brachiaria and both Panicum sect. Fasciculata and Eriochloa.

Brown (1977) also questioned the use of spikelet orientation for taxonomic delimitation. In his comparative [illegible] of foliar vascular anatomy and photosynthetic pat[illegible] he delimited a group of taxa characterized by the PEP-carboxykinase (PCK) variation of the C_4 photosynthetic pathway and a Kranz sheath derived from the parenchymatous sheath (P.S.) [photosynthetic carbon reduction sheath (PCR) that arises from the ground meristem (Dengler, Dengler, and Hattersly, 1985)]. This group is also defined by free style bases and a firm fertile lemma. Brown referred to this assemblage as the Brachiaria Group and included Brachiaria, Chaetium, Coridochloa, Eriochloa, Leucophrys, Oryzidium, Pseudobrachiaria, Psilochloa, Panicum sect. Fasciculata, Scutachne, and Urochloa.

Clayton and Renvoize (1986) in their treatment of the grass genera of the world comment on the difficulty of circumscribing Brachiaria and its affinities to other genera. Thompson (1988)notes that Brachiaria, Eriochloa, Panicum sect. Fasciculata, Pseudobrachiaria and Urochloa appear to form a monophyletic element, within Brown's Brachiaria Group. Therefore, the objective of the work embodied in this disseration was an elucidation of the relationship of the five taxa and description of their generic boundaries. The work comprises four parts: (1) a study of the anatomy of the spikelet callus of Eriochloa, Brachiaria, and Urochloa presented in Chapter II; (2) a study of the anthecial and foliar micromorphlogy and laminar anatomy of Urochloa and Panicum sect. Fasciculata presented in Chapter III; (3) an investigation of the anthecial and foliar micromorphlogy and laminar anatomy of eight additional species whose affinities with the Brachiaria complex is uncertain presented in Chapter IV; and (4) an examination of the taxonomic boundaries of the five taxa presented in Chapter V.

Chapters II-IV are being submitted for publication in the American Journal of Botany and the format of each is that required for submission. Chapter V is being submitted to Systematic Botany, and thus its format differs slightly from the others. References to Thompson, 1988 refer to this dissertation.

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ANATOMY OF THE SPIKELET CALLUS OF _ERIOCHLOA_, _BRACHIARIA_, AND _UROCHLOA_ (POACEAE: PANICEAE)

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Running Head: Panicoid callus anatomy

ABSTRACT

Anatomical investigation of the cup-shaped callus at the base of the spikelet in *Eriochloa* revealed a non-vascularized cup-shaped structure composed of large parenchyma cells surrounding a column of tissue that is continuous with the pedicel. The cup and column are fused only at the base of the cup. The stele branches above the cup at the rachillar node of the second glume. Therefore the cup-shaped callus characteristic of *Eriochloa* appears to be formed entirely of parenchymatous tissue and is not partly derived from the first glume as previously interpreted. The bead of callus at the base of the spikelet in *Brachiaria* is also an unbranched stele surrounded by parenchyma and the vascular tissue branches at the rachillar node of the first glume. The spikelet base of *Urochloa* has vascular tissue that branches initially at the first glume nodal plexus. This genus lacks an appreciable increase in girth due to callus parenchyma. Thus the cup-shaped callus of *Eriochloa* and the callus bead of *Brachiaria* appear to be homologous. The cup-shaped callus is the advanced character state, callus bead the intermediate state, and absence of callus parenchyma the primitive state.

Eriochloa H.B.K. is characterized by a distinct enlarged cup-like structure at the base of spikelet and the absence of the first glume (Stapf, 1934; Hitchcock, 1935). In their original description of the genus, Humbolt, Bonpland and Kunth (1815) referred to this structure at the base of the spikelet as an involucre. In 1883, Bentham and Hooker called it callose, while Hackel (1896) and Nash (1903) used the phrase annular callus. Vasey (1892) was the first to refer to the structure as cup-like swelling of the pedicel. Hitchcock and Chase (1917) interpreted the enlarged area to consist of an "...internode of the rachilla between the first and second glumes thickened forming a ring-like base to the spikelet, the first glume usually reduced to an obscure sheath adnate to the the ring...". Stapf (1934), Pilger (1940), Clayton (1975), and Gould and Shaw (1983) generally supported Hitchcock and Chase's hypothesis. On the basis of SEM studies, Shaw and Smeins (1979, 1983) reported that the epidermal patterns of the Eriochloa callus resembled those of the first glume of other panicoid grasses; therefore supporting Hitchcock and Chase's (1917) interpretation that the first glume is adnate to the callus.

In the closely related Brachiaria Griseb., the first glume is present and the cup-shaped callus typically absent. However, some species of the genus do have a small globose to elliptic bead of callus immediately below the first glume. Clayton (1975) suggested that it is homologous to the cup-shaped callus of *Eriochloa*. None of the species of *Urochloa* Beauv., which is closely related to both *Eriochloa* and *Brachiaria*, have a swelling at the base of the spikelet.

Hitchcock and Chase's hypothesis regarding the nature of the cup-shaped callus in *Eriochloa*, is not based on rigorous anatomical analyses. Consequently, an examination the anatomical organization of the cup-shaped callus of *Eriochloa* and the callus-bead of *Brachiaria* was undertaken to determine the possible origin of the structure and its relationship to the first glume. *Urochloa* was also examined and its anatomy compared to that of *Eriochloa* and *Brachiaria*.

Materials and Methods--Plants were grown from seed provided by the U.S.D.A. Plant Introduction Station, Experiment, GA. Inflorescences were collected immediately prior to anthesis from *Eriochloa australiensis* Stapf ex. Thellung, *E*. *borumensis* Hack. [= *E*. *meyerana* (Nees) Pilg.], *E*. *crebra* S. T. Blake, *Brachiaria brizantha* (A. Rich) Stapf, *B*. *decumbens* Stapf, *B*. *erucaeformis* (Smith) Griseb., *B*. *humidicola* (Rendle) Schweick, *B*. *xantholeuca* (Schinz) Stapf, *Urochloa oligotricha* (Fig. & De Not.) Henr. [= *U*. *bolbodes* (Steud.) Stapf], *U*. *brachyura* (Hack.) Stapf, and *U*. *pullulans* Stapf. Additionally, inflorescences with spikelets containing mature caryopses were collected from *E*. *borumensis*. Samples were fixed in FAA for 48 hr, stored in

70 % ethanol (EtOH), and pretreated in hydrofluoric acid and glycerin (3:7 v/v) for 5 days. This was followed by a 2 hr wash in distilled water and passage through an EtOH and tertiary buytl alcohol dehydration series (C. P. Daghlian, pers. comm.). The tissue was embedded in Paraplast after infiltration in a vacuum oven, serially sectioned at 10-25 μm on a rotary microtome, and stained in safranin (Johansen, 1940) and fast green (Boke, 1952) or rapid safranin (Gray and Pickle, 1956) and Sass's hemalum (Berlyn and Miksche, 1976). Spikelets of Eriochloa grandiflora (Trin.) Benth., E. nubica (Steud.) Stapf, E. crebra, E. polystachya Kunth, and Brachiaria humidicola were removed from herbarium specimens, rehydrated in 5 % Contrad 70, passed through a 70-90 % EtOH series, embedded in JB-4 resin, serially sectioned at 6-10 μm on an utlramicrotome, and stained with toluidine blue (Jensen, 1962). The parafin and plastic sections were examined and photographed using bright field, light microscopy.

Results--In Eriochloa, three vascular bundles enter the spikelet pedicel (Fig. 1d) from the rachis. These bundles are completely or partially fused, forming an amphicribal stele. This stele is unbranched until the node of the second glume (Fig. 1c, 1e). The cup consist of compact, parenchymatous tissue, and is positioned approximately 20-60 μm above the point where the spikelet disarticulation from the rachilla (Fig. 1a, 1c, 1e). At its maximum girth, the body of the cup is separated from a central column composed of the stele and associated parenchyma (Fig. 1b, 1c, 1e). Eriochloa crebra differs from the other species as a ring of spongy parenchyma occurs adjacent to the stele just below the the point where the cup separates from the column. Toward the apex, the wall of the cup bends inward on itself formning a false rim and a ventral projection (Fig. 1c, 1e, 1f). This projection then reascends to the level of the rim cup (Fig. 1c) or projects as a conspicuous flap of tissue above the main body of the cup (Fig. 1e). The cup is not vascularized (Fig. 1a-1f). The relative degree of development of the vascular tissue in the spikelet base is the only difference between vascular tissue in an immature spikelet (Fig. 2a) and in a spikelet with a mature grain (Fig. 2b). No new vascular traces arise later during spikelet development.

The vascular tissue in the pedicel and spikelet base of Brachiaria (Fig. 2c - 2f) is the result of the fusion of the three major bundles from the rachis. It is amphicribal and does not branch until the node of the first glume (Fig. 2f). The bead arises just above the point of disarticulation and is composed of parenchymatous tissue (Fig. 2c, 2d, 2f). In B. humidicola, B. xantholeuca, and B. erucaeformis, the parenchyma is contiguous with the stele (Fig. 2f). In B. brizantha and B. decumbens a small annular hollow area adjacent to the stele is present as the callus parenehyma is not completely fused to the central column (Fig. 2c). A ring of spongy parenchyma surrounds the stele immediately below the hollow area in B. decumbens (Fig. 2d). In all species, the veins to the first glume diverge from the stele at the apex of the bead (Fig. 2f).

The vascular tissue of Urochloa is essentially identical to that of Eriochloa and Brachiaria, as three major vascular bundles enter the pedicel and form an amphicribal stele (Fig. 2h). The stele of Urochloa is unbranched until the nodal plexus of the first glume similar to that of Brachiaria (Fig. 2g). However, there is no appreciable increase in girth due to a proliferation of parenchyma in Urochloa, such as found in the cup-shaped callus and callus bead.

Discussion--The cup of Eriochloa is formed via a proliferation of parenchymatous tissue and represents a modification of the spikelet base. A vestigial first glume does not sheath or form a part of the cup. This inference is based on the absence of vascular tissue in the cup and branching of the spikelet stele occuring first at the node of the second glume. Chandra (1962) in his examination of Eriochloa procera also found that the cup to lack vascular tissue.

Complete loss of the first glume and accompanying vascular tissue is well known in other genera in the Paniceae (Arber, 1931; Belk, 1939; Chandra, 1962). Thus it is not unreasonable to assume that the lack of any variation in vascular tissue between the two developmental stages of E. borumensis is also consistent with these observations. Therefore, we do not have any evidence of the involvement the first glume in the evolution of the development of the cup.

The callus bead of Brachiaria is anatomically similar to the cup of Eriochloa and the two are most likely homologous; these observations agree with Clayton's theory (1975). The spikelet base without a proliferation of parenchyma, as seen in Urochloa, represents the primitive condition, the callus bead of Brachiaria being intermediate, and the cup-shaped callus of Eriochloa being adavanced.

A possible function for the unusual spikelet base in Eriochloa has been suggested by Davidse (1978). He contends that the cup-shaped callus functions in an elaisome-like manner, as an ant-attractor that would subsequently facilitate spikelet dispersal by ants. A preliminary survey of fresh material revealed lipid droplets in the cells of the cup's ventral projection when free-hand sections were stained with rhodamine B (R. A. Thompson, unpublished). Lipids might be secreted into the cavity between the cup and central column or toward the outside of the cup via the ventral flap of tissue. This phenomenon, however, needs more thorough examination.

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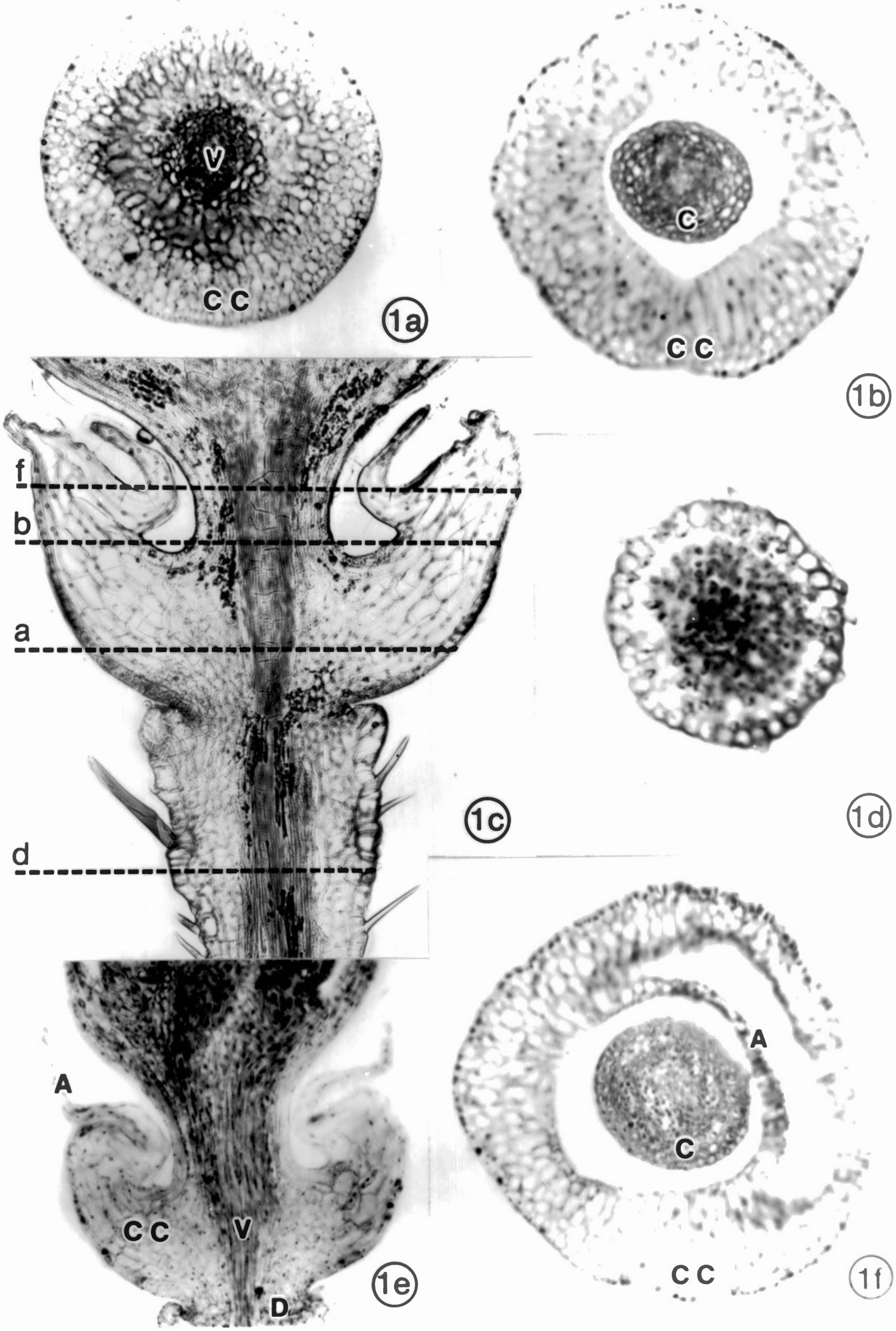
Fig. 1. Anatomy of Eriochloa callus. 1a. X.S. through callus base of E. borumensis. X 124. 1b. X.S. through middle portion of callus. X 136. 1c. L.S. of E. crebra spikelet base; dashed lines f, b, a, and d indicate approximate location of sections 1f, 1b, 1a, and 1f, respectively. X 124. 1d. X.S. of pedicel. X 153. 1e. L.S. of E. borumensis spikelet base. X 125. 1f. X.S. of apical portion of callus. X 135. A = ascending projection; C = central column; CC = cup-shaped callus; D = disarticulation region; V = vascular tissue.

Fig. 2. 2a-2b. Vascular tissue of Eriochloa callus. 2a. E crebra before spikelet anthesis. X 300. 2b. E. borumensis immediately before spikelet disarticulation. X 436. 2c-2f. X.S. of spikelet base of Brachiaria. 2c. B. decumbens. X 109. 2d. X 107. 2e. Pedicel. X 104. 2f. B. xantholeuca. X 78. 2g-2h. Spikelet base of Urochloa oligotricha. 2g. X 100. 2h. X 123. Arrows point to first glume vascular traces; BC = bead of callus; P = phloem; PC = procambium; S = spongy parenchyma; V = vascular tissue; X = xylem.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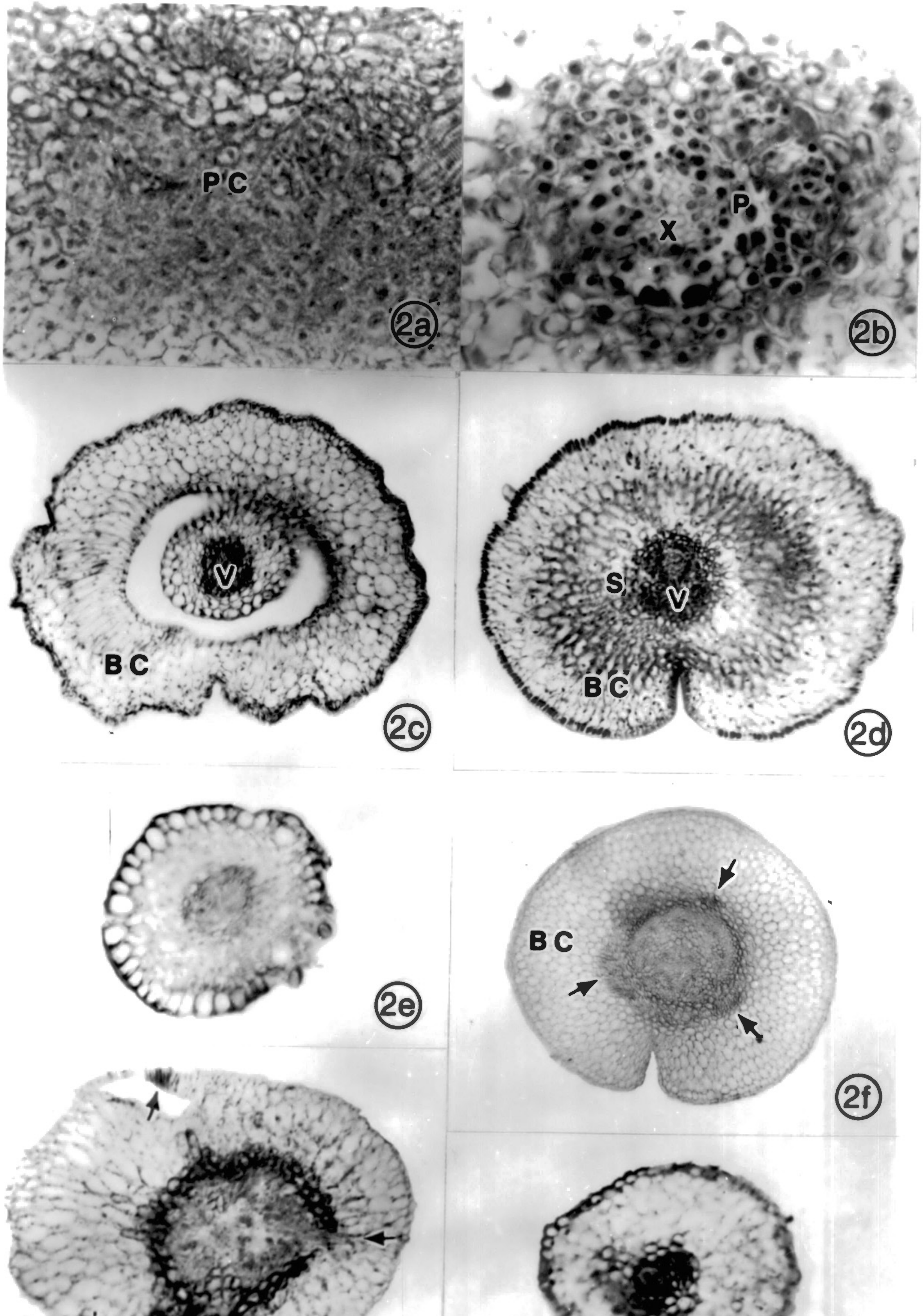

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ANTHECIAL AND FOLIAR MICROMORPHOLOGY AND LAMINA OF *UROCHLOA* AND *PANICUM* SECTION *FASCICULATA* (POACEAE: PANICEAE)

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Running Head: <u>Urochloa</u> and <u>Panicum</u> sect. <u>Fasciculata</u>

ABSTRACT

Species of *Urochloa* exhibit the Brachylopha and the Urochloa anthecial patterns. Laminar anatomy of *Urochloa* includes: (1) a 7 to 1 arrangement of vascular bundles; (2) a reduced mesophyll; (3) deeply penetrating fans of bulliform cells; (4) 5-6 celled intercostal regions; and (5) costal regions with typically one row of dumbell-shaped silica cells. This unique complex of characters provides evidence that the genus has evolved as a discrete lineage from *Brachiaria*. An examination of all four species of *Panicum* sect. *Fasciculata*, revealed that the section includes an anthecial pattern and variable epidermal microcharacters, both which occur within *Brachiaria* and *Panicum*. However, the section and *Brachiaria* both possess PCK anatomy, a ribbed to slightly ribbed laminae with radiated mesophyll, and a band of parenchyma connecting the bulliform fans and abaxial epidermis. This study supports placement of *Panicum* sect. *Fasciculata* within *Brachiaria*.

Within the Paniceae, spikelet orientation may be abaxial or adaxial. Butzin (1970), Chase (1920), and Stapf (1934a, 1934b) used spikelet orientation as a generic character. The segregation of Urochloa Beauv. with abaxial spikelet orientation and Brachiaria Griseb. with adaxial represents such an interpretation (Butzin, 1970; Chase, 1920; Stapf, 1934a, 1934b). Both genera have a racemose inflorescence, ovoid to elliptic spikelets, and a firm rugose fertile anthecium (lemma and palea). Therefore, separation of these two genera may be based largely on spikelet orientation. However, Urochloa typically does have an awned fertile lemma and a more ovoid spikelet whereas Brachiaria usually has an awnless fertile lemma and a more elliptic spikelet (Butzin, 1970; Chase, 1920; Stapf, 1934a, 1934b; Clayotn and Renvoize, 1986).

Hsu (1965) and Brown (1977) have contended that spikelet orientation was not a suitable character upon which to base generic boundaries, and both authors emphasized the similarities exhibited between Urochloa and Brachiaria as an example. Hsu described Urochloa and Brachiaria as both having papillose-rugose fertile lemmas with transverse ridges; styles free at the base; plicate, papery lodicules with distinct veins; and caryopses with a punctiform hilum. He also noted that the spikelet orientation of long-pedicelled Brachiaria species was difficult to determine. Brown reported that both genera utilized a high level of PEP carboxykinase (PCK) during C_4 photosynthesis and that both had an outer sheath derived from a parenchymatous bundle sheath (PS) [= the photosynthetic carbon reduction sheath (PCR) that arises from ground meristem (Dengler, Dengler, and Hattersley, 1985)].

Brown (1977) additionally suggested that Panicum section Fasciculata Hitchc.--also a PCK, PS taxon--was more closely allied to Brachiaria than to Panicum L. He did not, however, make a formal transfer of the taxa. Parodi (1969) had placed two species of the section--P. adspersum and P. fasciculatum--in Brachiaria based on spikelet orientation. Independently, Blake (1969, 1973) transferred all four species of the section to Brachiaria. Panicum sect. Fasciculata has a tight, paniculate inflorescence; an elliptical, transversely rugose fertile floret; an awnless or mucronate fertile lemma; free style bases; and a caryopsis with a punctiform hilum (Hitchcock and Chase, 1910, 1915; Hsu, 1965). Spikelet orientation is abaxial according to Hitchcock and Chase (1910, 1915), but adaxial according to Parodi and Blake, indicating the difficulty in determining spikelet orientation.

The close relationship of Urochloa, Brachiaria, and Pancium sect. Fasciculata was further suggested by Thompson and Estes (1986). In an examination of the anthecial micromorphology of Brachiaria, they discovered more variation in the genus than had been previously discerned.

Furthermore, they proposed morphological intergradation between *Brachiaria* and both *Urochloa* and *Panicum* sect. *Fasciculata*. Although the three taxa form an assemblage of closely related phenetic elements, formal recognition of ge[illegible]s problematic and different classifications have been proposed recently. Clayton and Renvoize (1986) positioned PCK species in *Panicum* and recognized *Brachiaria* and *Urochloa* as distinct. Webster (1987), however, considered *Brachiaria* a monotypic genus based on *B. erucaeformis*. The Australian species of *Brachiaria* plus those of *Panicum* sect. *Fasciculata* were placed in *Urochloa*. In order to resolve generic boundaries among these three taxa, a detailed examination of the laminae and anthecia of the full range of *Urochloa* and *Panicum* sect. *Fasciculata* was undertaken.

MATERIALS AND METHODS--Taxa studied were *Urochloa brachyura* (Hack.) Stapf, *U. echinolaenoides* Stapf, *U. mosambicensis* (Hack.) Dandy, *U. panicoides* Beauv., *U. pullulans* Stapf, *U. reptans* (L.) Stapf [= *Brachiaria reptans* (L.) Gardner & Hubbard; = *Panicum reptans* L.], *U. rhodesiensis* Stent., *U. stolonifera* (Goossen) Chippind., *U. trichopus* (Hochst.) Stapf, *Panicum adspersum* Trin., *P. arizonicum* Scribn. & Merr., *P. fasciculatum* Swartz., and *P. texanum* Buckl. Specific names were taken from herbarium labels. A list of specimens examined is presented in

Thompson, 1988. Spikelet and leaf material was removed, with permission, from specimens from K and MO.

Anthecial micromorphlogy--Intact anthecia or separated fertile lemmas and paleas were placed on aluminum stubs using double-stick tape. Specimens were coated with gold-paladium (Thompson and Estes, 1986). JEOL JSM-2 and ETEC Autoscan scanning electron microscopes were used to examine the specimens, and photographs were taken of the apical, middle, and basal portions of each bract. One or two anthecia were examined for each taxon; if anything unusual was observed additional anthecia were scanned until an understanding of the pattern of variation was obtained.

Leaf epidermis--Abaxial and adaxial epidermal peels were made primarily from middle portions of blades. The specimens were rehydrated in 5 % Contrad 70 for 5-10 min, and extraneous tissue was removed with a scalpel. The epidermis was then mounted in Hoyer's Mounting Medium and examined using phase-optics (Thompson and Estes, 1986).

Leaf anatomy--Free-hand cross-sections were made from the rehydrated material described above. Sections were stained in safranin and Delafield's haematoxylin using the procedure of Thompson and Estes (1986).

Maximum lateral cell count, the maximum number of cells separating any mesophyll cell from a bundle sheath cell, and maximum cell distance, the maximum number of cells between adjacent bundle sheaths (Hattersley and Watson, 1975) were used as indicators of the presence of the C_3 or C_4 photosynthetic pathway. Specimens were also scored for presence (XyMS+) or absence (XyMS-) of a complete inner sheath as an indicator of PCK/NADP-malic enzyme or NAD-malic enzyme activity (Hattersley and Watson, 1976).

RESULTS--Urochloa--Anthecial micromorphology: Species of Urochloa exhibit two anthecial epidermal patterns. The first is the Brachylopha pattern (Fig. 1) described for Brachiaria brachylopha and B. kotschyana (Thompson and Estes, 1986). This pattern is possessed by U. brachyura, U. mosambicensis, U. panicoides, U. pullulans, U. rhodesiensis, and U. stolonifera. It is characterized by large, compound or simple papillae (11.0-37.2 μm) situated on the transverse anticlinal cell walls. Transverse ridges 2-4(5) cells wide frequently connect the papillae. These ridges impart a transversely rugose appearance and occur most frequently on the anthecial midsection. Longitudinal ridges are adorned with simple papillae (2.3-9.7 μm). Ridge height varies with the species. Additionally, each of the longitudinal anticlinal cell wall extensions bears a small, simple papilla (1.0-5.4 μm). These papillae may be absent on U.

stolonifera. Additionally, panicoid bicellular hairs are frequent along the fertile palea's apical margin (Fig. 8).

The Urochloa pattern (Thompson and Estes, 1986) is displayed by U. echinolaenoides and U. trichopus (Fig. 2). Transverse ridges are absent, otherwise distribution of bicellular hairs and stoma, are essentially the same as the Brachylopha pattern.

Urochloa reptans exhibits two anthecial micromorphological patterns. Some plants exhibit the Brachylopha pattern (Fig. 4) but lack papillae on the cell wall extensions, while other plants exhibit a pattern intermediate between that of the Brachylopha pattern and the Urochloa pattern (Fig. 3). This variation has only a few transverse ridges that are only 2 cells wide. It also lacks the small, simple papillae on the longitudinal anticlinal cell wall extensions.

Awns, present on most of the species, have prickle hairs (Fig. 5-8) that arise adjacent to transverse anticlinal cell walls. Their density varies with the species. Papillae often surround the base of the hair (Fig. 5). The pattern of papillae seen on the body of the anthecium is also visible on the lower portion of the awn, but tends to disappear toward the apex. Stomata occur on the awns (Fig. 5), but are not present on the body of the anthecium. Panicoid bicellular hairs are common.

Two bladder-like structures are present in some species (Fig. 6). They occur along the apical margin on the adaxial side of the fertile lemma and overlap the fertile palea. These bladders are quite large in _U. panicoides_ and _U. pullulans_, but are smaller in _U. reptans_ and _U. trichopus_. Only small folds of tissue occur in _U. echinolaenoides_ and _U. stolonifera_ (Fig. 7). _Urochloa brachyura_, _U. mosambicensis_, and _U. rhodesiensis_ lack bladders and folds (Fig. 8).

Leaf epidermis: The epidermal anatomy of _Urochloa_ is relatively uniform. The costal regions typically have one row of silica cells which are generally dumbbell-shaped (Fig. 9), although nodular and cross-shaped cells also occur. Barbed prickle hairs frequently are positioned on top of these silica cells. Cork cells alternate with the silica cells in _U. mosambicensis_, _U. rhodesiensis_, and _U. stolonifera_.

Intercostal regions are narrow, normally 5-6 cells wide. The long cells have smooth or crenate to sinuous margins and concave ends when they are adjacent to a stoma. Short cells generally are infrequent. Macrohairs, if present, arise adjacent to the stomatal rows. The presence and abundance of panicoid bicellular microhairs and prickle hairs varies with the species. There are generally two rows of stomata which have triangular to low-domed subsidiary cells that are separated by 1-4 rows of long cells (Fig. 9).

Again, U. reptans is slightly different from other species of the genus. The intercostal regions of some individuals are 4-10 cells wide, while those of other plants are the typical 5-6 cells wide. The abundance of microhairs also varies considerably from individual to individual. Silica cells are generally dumbbell-shaped, but nodular and cross-shaped cells do occur.

Leaf anatomy: The laminae of Urochloa are either keeled or unkeeled and have adaxial ribs. Additionally, they have abaxial ribs that are equal in size. Vascular bundles are arranged in a pattern of seven secondary bundles between each primary vascular bundle (a 7 to 1 pattern); this pattern disappears near the margins. Some plants of Urochloa reptans have a 6-7 to 1 or a 10-11 to 1 arrangement.

With an outer sheath of 6-13 parenchymatous cells, the primary vascular bundles are triangular, ovoid, or rectangular in shape. The inner sheath is complete and the cells are smaller than those of the outer sheath. The xylem comprises 0-2 protoxylem lacunae and 2-3 metaxylem vessels and the phloem is ovoid to oblong in outline.

Four to seven parenchymatous cells compose the outer sheath of the secondary bundles. The bundle sheath cell(s) closest to one or both of the epidermal layers is usually larger than the others (Fig. 10). Frequently, these larger cells are triangular in outline with the apex of the triangle pointing outward, while the lateral cells are ovoid to rectangular. The xylem comprises 1-2 vessels or is not distinguishable from the phloem and inner sheath.

Primary vascular bundles have 0-6 cells of sclerenchyma in 1-2 rows on the adaxial side and 0-8 cells in 1-2 rows on the abaxial side (Fig. 10). The adaxial side of secondary vascular bundles has 0-3 sclerenchyma cells in one row, while the abaxial side has 0-4 cells also in one row.

A subradiate, single layer of mesophyll cells surrounds each vascular bundle. It abuts the mesophyll layers around adjacent vascular bundles. Maximum lateral cell count is 0-1 and maximum cell distance is 1-2(3). Some plants of Urochloa reptans have radiated mesophyll that composes a greater volume of the blade and is similar to that found in Panicum sect. Fasciculata and Brachiaria.

Between each vascular bundle is a fan of 3-5 bulliform cells. The large, central cell(s) is triangular in outline. These fans penetrate 1/2 to 2/3 the thickness of the blade. A macrohair, with its bulbous base, may arise within the fan.

Panicum section Fasciculata--Anthecial micromorphology: The anthecial micromorphology of Panicum sect. Fasciculata resembles the SE pattern described by Hsu (1965) and the

Ciliatissima pattern of Thompson and Estes (1986) (Fig. 13). The anthecia of all species have swellings over the transverse anticlinal cell walls that coalesce to form transverse ridges (Fig. 14, 15). Situated on these ridges, adjacent to the transverse anticlinal cell walls are simple (Fig. 15) or compound papillae (Fig. 14). Immature anthecia of some P. fasciculatum plants are soft enough to allow wrinkling, which produces short longitudinal extensions of the transverse ridges (Fig. 16).

The fertile palea apex of P. adspersum has panicoid bicellular microhairs and prickle hairs (Fig. 17), whereas that of P. arizonicum has bicellular bottle hairs [a bottle-shaped microhair where the two cells are both short and approximately equal in length (Zuloaga, 1987)] (Fig. 18) similar to those described in Panicum sect. Parvifolia (Zuloaga, 1987). Hairs are absent on the fertile palea apices of P. fasciculatum and P. texanum.

The fertile lemmas of P. arizonicum and P. texanum have mucronate apices. Panicoid bicellular microhairs and stomata occcur on the apex of the fertile lemma in P. arizonicum. Panicum texanum lacks stomata, but does have bottle hairs. The apex of the fertile lemma of P. fasciculatum is recurved and overlaps the fertile palea (Fig. 13); hairs and stomata are absent. The lemmental apex of P. adspersum does not possess a terminal projection, hairs, or stomata.

Leaf epidermis: The costal region typically consists of one, usually continuous, row of nodular to cross-shaped silica cells (Fig. 12). _Panicum texanum_ may have two rows of silica cells over primary vascular bundles and one row over secondary vascular bundles. Prickle hairs plus widely spaced dumbbell-shaped silica cells may occur on the adaxial epidermis in _P_. _arizonicum_. The discernible midrib has a costal zone of 2-4(5) rows of silica cells, which may occur alone or be widely spaced between cork cells.

The intercostal zone is (6)7-10 cells wide with almost smooth to sinuous long cells (Fig. 12). Two to three rows of stomata with low-domed to triangular subsidiary cells are regularly interspersed with long cells. _Panicum fasciculatum_ and _P_. _texanum_ have rectangular cork cells paired with dumbbell-shaped silica cells; the pairs randomly occurr between long cells in nonstomatal rows. Macrohairs are abundant on leaf margins, whereas the presence and abundance of prickle hairs, panicoid bicellular microhairs, and intercostal macrohairs varies among species.

Leaf anatomy: Laminae of _Panicum_ sect. _Fasciculata_ are usually keeled (Fig. 11). The adaxial side is ribbed, while the abaxial side is undulate or ribbed. Between each primary vascular bundle, 3-10 secondary vascular bundles occur; the number is not constant in any species.

The outer sheath of the primary vascular bundles is usually complete and composed of 8-15 cells. *Panicum fasciculatum* has the fewest cells. The cells are ovoid, rectangular, or triangular in shape and larger than the cells of the inner sheath which is complete. The xylem consists of 1-2 protoxylem lacunae and 2-4 metaxylem vessels. In foliar cross-section, the phloem is ovoid in outline.

Secondary vascular bundles have an outer sheath of 4-12 parenchymatous cells with *P. texanum* having 1.5-2 times more cells than *P. fasciculatum*. The cells are rectangular to triangular with the outer edges being either smooth or lobed. The inner sheath is either distinct and complete or not discernible. Xylem comprises 1-3 vessels and the phloem may or may not be distinguishable.

Sclerenchyma occurs as 1-3 rows of 2-8 cells on the adaxial side and 1-3 rows of 5-8 cells on the abaxial side of the primary vascular bundles. Secondary vascular bundles have 1-10 cells in 1-3 rows on the adaxial side and 1-6 cells in 1(2) row on the abaxial side. A single layer of parenchyma radiates from each vascular bundle. Between the radiate parenchyma, a parenchymatous column of cells usually extends from the abaxial epidermis to the adaxial bulliform cells. This column is 1-2 cells wide and the cells are circular to ovoid. Maximum lateral cell count is 1-4 and maximum cell distance is 0-2. Bulliform fans of 3-5 cells occur between all vascular bundles. The central cell(s) is usually largest and triangular in outline. The base of a macrohair may penetrate the bulliform cells.

The triangular midrib contains only one primary vascular bundle with a 13-17 celled outer sheath that is interrupted by a triangular to ovoid sclerenchymatous girder. The width of the girder is equal to or slightly greater than that of the vascular bundle.

DISCUSSION--Urochloa--The anthecial micromorphology of this genus is relatively uniform with two similar patterns that are linked by the intermediate forms of U. reptans. These observations are similar to but reversed from those of Hsu (1965). That is, what he termed ridges are called depression in this manuscript and vice-versa.

Urochloa with only two anthecial patterns and an intermediate form is less variable than Brachiaria, which has with ten discrete patterns. However, the variation found in Urochloa is within the boundaries of the larger genus. The Brachylopha pattern is found in B. brachylopha, B. kotschyana, and B. gilesii (Thompson and Estes, 1986; Thompson, 1988) as well as Urochloa. Brachiaria brachylopha and B. kotschyana share are morphologically distinct from Urochloa. However, B. gilesii possesses laminae similiar to those of U. reptans and its spikelet morphology is more typical of _Urochloa_ than _Brachiaria_ (Thompson, 1988).

Brachiaria platyrhachis displays the Urochloa pattern of anthecial micromorphology (Thompson and Estes, 1986). This observation supports Hubbard's (1934) placement of this species in _Urochloa_ on the basis of gross morphology. _Brachiaria platyrhachis_ differs from other species of _Urochloa_ by having cubical silica cells rather than dumbbell, nodular, or cross-shaped. It is also unlike other species in _Brachiaria_ because of the differences in spikelet morphology, anthecial micromorphology, and silica cell shape.

The bladders and folds at the apical margin on the adaxial side of the fertile lemma found in some species of _Urochloa_ also occur in other panicoid taxa (G. Davidse, personal communication), but are not present in _Brachiaria_ or _Panicum_ sect. _Fasciculata_. These structures may hold the anthecium more securely around the caryopsis and retard germination. Germination rates in _Urochloa_ are exceedingly low without scarification (R. Thompson, unpublished).

Observations of the uniformity of the foliar epidermis of _Urochloa_--costal regions with one row of silica cells and intercostal regions with 5-6 rows of sinous long cells--is supported by Chen, Jin, and Wu's (1986) recognition of the same pattern in Chinese species of the genus. Palmer and Gerbeth-Jones' (1986) observation of the epidermis of African samples of _U. mosambicensis_ also corresponds with this study. Thompson and Estes (1986) reported an absence of nodular silica cells in _U_. _reptans_ (as _B_. _reptans_). Metcalfe (1960) also reported only cross and dumbbell-shaped silica cells in his description of _Urochloa_ epidermal anatomy. But this study reveals that their presence varies from plant to plant and that both nodular, cross, and dumbbell-shaped silica cells are frequent in all species.

The leaf anatomy of _Urochloa_ is characteristic of a C_4, PCK grass similar to that found in _Brachiaria_ and _Pancium_ sect. _Fasciculata_. _Urochloa_ differs from the other two taxa in the amount of mesophyll present; the genus has a single subradiate layer of cells, composed of cells whose length is not much greater than its width, when viewed in cross-section. _Brachiaria_ (Thompson and Estes, 1986) and _Panicum_ sect. _Fasciculata_ have more mesophyll, a single radiate to subradiate layer of cells composed of cells whose length is almost twice that of its width. The 7 to 1 arrrangement of vascular bundles prevails in _Urochloa_, except in some plants of _U_. _reptans_. Additionally, the bulliform fans penetrate deeply into the mesophyll in _Urochloa_, a feature Metcalfe (1960) also noted. This reduction in the amount of mesophyll may be an adaption to drier habitats (Ellis, 1976). However, these _Urochloa_ species are found in both mesic and xeric habitats.

The generic affinities of _Urochloa reptans_ have been difficult to ascertain. It has been placed in _Brachiaria_, Panicum sect. Fasciculata, and Urochloa (Hitchock and Chase, 1910; Stapf, 1934b; Gardner and Hubbard, 1938). Although individual plants are variable with respect to anthecial and leaf features, the species displays all the characteristics in Urochloa and exhibits a greater affinity to species of that genus than to species of Brachiaria or Panicum sect. Fasciculata.

The results of this study suggest that Urochloa is a distinct genus. The anatomically uniform leaf of Urochloa with its reduced mesophyll, a 7 to 1 arrangement of vascular bundles, deep penetration by bulliform fans, 5-6 celled intercostal regions, and narrow costal regions with typically one row of dumbell-shaped silica cells differs markedly from the variable leaf characteristic of Brachiaria and Panicum sect. Fasciculata. This suite of foliar features may be coupled with the genus's radiation into drier habitats as suggested by Ellis (1976).

Panicum section Fasciculata--Panicum sect. Fasciculata possesses features characteristic of both Brachiaria and Panicum. The SE or Ciliatissima pattern exhibited by species of the section commonly occurs in Brachiaria (Hsu, 1965; Thompson and Estes, 1986) and more rarely in Panicum [P. sect. Maxima, sect. Bulbosa, and sect. Monticola (Zuloaga, 1987)].

The foliar anatomy of the section is characteristic of a C_4, PCK grass but it is highly variable. The leaves of the species in the section resemble those of Brachiaria eruceaformis, B. deflexa, B. lata, B. nigropedata, B. ramosa, and B. rugulosa. They all exhibit ribbed to slightly ribbed laminae containing radiate parenchyma (Thompson, unpublished). Brachiaria deflexa also occasionally exhibits columns of parenchyma connecting the fans of bulliform cell and the abaxial epidermis. This study, therefore supports Parodi (1969) and Blake's (1969, 1973) placement of Panicum sect. Fasciculata in Brachiaria.

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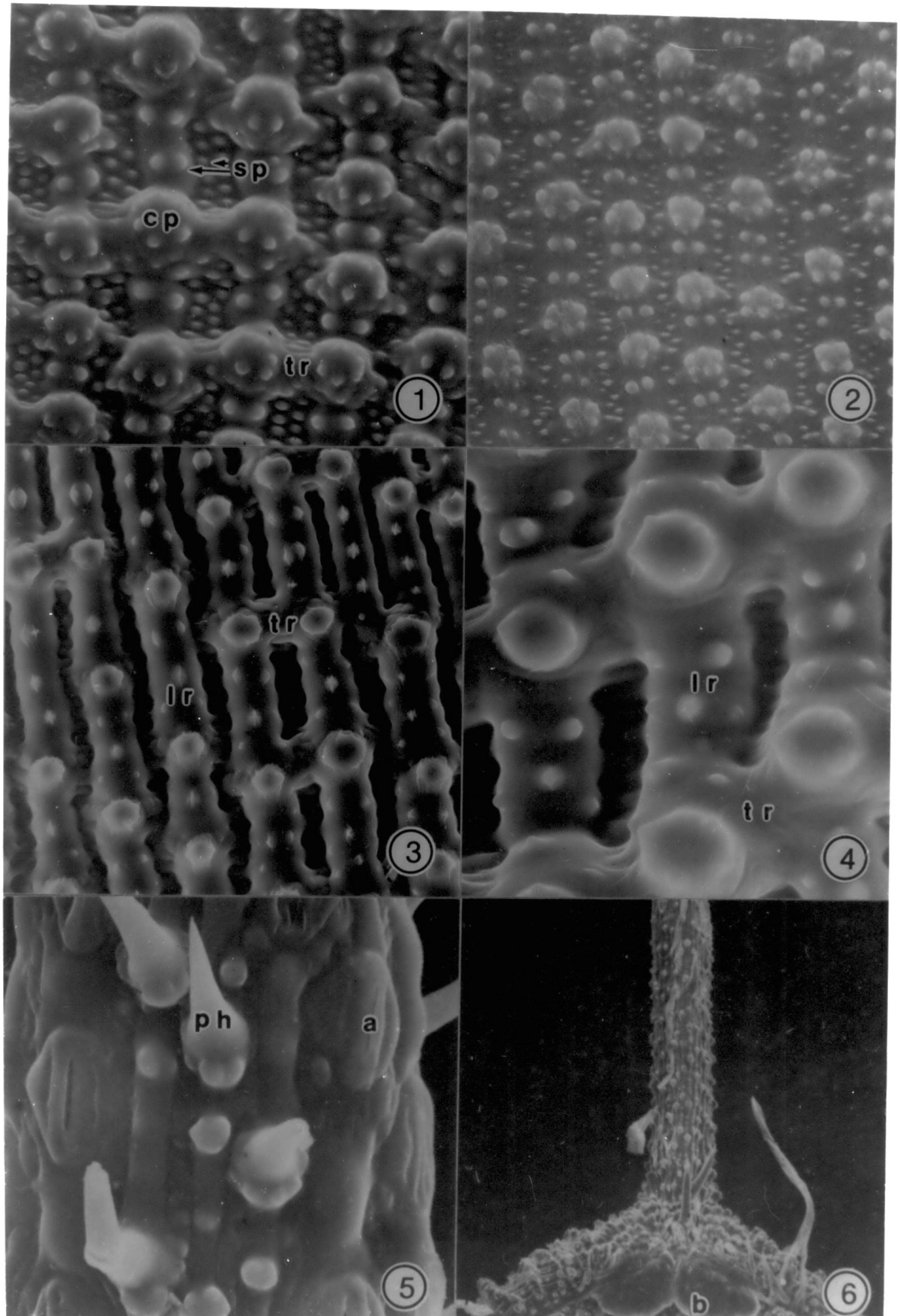
Fig. 1-6. Urochloa anthecial micromorphology. 1. Fertile palea of U. stolonifera. X 360. 2. Fertile palea of U. echinolaenoides. X 360. 3-4. Fertile palea of U. reptans. 3. X 400. 4. X 780. 5. U. echinolaenoides awn. X 1800. 6. U. panicoides fertile lemma overlapping the fertile palea. X 60. a = stoma; b = bladder; cp = compound papilla; lr = longitudinal ridge; ph = prickle hair; sp = simple papilla; tr = transverse ridge.

Fig. 7-12. Urochloa anthecial micromorphology and Urochloa and Pancium sect. Fasciculata leaf anatomy. 7. U. stolonifera fertile lemma overlapping the fertile palea. X 180. 8. U. brachyura fertile lemma overlapping the fertile palea. X 120. 9. U. stolonifera adaxial leaf epidermis. X 340. 10. U. reptans leaf cross section. X 420. 11. P. texanum leaf cross section. X 160. 12. P. fasciculatum adaxial leaf epidermis. X 290. a = stoma; b = bicellular hair base; c = cork cell; F = folds of tissue; f = bulliform fans; i = inner sheath; l = long cell; mh = macrohair; ph = prickle hair; o = outer sheath; s = silica cell; x = xylem; y = phloem.

Fig. 13-18. Pancium sect. Fasciculata anthecial micromorphology. 13. Fertile palea of P. fasciculatum. X 40. 14. Fertile palea of P. arizonicum. X 600. 15. Fertile palea of P. adspersum. X 300. 16. Immature fertile palea of P. fasciculatum. X 300. 17. P. adspersum fertile palea apex. X 400. 18. P. arizonicum fertile palea apex. X 600. ph = prickle hair; bo = bottle hair; bm = bicellular microhair; cp = compound papilla; sp = simple papilla; tr = transverse ridge.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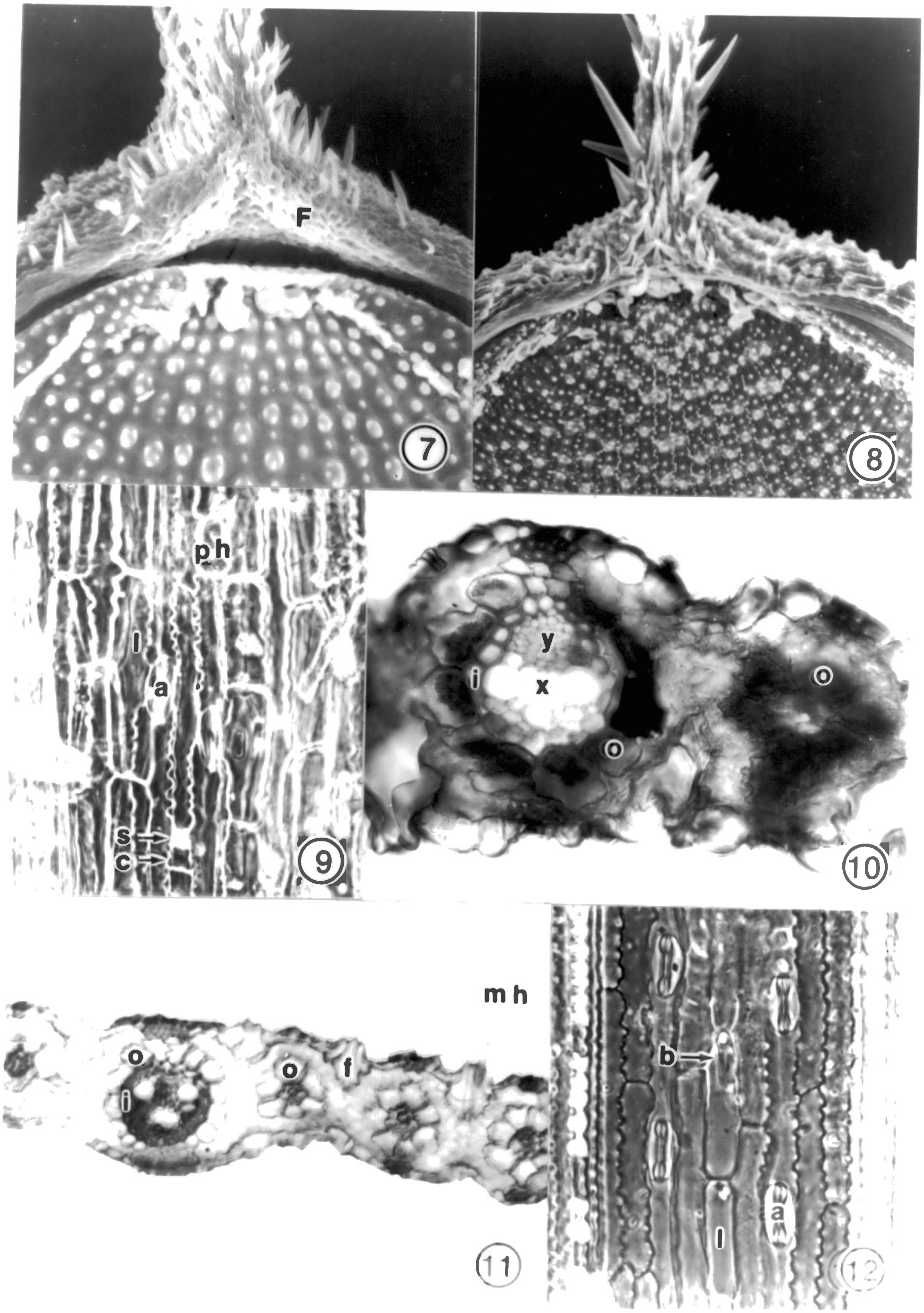
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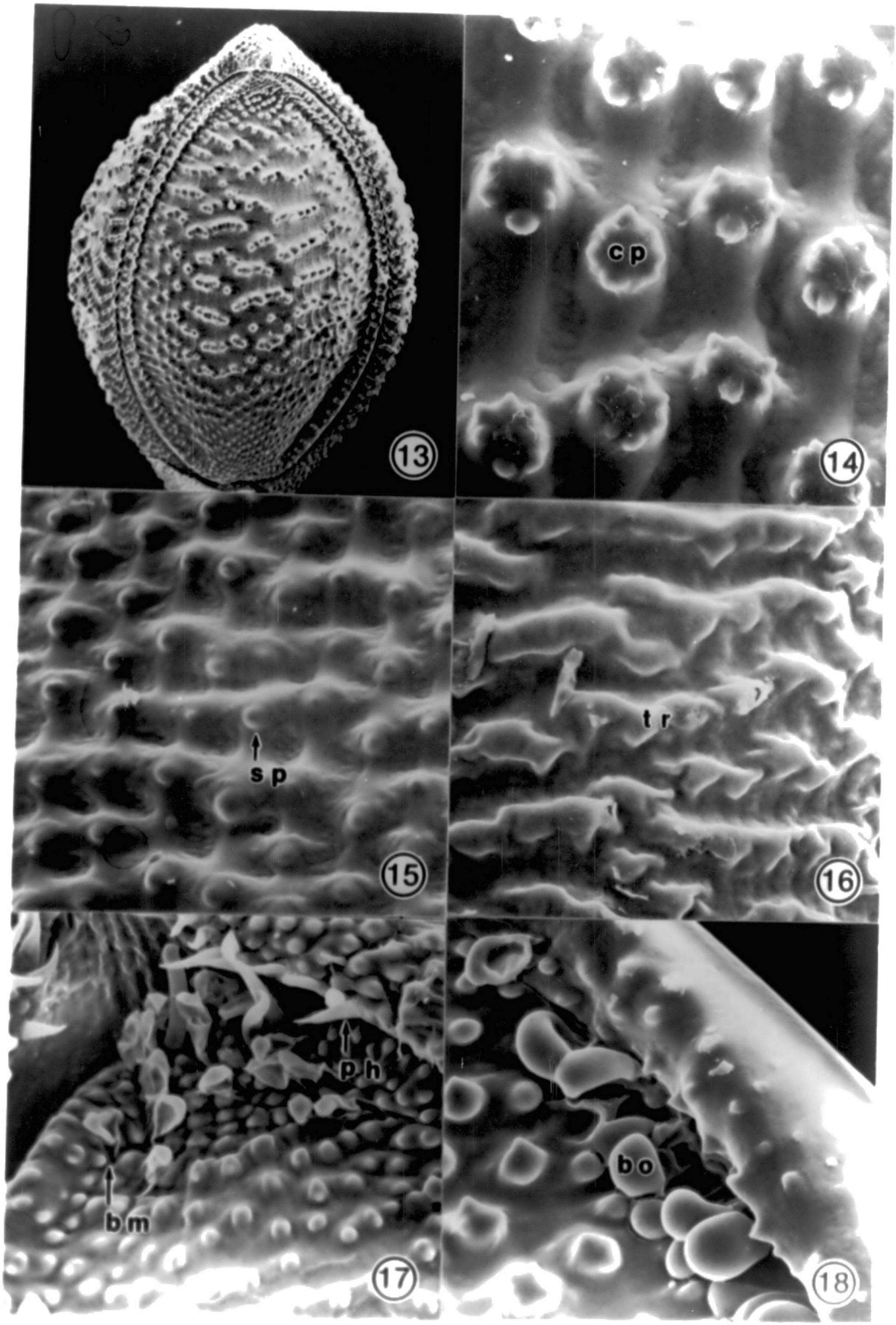
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ANTHECIAL AND FOLIAR MICROMORPHOLOGY AND FOLIAR ANATOMY OF BRACHIARIA (POACEAE: PANICEAE). II.

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Running Head: *Brachiaria* II

ABSTRACT

Observations of anthecial and foliar micromorphology and laminar anatomy of eight *Brachiaria* species reveal that: (1) *B. callopus* and *B. obtusiflora* exhibit anthecia with the Echinochloa pattern and a single papilla in the center of [illegible]nar, epidermal long cell; (2) *B. gilesii* is similar to *Urochloa reptans*, as both have anthecia with the Brachylopha pattern and leaf anatomy with ribs, radiate mesophyll, and an epidermal, intercostal width that is sometimes 5-6 cells wide; (3) *B. breviglumis* and *B. deflexa* display the Cilitissima anthecial pattern; (4) *B. longiflora* and *B. subulifolia* have anthecia with the Dura pattern; (5) *B. umbellata* has anthecia with the Eriochloa pattern; and (6) the latter four species have lamiar features found in *Brachiaria*. This study supports the transfer of *B. callopus* and *B. obtusiflora* to *Echinochloa*; the placement of *B. gilesii* in *Urochloa*; and the retention of *B. breviglumis*, *B. longiflora*, *B. subulifolia*, and *B. umbellata* in *Brachiaria*. Recognition of *Pseudobrachiaria deflexa* is not warranted and the placement of this species in *Brachiaria* is accepted.

Bracharia Griseb. is characterized by the presence of an inflorescence of a panicle of racemes and spikeletes exhibiting adaxial orientation--a characteristic that is in contrast to most of the other panicoid genera. Trinius (1826) originally recognized Brachiaria as a section of Panicum, comprising 29 species, eight of which most authors still retain in Brachiaria. Grisebach (1853) raised the taxon to generic rank and described one species. As floristic endeavors have been completed, the number of described species has increased. In her monograph on the North American species of Brachiaria, Chase (1920) recognized 6 species, and commented that there were approximately 70 species world-wide. In contrast, Stapf (1934) in his treatment of tropical African grasses recognized 48 species; either new combinations or new species. Some 164 species names appear in Index Kewensis, however Clayton and Renvoize (1986) recognize approximately 100 species.

Species of Brachiaria display a wide range of morphological characteristics. They range in habit from small annuals (e.g. B. erucaeformis) to robust perennials (B. brizantha); in inflorescence type from those with racemes (B. decumbens) to those with one-sided panicles (B. poaeoides); and in spikelet orientation from solely adaxial (B. nigropedata) to adaxial and abaxial (B. adspersa) to solely abaxial (B. gilseii) (Thompson, 1988).

Species of the genus also display variation in anatomical features. Studies of panicoid anthecial micromorphology, laminar anatomy, and laminar epidermal micromorphology revealed a variety of patterns and similarities between *Brachiaria* and other genera of the Paniceae. Hsu (1965) discovered that *Brachiaria* and *Urochloa* shared the same lemmatal surface patterns and that spikelet orientation seemed to be the only feature separating the two taxa. Thompson and Estes (1986) and Thompson (1988) found even more variation than had been discerned by Hsu. Thompson (1988) suggested that *Brachiaria*, *Eriochloa*, *Panicum* sect. *Fasciculata*, and *Urochloa* appear to form a monophyletic assemblage.

As a result of this variational pattern and the apparent overlap in variation with other panicoid taxa, Clayton and Renvoize (1982, 1986), Thompson and Estes (1986), and Webster (1987) all contend that the generic boundaries of *Brachiaria* are problematic. This report describes observations of eight species which were not included in a previous study of the genus (Thompson and Estes, 1986). Three are morphological intermediates between *Brachiaria* and other taxa (Clayton and Renvoize, 1982; Thompson, 1981); four are recently erected taxa (Clayton, 1979); and one is segregated as the monotypic *Pseudobrachiaria* (Launert, 1970). These data will be combined with those from previously examined species of

Brachiaria, Eriochloa, Panicum sect. Fasciculata, and Urochloa in an examination of generic boundaries in the Brachiaria complex (Thompson, 1988).

MATERIALS AND METHODS--Species examined include Brachiaria breviglumis Clayton, B. callopus (Pilger) Stapf [= Echinochloa callopus (Pilger) Clayton], B. deflexa (Schumach.) C.E. Hubbard [= Pseudobrachiaria deflexa (Schumach.) Launert], B. gilesii (Benth.) Chase [= Urochloa gilesii (Benth.) Hughes], B. longiflora Clayton, B. obtusiflora (A. Rich) Stapf [= Echinochloa rotundiflora Clayton], B. subulifolia (Mez) Clayton, and B. umbellata (Trin.) Clayton. Spikelet and leaf material was removed, with permission, from specimens from K and MO. Specfic names were taken from herbaium labels. A list of specimens examined is presented in Thompson (1988).

Anthecial micromorphology--Intact anthecia or separated fertile lemmas and paleas were placed on aluminum stubs using double-stick tape. Specimens were coated with gold-paladium (Thompson and Estes, 1986). JEOL JSM-2 and ETEC Autoscan scanning electron microscopes were used to examine the specimens, and photographs were taken of the apical, middle, and basal portions of each valve. One or two anthecia were examined for each taxon; if anything unusual was observed additional anthecia were scanned until an understanding of the pattern of variation was obtained.

Leaf epidermis--Abaxial and adaxial epidermal peels were made primarily from middle portions of blades. The specimens were rehydrated in 5 % Contrad 70 and extraneous tissue was removed with a scalpel. The epidermis was then mounted in Hoyer's Mounting Medium and examined using phase (Thompson and Estes, 1986) or interference-contrast optics.

Leaf anatomy--Free hand cross-sections were made from the rehydrated material described above. Sections were stained in safranin and Delafield's haematoxylin using the procedure of Thompson and Estes (1986).

Maximum lateral cell count--the maximum number of cells separating any mesophyll cell from a bundle sheath cell--and maximum cell distance--the maximum number of cells between adjacent bundle sheaths (Hattersley and Watson, 1975)--were used as an indicator of the presence of the C_3 or C_4 photosynthetic pathway. Specimens were also scored for presence (XyMS+) or absence (XyMS-) of a complete inner sheath as an indicator of PEP-carboxykinase/NAD-malic enzyme (PCK/NAD-me) or NADP-malic enzyme (NADP-me) activity (Hattersley and Watson, 1976).

RESULTS--*Anthecial micromorphology*--*Brachiaria callopus* and *B. obtusiflora* exhibit an anthecium with a smooth, striate surface and a typically green, more hyaline, wrinkled apex similar to that possessed by *Echinochloa* (Fig. 1-2). Sinuous anticlinal walls of the long cells are evident. Apical spicules or prickle hairs similar to those described by Clark and Gould (1975) from the paleas of *E. crusgalli* and silica cells similar to those noted by Hsu (1965) noted on the fertile lemmas of *Echinochloa* are present on the apices of the fertile lemmas of both species. Silica cells may also be present along the edges of the upper 2/3 of the fertile paleas. Using the terminology established earlier (Thompson and Estes, 1986), this pattern is designated here as the Echinochloa pattern.

Brachiaria gilesii displays the Brachylopha pattern recognized by Thompson and Estes (1986). Compound papillae are present on the transverse ridges and smaller simple papillae are on the longitudinal ridges (Fig. 7). Papillae on the longitudinal anticlinal cell wall extensions are absent. This species also bears an awn which has bristle hairs, simple papillae, and stomata (Fig. 8).

The Ciliatissima pattern (Thompson and Estes, 1986) or the SE pattern (Hsu, 1965) characterizes the anthecia of *B. breviglumis* and *B. deflexa*. *Brachiaria breviglumis* exhibits the typical Ciliatissima pattern (Fig. 9)--coalesced transverse ridges that are higher than the longitudinal ridges. Pappillae on the transverse ridges are usually compound although simple ones do occur. Silica cells, bicellular microhairs, bristle hairs, and stomata may be present on the mucronate apex of its fertile lemma (Fig. 10). The anthecia of B. deflexa display a variation of the Ciliatissima pattern (Fig. 11-12). Papillae are present on the transverse ridges only near the apex of the fertile lemma. Those nearest the apex are compound while those farther away are simple. Simple papillae are also present on the longitudinal anticlinal cell wall extensions. Panicoid bicellular microhairs are common along the apical edges of the fertile palea, but less frequently on the fertile lemma apex. Stomata also may be present on the fertile lemma apex.

The Eriochloa pattern of Thomspon and Estes (1986)--longitudinal rows of papillae--characterizes the anthecia of B. umbellata (Fig. 13). The apex of its bracts are only papillate, silica cells, bicellular microhairs, bristle hairs, and stomata are not present (Fig. 14).

Brachiaria longiflora and B. subulifolia have anthecia displaying the Dura pattern (Thompson and Estes, 1986), i.e., small papillae are present only on the upper 1/3 to 1/2 of both bracts (Fig. 15-16). The apex of the fertile palea of both species is truncate. The fertile lemma apex of B. subulifolia has silica cells and bristle hairs while both species have a truncate fertile palea apex (Fig. 16).

Leaf epidermis--With one exception, the epidermal features are relatively uniform among the eight species (Fig. 3, 6, 17). In all species, intercostal and costal regions vary in width on all laminae. *Brachiaria gilesii* does have some intercostal regions that are 5 to 6 cells wide. Silica cells, particularly dumbbell-shaped cells, and prickle hairs are common in the costal regions. Long cells have smooth to sinuous margins and concave ends when they are adjacent to a stoma. Cross-shaped silica cells, often paired with a cork cell, are common between long cells. Panicoid bicellular microhairs, prickle hairs, and macrohairs occurr regularly. *Brachiaria callopus*, and *B. obtusiflora* differ from the other species as they have a single papilla on the anticlinal cell wall of each long cell (Fig. 3).

Leaf anatomy--*Brachiaria callopus* and *B. obtusiflora* have anatomy typical of the NADP-me pathway of C_4 photosynthesis (Fig. 4) while the other six species have anatomy indicative of the PCK/NAD-me pathway (Fig. 5, 18). Lamina of *B. longiflora* (Fig. 18) display a reduced amount of mesophyll similar to that typically seen in *Urochloa*. *Brachiaria gilesii* (Fig. 5) has a ribbed lamina with radiate mesophyll similar to *Urochloa reptans* (Thompson, 1988). *Brachiaria subulifolia* is distinctive; its leaves are filiform (Fig. 18). Foliar characteristics of the eight species are summarized in Table 1.

DISCUSSION--The patterns of anthecial and foliar micromorphology and laminar anatomy described above permit placement of these eight taxa. Brachiaria callopus and B. obtusiflora display an anthecial pattern similar to that found in Echinochloa. Echinochloa also exhibits the NADP-me pathway of C_4 photosynthesis (Brown 1977) and has a single, simple papilla on the anticlinal cell wall of each long cell (Sánchez, 1968); characteristics which are also found in these two species. On the basis of spikelet and anthecial gross morphology, Clayton (1979) and Clayton and Renvoize (1982) placed B. callopus and B. obtusiflora in Echinochloa. This study supports their transfer.

Brachiaria gilesii bears an anthecial pattern and leaf anatomy similar to some specimens of Urochloa reptans (Thompson, 1988). This study indicates that B. gilesii is more closely allied with Urochloa, and Hughes' (1923) placement of the species in Urochloa is accepted.

Recognition of Pseudobrachiaria is not warranted. Launert (1970) segregated P. deflexa, a minor cereal of West Africa, based on the presence of an internode between the two florets. Despite the separation of the florets, the conspicuous similarities in micromorphology indicate placement in Brachiaria, a conclusion in agreement with that of Clayton and Renvoize (1982, 1986).

The remaining four species--*B*. *breviglumis*, *B*. *longiflora*, *B*. *subulifolia*, and *B*. *umbellata* exhibit anthecial patterns found in *Brachiaria*; all except *B*. *longiflora* possess laminar mesophyll that occupies a significant portion of the blade; and all except *B*. *subulifolia* have bulliform fans that penetrate less than 1/2 the width of the blade between vascular bundles. Although reduced mesophyll of *B*. *longiflora* is typical of *Urochloa*, this and all of the species other laminar features can be found in *Brachiaria* (Thompson and Estes, 1986). The distinctive leaf shape of *B*. *subulifolia* appears to be an environmental adaptation. Therefore, on the basis of their micromorphological and foliar anatomical features, these four species appear to be properly placed and boundaries of *Brachiaria* further clarified.

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Table 1. Comparison of leaf anatomy.

	BREVIGLUMIS	CALLOPUS	DEFLEXA	GILESII	LONGIFLORA	OBTUSIFLORA	SUBULIFOLIA	UMBELLATA
LAMINA OUTLINE	no midrib	V-shaped	flat	flat	monofiliform	V-shaped	filiform	no midrib
MAXIMUM LATERAL CELL COUNT	0-1	2-4	2	2	1-2	3-4	0-2	2-4
MAXIMUM CELL DISTANCE	2-3	3-5	0	0	1	1-2	2	1-3
C_4 PATHWAY	PCK/NAD-me	NADP-me	PCK	PCK/NAD-me	NADP-me	PCK/NAD-me	PCK/NAD-me	
MESOPHYLL								
Arrangement of Chlorenchyma	radiate	irradiate	subradiate	subradiate	subradiate	subradiate	subradiate	radiate
Cell Shape in Chlorenchyma	cubical to rectangular	irregular	rectangular	rectangular	rectangular	rectangular to irregular	cubical to rectangular	rectangular
Additional Parenchyma	a few iso-diameteric cells	none	none	none	none	none	center of filiform blades filled with large parenchyma cells	none

Table 1. Comparison of leaf anatomy.

	BREVIGLUMIS	CALLOPUS	DEFLEXA	GILESII	LONGIFLORA	OBTUSIFLORA	SUBULIFOLIA	UMBELLATA
LAMINA OUTLINE	no midrib	V-shaped	flat	flat	monofiliform	V-shaped	filiform	no midrib
MAXIMUM LATERAL CELL COUNT	0-1	2-4	2	2	1-2	3-4	0-2	2-4
MAXIMUM CELL DISTANCE	2-3	3-5	0	0	1	1-2	2	1-3
C_4 PATHWAY	PCK/NAD-me	NADP-me	PCK	PCK/NAD-me	NADP-me	PCK/NAD-me	PCK/NAD-me	
MESOPHYLL								
Arrangement of Chlorenchyma	radiate	irradiate	subradiate	subradiate	subradiate	subradiate	subradiate	radiate
Cell Shape in Chlorenchyma	cubical to rectangular	irregular	rectangular	rectangular	rectangular	rectangular to irregular	cubical to rectangular	rectangular
Additional Parenchyma	a few iso-diameteric cells	none	none	none	none	none	center of filiform blades filled with large parenchyma cells	none

Table 1. Cont.

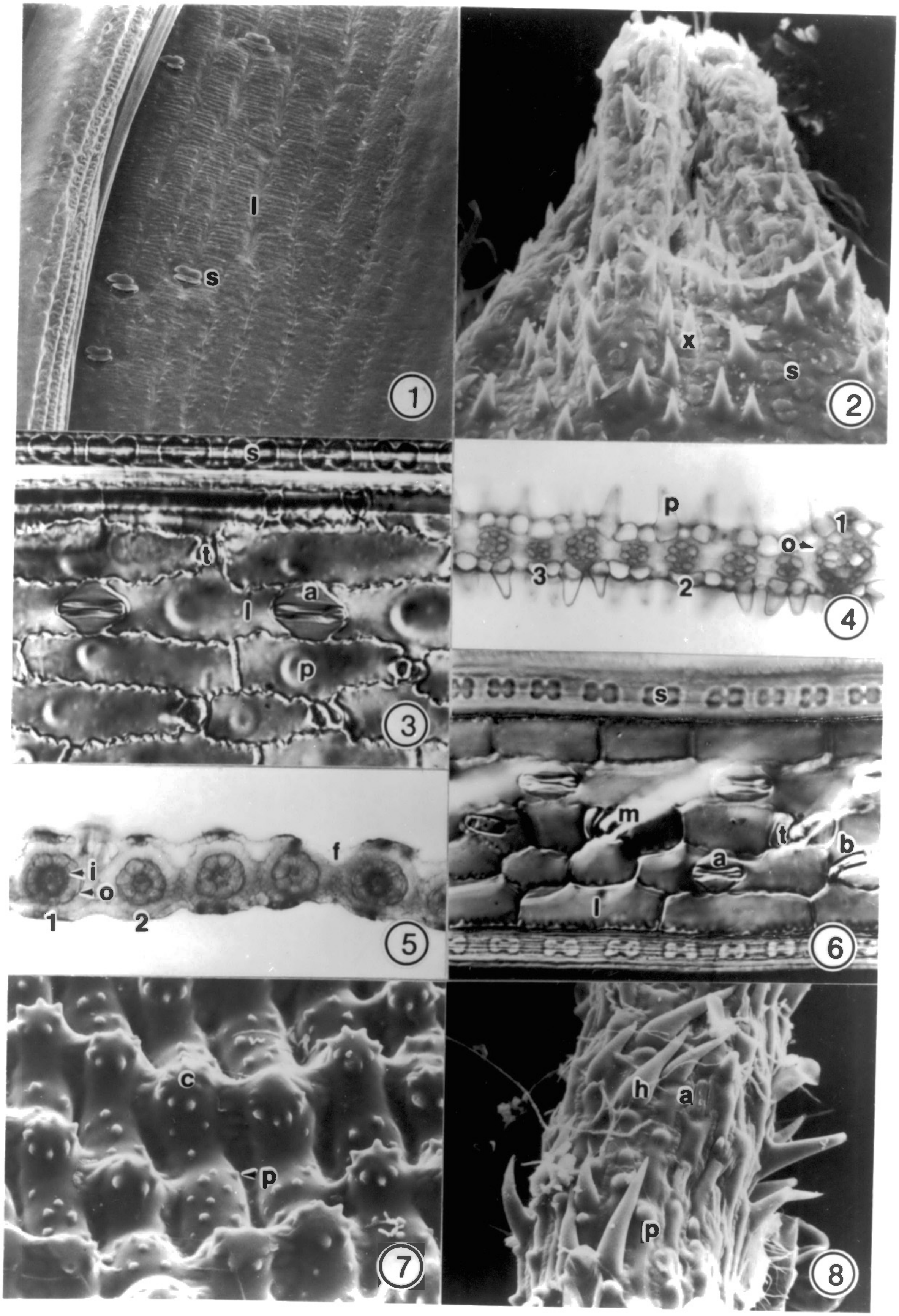
	BREVIGLUMIS	CALLLOPUS	DEFLEXA	GILESII	LONGIFLORA	OBTUSIFLORA	SUBULIFOLIA	UMBELLATA
VASCULAR BUNDLES RATIO	4 secondary to 1 primary vascular bundle	7 secondary to 1 primary vascular bundle	4-15 secondary to 1 primary vascular bundle	9 secondary to 1 primary vascular bundle	6-8 secondary to 1 primary vascular bundle	1 secondary to 1 tertiary vascular bundle	1 secondary to 1 tertiary vascular bundle	5 secondary to 1 primary vascular bundle
TERTIARY VASCULAR BUNDLES	absent	present	absent	absent	absent	present	present	absent
BULLIFORM FANS								
Number of Cells	3-5	3	3-4	3-5	3-4	0	4-6	5-6
Position of Fans	between vascular bundles	over tertiary vascular bundles	between vascular bundles	between vascular bundles	between vascular bundles	absent	in notch of filiform blade	between vascular bundles

Fig. 1-8. Characteristics of B. callopus, B. obtusiflora, and B. gilesii. 1-3. B. callopus. 1. Fertile palea. X 200. 2. Fertile lemma. X 240. 3. Adaxial leaf epidermis. X 378. 4. Leaf cross section of B. obtusiflora. X 120. 5-8. B. gilesii. 5. Leaf cross section. X 110. 6. Abaxial leaf epidermis. X 302. 7. Fertile lemma. X 400. 8. Awn. X 400. a = stoma; b = bicellular hair base; c = compound papilla; f = fan of bulliform cells; h = bristle hair; i = inner sheath; l = long cell; m = macrohair; o = outer sheath; p = simple papilla; s = silica cell; t = short cell; x = prickle hair; 1 = primary vascular bundle; 2 = secondary vascular bundle; 3 = tertiary vascular bundle.

Fig. 9-14. Anthecial micromorphology of B. breviglumis, B. deflexa, and B. umbellata. 9-10. Fertile lemma of B. breviglumis. 9. X 600. 10. X 300. 11-12. B. deflexa. 11. Fertile palea. X 200. 12. Fertile lemma. X 400. 13-14. Fertile lemma of B. umbellata. 13. X 400. 14. X 500. a = stoma; b = bicellular hair; c = compound papilla; h = bristle hair; p = simple papilla; s = silica cell.

Fig. 15-18. Characteristics of B. longiflora and B. subulifolia. 15.Fertile palea of B. subulifolia. X 200. 16-17. B. longiflora. 16. Fertile palea. X 100. 17. Abaxial leaf epidermis. X 97. 18. Cross section of B.

<u>subulifolia</u> leaf. X 40. a = stoma; f = fan of bulliform cells; i = inner sheath; l = long cell; o = outer sheath; p = simple papilla; t = pair of short cells.



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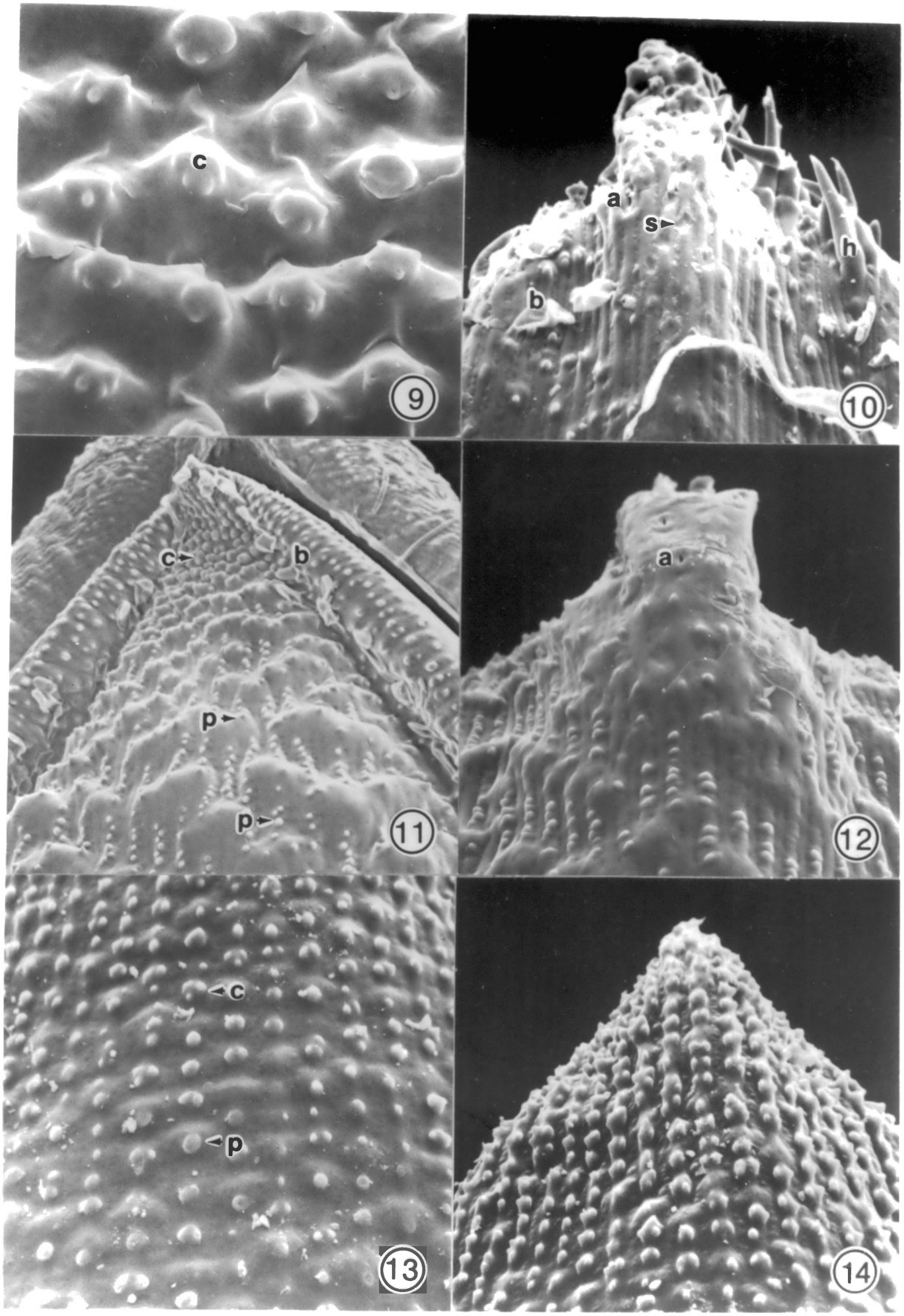
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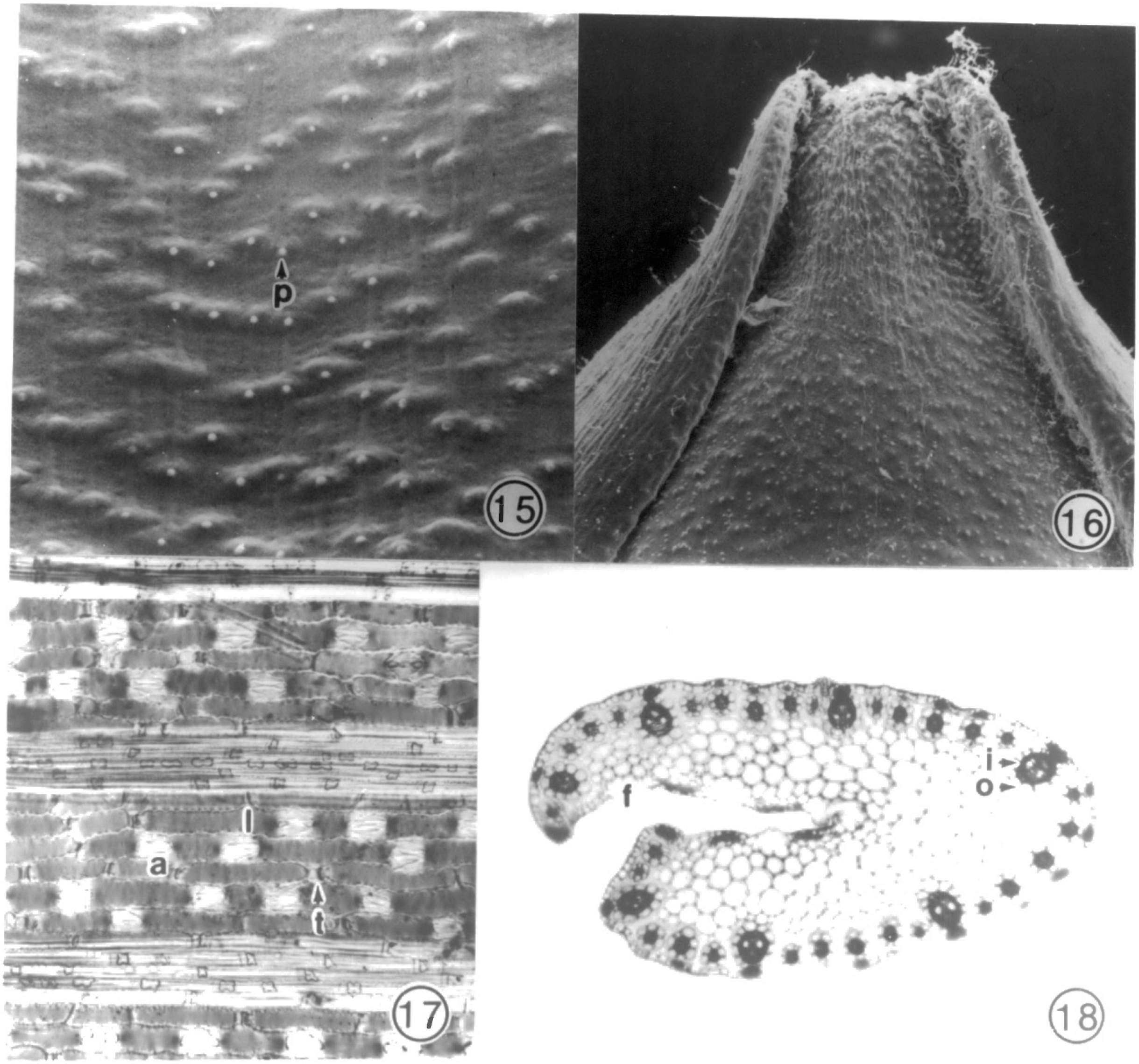
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TAXONOMY OF THE *BRACHIARIA* COMPLEX

(POACEAE: PANICEAE)

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ABSTRACT. The Brachiaria complex includes three taxa: Eriochloa, Urochloa, and Brachiaria. Panicum sect. Fasciculata and Pseudobrachiaria are submerged in Brachiaria. Eriochloa is distinct because of: (1) bulliform fans over the vascular bundles; (2) a tight panicle; (3) a cup-shaped callus; (4) an adaxially orientated, elliptic spikelet; (5) a papillose anthecium; and (6) an awned fertile lemma. Urochloa possesses (1) a racemose to occasionally paniculate inflorescence; (2) a complex of laminar characters that includes (a) a reduced mesophyll, (b) a 7 to 1 ratio of secondary to primary vascular bundles, (c) bulliform fans that penetrate deeply into the mesophyll, (d) an intercostal width of 5 or 6 cells, and (e) single, costal rows of dumbbell-shaped silica cells; (3) an ovate to elliptic spikelet; (4) typically adaxial spikelet orientation; (5) rugose anthecia; and (6) awnless to awned fertile lemmas. Brachiaria remains a highly variable genus with: (1) a racemose to one-sided, paniculate inflorescence; (2) variable, C_4, PCK leaf anatomy; (3) variable spikelet shape; (4) primarly adaxially orientated spikelet; (5) a papillose to rugose anthecium; and (6) awnless to awned fertile lemma.

Among the subfamilies of grasses, the circumscription of the Panicoideae has remained essentially unchanged since its recognition as a distinct taxon by Brown (1814). The same is true for the circumscription of the Paniceae, a tribe characterized by an indurate upper lemma and palèa which tightly enclose the flower and later the caryopsis. Within the tribe, however, delimitation of genera can be problematic. As Clayton and Renvoize (1986) noted, the relative uniformity of spikelet structure hinders partitioning of the tribe.

Definition of Brachiaria Griseb. has proven especially difficult. It has been most often characterized by: (1) a panicle of racemes; (2) an adaxial spikelet orientation; (3) the presence of both glumes; (4) a papillose to papillose-rugose fertile floret; and (5) an awnless to mucronate fertile lemma (Clayton and Renvoize 1986; Thompson and Estes 1986). Proposed affinities, both phenetic and phylogenetic, between Brachiaria and Urochloa Beauvious, Panicum sect. Fasciculata Hitchcocok & Chase,and Eriochloa H.B.K. have been recognized. In addition, relationships between Brachiaria, and Acroceras Stapf, Alloteropsis Presl, Anthaenantiopsis Pilger, Axonopus Beauvious, Chaetium Nees, Coridochloa Nees, Eccoptocarpha Launert, Entolasia Stapf, Leucophrys Rendle, Louisiella Hubbard & Leonard, Neurachne R. Brown, Oryzidium Hubbard & Schweick, Pseudobrachiaria Launert, Psilochloa Launert, Remaria Flugge, Scutachne

Hitchcock & Chase, Thuarea Pers., and Yvesia A. Camus are recognized. Various interpretations of its generic boundaries and relationships have been offered for more than 150 years (Trinius 1826; Grisebach 1853; Chase 1920; Stapf 1934a, 1934b; Pilger 1940; Hsu 1965; Parodi 1969; Blake 1969, 1973; Butzin 1970; Brown 1977; Shaw and Smiens 1980; Clayton and Renvoize 1982, 1986; Thompson and Estes 1986; Shaw and Webster 1987; Webster 1987).

Trinius (1826) originally recognized Brachiaria as a section of Panicum on the basis of its racemose inflorescence. The section was elevated to generic level by Grisebach (1853). Nash (1903) was the first to note the adaxial orientation of the spikelet in a treatment of the genus in the southeastern United States. Chase (1920) and Stapf (1934a) expanded the circumscription of Brachiaria by emphasizing this feature. They de-emphasized morphology of the inflorescence.

Parodi (1969) formally recognized the similarity between Panicum sect. Fasciculata and Brachiaria when he transferred P. adspersum and P. fasciculatum to Brachiaria on the basis of the adaxial orientation of the second and third spikelets below the apex of the inflorescence. Independently, Blake (1969) placed the entire section in Brachiaria on the basis of overall similarity. Hsu (1965) and Brown (1977) also believed that these two taxa should be combined. Webster (1987) transferred all the Australian species of _Brachiaria_ with the exception of _B_. _erucaeformis_, including those of section _Fasciculata_, to _Urochloa_.

Shaw and Smiens (1980), Clayton and Renvoize (1986), and Shaw and Webster(1987) noted a similar close relationship in morphology between _Eriochloa_ and _Brachiaria_. All species of _Eriochloa_ and some species of _Brachiaria_ possess a tight panicle; an elliptical, adaxial spikelet; a papillose anthecium; and an awned fertile lemma. The presence of a cup-shaped callus at the base of the spikelet in _Eriochloa_ is traditionally used to separate the two taxa, but several species of _Brachiaria_ possess a callus bead that Clayton (1975) believed to be an ealier evolutionary stage of the cup.

Urochloa also exhibits considerable similarity to _Brachiaria_. It has a racemose inflorescence, both glumes, a rugose fertile floret, and a mucronate to awned fertile lemma, but differs in abaxial spikelet orientation (Burt et al. 1980; Clayton and Renvoize 1986; Stapf 1934b). Several species of _Brachiaria_ possess all of these characters of _Urochloa_ except for the orientation of the spikelet (Clayton and Renvoize 1986). As a result of his extensive study of panicoid anthecial micromorphology, leaf epidermal anatomy, and lodicule morphology, Hsu (1965) questioned the emphasis placed on spikelet orientation. He noted that _Brachiaria_ and _Urochloa_ shared the same lemmatal surface pattern and that spikelet orientation seemed to be the only feature separating the two taxa. In their examination of Brachiaria's anthecial micromorphology and laminar epidermal micromorphology, Thompson and Estes (1986) found even more variation in the genus than had been discerned by Hsu, however, they confirmed similarities between Brachiaria and Urochloa. They also noted similarities between Brachiaria and both Panicum sect. Fasciculata and Eriochloa.

Brown (1977) questioned the use of spikelet orientation for taxonomic delimitation. In his comparative study of foliar vascular anatomy and photosynthetic pathways, he delimited a group of taxa characterized by the PEP-carboxykinase (PCK) variation of the C_4 photosynthetic pathway and a Kranz sheath derived from the parenchymatous sheath (P.S.) [photosynthetic carbon reduction sheath (PCR) that arises from the ground meristem (Dengler, Dengler, and Hattersly, 1985)]. This group is also defined by free style bases and a firm fertile lemma. Brown referred to this assemblage as the Brachiaria group and included Brachiaria, Chaetium, Coridochloa, Eriochloa, Leucophrys, Oryzidium, Pseudobrachiaria, Panicum sect. Fasciculata, Scutacne and Urochloa.

Thompson (1988) and Thompson and Estes (1986) have indicated that within the Brachiaria group, Brachiaria, Eriochloa, Pseudobrachiaria, Panicum sect. Fasciculata, and Urochloa appear to form a monophyletic complex with problematic taxonomic relationships. An examination of the relationships among these taxa was undertaken (Thompson 1988). This paper presents a tentative delimitation of the taxa within the complex based on anthecial and foliar micormorphology, foliar anatomy, and gross morphology. Relationships among the other taxa thought to be related to Brachiaria will be described in subsquent publications.

MATERIAL AND METHODS

The gross morphology, anthecial and laminar micromorphology, and laminar anatomy of 76 species of Brachiaria, Eriochloa, Panicum sect. Fasciculata, Pseudobrachiaria, and Urochloa were examined using the techniques presented in Thompson (1988) (table 1). Both living and dried material were examined. Hebarium specimens are listed in Thompson (1988). The data from this investigation were combined with those of from Hsu (1965), Brown (1977), Shaw and Smiens (1981), Clatyon and Renvoize (1982, 1986), Zuloaga and Soderstrom (1985), Thompson and Estes (1986), Shaw and Webster (1987), Zuloaga (1987), and Thompson (1988) and a classification produced.

RESULTS AND DISCUSSION

On the basis of the information accumulated, Eriochloa, Urochloa and Brachiaria are recognized as distinct genera. Pseudobrachiaria and P. sect. Fasciculata are submerged in Brachiaria. In the following paragraphs, the bases for these decisions are presented.

Eriochloa Kunth in Humb. & Bonpl., Nov. Gen. Sp. 1:94 (1816)

Eriochloa encompasses approximately 30 species distributed in the tropical and temperate regions of the southern hemisphere and North America. The genus was originally delimited on the basis of the absence of the first glume and the presence of a cup-shaped callus (Humbolt, Bonpland, and Kunth 1815). Three species, E. biglumis Clayton, E. borumensis, and E. meyerana, differ from the others by possessing both the cup-shaped callus and a flap of tissue that has been called the first glume. Species of the genus exhibit: (1) a tight panicle; (2) an elliptical spikelet; (3) an adaxially orientated spikelet; (4) a papillose fertile floret; and (5) an awned fertile lemma (Shaw and Smiens 1980; Clayton and Renvioze 1986; Shaw and Webster 1987).

However, there are several species of Brachiaria with some combination of tight panicles, elliptical spikelets, papillose anthecia, and/or awned fertile lemmas.

Additionally, *B. brizantha*, *B. decumbens*, *B. erucaeformis*, *B. humidicola*, and *B. xantholeuca* have a bead of callus that is homologous to the cup-shaped callus of *Eriochloa* and perhaps a more primitive state of the character (Thompson 1988). The distinction between these two genera seems to be obscured further by *Brachiaria callopus*, which bears a cup-shaped callus and a first glume. Clayton (1975), however, placed *B. callopus* in *Echinochloa* because it has a smooth anthecium with a green, wrinkled apex. The species has C_4, NADP-malic acid (NADP-me) leaf anatomy and the Echinochloa anthecial pattern (Thompson 1988). All are characteristics of *Echinochloa*, whereas *Eriochloa* and *Brachiaria* have C_4, PCK anatomy, different anthecial patterns, and no foliar papillae. Shaw and Webster (1987) also supported placement of this species in *Echinochloa*. They noted the nerves of the second glume and sterile lemma are spiculate, a feature that is common in *Echinochloa* but not in *Eriochloa* or *Brachiaria*. Thus, proper placement of *B. callopus* appears to be in *Echinochloa*.

Thompson and Estes (1986) noted that bulliform fans occur over the smaller vascular bundles in *Eriochloa*, but in Brachiaria, they generally occur between the bundles. As a result, the distinction between *Eriochloa* and *Brachiaria* can be clarified. *Eriochloa* is a taxon with: (1) bulliform fans over the vascular bundles; (2) a tight panicle inflorescence; (3) a cup-shaped callus; (4) an adaxially oriented spikelet; (5) an elliptical spikelet; (6) a papillose anthecium; and (7) an awned fertile lemma.

Panicum sect. Fasciculata Hitchcock & Chase, 1910: 35

Panicum sect. Fasciculata is a small taxon of four, annuals, P. adspersum, P. arizonicum, P. fasciculatum, and P. texanum. Characteristic of this taxon are: (1) a tight, one-sided panicle; (2) an abaxially or/and adaxially oriented spikelet; (3) an elliptical spikelet; (4) a rugose anthecium; and (5) a beaked to unawned fertile lemma. These species are circumtropical, but occur primarily in temperate and tropical regions of the Americas.

The section has the C_4, PCK photosynthetic pathway and its foliar anatomy is similar to that of B. erucaeformis, B. deflexa, B. lata, B. nigropedata, B. ramosa, and B. rugulosa. All exhibit ribbed to slightly ribbed laminae containing radiate parenchyma. In addition, B. deflexa and the members of this section both have in common columns of parenchyma connecting the bulliform fans and the abaxial epidermis. The only features that separate it from Brachiaria are the type of inflorescence and the orientation of the spikelet. However, some species of Brachiaria have tight, one-sided panicles which do not always have adaxially oriented spikelets. The gross morphology of the species of section Fasciculata is so similar to that of B. ramosa that Hitchcock (1935), at one time, placed B. ramosa in the section. Clayton and Renvoize (1982, 1986) noted that B. ramosa intergrades with B. deflexa, which then intergrades with B. xantholeuca.

The Ciliatissima pattern of anthecial micromorphology is displayed in P. sect. Fasciculata, B. deflexa and B. xantholeuca (Thompson and Estes 1986; Thompson 1988). This pattern is also displayed by other species of Brachiaria including: B. advena, B. arrecta, B. cilitissima, B. mutica, and B. plantaginea (Thompson and Estes 1986). These similarities in laminar anatomy, anthecial micromorphology, and gross morphology suggest that the four species of the section belong in Brachiaria. This is in agreement with Parodi's (1969) and Blake's (1969, 1973) treatments.

Urochloa P. Beauv, Ess. Agrost: 52 (1812)

With approximately 12 to 15 species, Urochloa is common in temperate and tropical Africa and Australia, however, some species have a world-wide distribution. The genus traditionally has been described as having: (1) a racemose inflorescence; (2) an ovate spikelet with a cuspidate apex; (3) adaxial spikelet orientation; (4) a rugose anthecium; and (5) a mucronate to awned fertile lemma (Stapf 1934b; Clayton and Revoize 1982, 1986). Problems of classification do exist. For example, U. reptans has a tight paniculate inflorescence, elliptical spikelet, mucronate to beaked fertile lemma, and intergrades morphologically with P. sect.

Fasciculata, B. deflexa, and B. ramosa. Urochloa gilesii exhibits the adaxially oriented, ovate spikelet with a cuspidate apex, racemose inflorescence, and short, tufted growth form of B. cilitissima. Brachiaria platyrhachis, on the otherhand, has the traditional Urochloa gross morphology except that it has an oblong spikelet and a beaked fertile lemma.

Examination of foliar anatomy revealed that species of Urochloa possess all or part of a suite of laminar characters including: (1) a reduced amount of mesophyll; (2) a 7 to 1 ratio of secondary to primary vascular bundles; (3) bulliform fans that penetrate deeply into the mesophyll; (4) an intercostal width of 5 or 6 cells; and (5) single costal rows of dumbbell-shaped silica cells (Thompson 1988). Additionally, all species bear anthecia with either the Brachylopha or Urochloa pattern of micromorphology. Urochloa reptans and U. gilesii display the Brachylopha pattern and B. platyrhachis the Urochloa pattern (Thompson and Estes 1986; Thompson 1988). These three species also possess combinations of the foliar characters listed above and therefore in Urochloa.

Urochloa can be circumscribed by the presence of (1) a racemose to occassionally a paniculate inflorescence; (2) the suite of laminar characters listed above; (3) an ovate spikelet with a cuspidate apex to elliptical spikelet; (4) typically adaxial spikelet orientation; (5) a rugose anthecium; and (6) an unawned to awned fertile lemma.

Pseudobrachiaria Launert in Mitt. Bot. Staats. Munch. 8: 158(1970)

Launert (1970) segregated Brachiaria deflexa (Schumach.) C.E. Hubbard as the monotypic Pseudobrachiaria because of the separation of the two florets by a distinct internode. Other features exhibited by P. deflexa are: (1) a panicle with spikelet arising from one side of the rachis; (2) a generally adaxially orientated spikelet; (3) an elliptical spikelet; (4) a rugose anthecium; and (5) an awnless fertile lemma. Clayton and Renvoize (1982, 1986) treated the species as a member of Brachiaria noting that it intergrades into B. ramosa. Webster (1987) placed Pseudobrachiaria in Urochloa when he transferred all but one of the Australian species of Brachiaria to Urochloa. In his generic description of Urochloa, he stated that the rachilla is not well developed between the lower and upper florets.

Clayton and Renvoize's placement of P. deflexa in Brachiaria is supported by its possession of the Ciliatissima antheical pattern, which is common in Brachiaria. Additionally, the foliar anatomy of P. deflexa is similar to that found in B. ramosa--ribbed to slightly ribbed laminae containing radiate parenchyma (Thompson and Estes 1986; Thompson 1988). Pseudobrachiaria deflexa is also unlike species of Urochloa which possess anthecia with either the Brachylopha or Urochloa pattern of micromorphology and all or part of a complex of laminar characters including: (1) a reduced amount of mesophyll; (2) a 7 to 1 ratio of secondary to primary vascular bundles; (3) bulliform fans that penetrate deeply into the mesophyll; (4) an intercostal width of 5 or 6 cells; and (5) single costal rows of dumbbell-shaped silica cells (Thompson 1988). Therefore, *Pseudobrachiaria* is relegated to synonymy with *Brachiaria*.

Brachiaria (Trin.) Griseb. in Ledeb., Fl. Ross. 4: 496 (1853)

As noted above, *Brachiaria* was originally recognized by Trinius (1826) as a section of *Panicum* displaying an inflorescence of racemes. Grisebach (1853) elevated the taxon to generic rank and Chase (1920) and Stapf (1934a) subsequently expanded its circumscription. *Brachiaria* (*sensu lato*) is a variable taxon, more variable than most generic descriptions indicate. Species range in habit from small annuals (e.g. *B. erucaerformis*) to robust perennials (*B. brizantha*); in inflorescence type from those with racemes that are winged (*B. jubata*) or triquetrous (*B. bovonei*) to those with one-sided panicles that are open (*B. poaeoides*) or tight (*B. adspersa*). Spikelet orientation varies from solely adaxial (*B. nigropedata*) to adaxial and abaxial (*B. adspersa*) with spikelets borne solitary (*B.

arrecta), in pairs (B. occidentalis), or solitary and paired on the same inflorescence (B. mutica). Solitary spikelets are generally sessile to subsessile; but may have long pedicels as in B. longiflora. When the spikelets are paired there is always an upper and lower spikelet. The length of the pedicels varies from species to species and even within an inflorescence.

Based solely on gross morphology, Brachiaria intergrades with Urochloa. Indeed, Webster (1987) placed all of the Australian species of Brachiaria into Urochloa except B. erucaeformis which he maintained in a monotypic Brachiaria. The characters he uses to delimit Brachiaria (sensu stricto) were: (1) that the upper floret is the primary point of disarticulation; (2) that the anthecium is smooth with a broadly rounded apex that is not awned or mucronate; (3) that the base of the upper floret is not constricted; and (4) that the apex of the upper palea is not clasped by the fertile lemma. These characters, however, are not unique to B. erucaeformis. For example, B. longiflora also has a disarticulating anthecium and B. poaeoides has a smooth anthecium with a broadly rounded apex (Thompson and Estes 1986). The degree of constriction at the base of the anthecium is also variable in the genus (sensu lato),and is a function of the type of anthecial patterning present and the degree of definition of the germination lid. Finally, the degree of clasping of the fertile palea by the fertile lemma changes. During the maturation of the caryopsis, the entire palea is clasped by the lemma, however during anthesis the gap between the lemma and palea is more pronounced because the anthecium is softer, i.e. unadorned with cuticular features such as papillae or ridges and/or the lemma has no modifications such as a beak, fold of tissue, or bladders to facilitate clasping the palea (Thompson unpublished).

As noted above, Urochloa displays a distinctive suite of foliar characters. With respect to its foliar anatomy, Brachiaria (sensu lato) is considerabley variable. Laminae are ribbed or unribbed; keeled or unkeeled; have reduced or extensive mesophyll; have deeply penetrating or superfical bulliform fans; have radiate, irradiate or subradiate mesophyll; and have consistant or variable vascular bundle ratio. Suites of foliar characters do not occur as they do in Urochloa.

Brachiaria (sensu lato), therefore appears to be a highly variable genus with: (1) a racemose to one-sided, paniculate inflorescence; (2) variable, C_4, PCK leaf anatomy; (3) variable spikelet shape; (4) a primarily adaxially orientated spikelet; (5) a papillose to rugose anthecium; and (6) an unawned to awned fertile lemma.

Thus, the Brachiaria complex comprises three taxa, Brachiaria, Eriochloa, and Urochloa. Panicum sect. Fasciculata and Pseudobrachiaria are submerged in Brachiaria.

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TABLE 1. Species and nomenclature used in this study.

Brachiaria (Trin.) Griesb.

B. adspersa (Trin.) Parodi

[*Panicum adspersum* Trin.]

B. advena Vick.

[*Urochloa advena* (Vick.) R. Webster]

B. arizonica (Scribn. & Merr.) S.T. Blake

[*Panicum arizonicum* Scribn. & Merr.]

B. arrecta (Th. Dur. & Schinz) Stent

[*B. latifolia* Stapf]

[*B. radicans* Napper]

B. bovonei (Chiov.) Robyns

[*B. hians* Stapf]

[*B. virdula* Stapf]

B. brachylopha Stapf

B. breviglumis Clayton

B. brizantha (A. Rich.) Stapf

[*Urochloa brizantha* (A. Rich.) R. Webster]

B. chusqueoides (Hack.) Clayton

B. ciliatissima (Buckl.) Chase

B. comata (A. Rich) Stapf

[*B. kotschyana* (Steud.) Stapf]

[*B. epaleata* Stapf]

[*B. secernenda* Henr.]

B. decumbens Stapf

[*Urochloa decumbens* (Stapf) R. Webster]

B. deflexa (Schumach.) Hubbard

[*Pseudobrachiaria deflexa* (Schumach.) Launert]

B. dictoyneura (Fig. & DeNot.) Stapf

[*B. ovoluta* Stapf]

[*B. keniensis* Henr.]

B. distachyoides Stapf

B. distichophylla (Trin.) Stapf

B. dura Stapf

B. erucaeformis (Smith) Griseb.

[*B. isachne* Stapf]

B. fasciculata (Swartz) Parodi

[*Panicum fasciculatum* Swartz]

[*Urochloa fasciculata* (Swartz) R. Webster]

B. foliosa (R. Br.) Hughes

[*Urochloa foliosa* (R. Br.) R. Webster]

TABLE 1 Continued. Species and nomenclature used in this study.

Brachiaria (Trin.) Griseb.

B. glomerata (Hack.) A. Camus

B. grossa Stapf

B. hangerupii Hitchc.

B. heterocraspeda (Peter) Pilger

B. holosericea (R. Br.) Hughes

[Urochloa holosericea (R. Br.) R. Webster]

B. humbertiana A. Camus

B. humidicola (Rendle) Schweick

B. jubata (Fig. & DeNot.) Stapf

[B. fulva Stapf]

[B. brevis Stapf]

[B. soluta Stapf]

[B. bomaensis Vanderyst]

B. lachnantha (Hochst.) Stapf

B. leersiodies (Hochst.) Stapf

B. leucacrantha (Schumach.) Stapf

B. longiflora Clayton

B. mutica (Forssk.) Stapf

[B. purpurascens (Radd.) Henr.]

[B. nunidianum (Lam.) Henr.]

[Urochloa mutica (Forssk.) Nguyen]

B. nigropedata (Munro) Stapf

B. occidentalis Gardn. & Hubbard

B. pilgera (F. Muell. ex Benth.) Hughes

[Urochloa pilgera (F. Muell. ex Benth) R. Webster]

B. plantaginea (Link) Hitchc.

B. platynota (Schumach.) Robyns.

[Urochloa bifalcigera (Stapf) Stapf]

[Urochloa platynota (Schumach.) Pilger]

B. platyphylla (Griseb.) Nash

B. platyaenia Stapf

B. poaeoides Stapf

B. pubifolia (Mez) Stapf

B. pungipes Clayton

B. ramosa (L.) Stapf

[Panicum ramosa L.]

[Urochloa ramosa (L.) R. Webster]

B. rugulosa Stapf

B. ruziziensis Germain & Evrard

TABLE 1 Continued. Species and nomenclature used in this study.

Brachiaria (Trin.) Griseb.

- B. scalaris (Mez) Pilger
- B. semiundulata (A. Rich.) Stapf
- B. serrata (Thunb.) Stapf
- B. serrifolia (Hochst.) Stapf
- B. subulifolia (Mez) Clayton
  - [B. filifolia Stapf]
- B. subquadripara (Trin.) Hitchc.
  - [B. miliiformis (J. & C. Presl) Chase]
  - [Urochloa subquadripara (J. & C. Presl) R. Webster]
- B. texana (Buckl.) S.T. Blake
  - [Panicum texanum Buckl.]
  - [Urochloa texana (Buckl.) R. Webster]
- B. umbellata (Trin.) Clayton
- B. whiteana (Domin) Hubbard
  - [Urochloa whiteana (Domin) R. Webster]
- B. xantholeuca (Schinz) Stapf

Echinochloa Beauv.

- E. callopus (Pilger) Clayton
  - [Brachiaria callopus (Pilger) Stapf]
  - [Brachiaria stipitata Hubbard]
- E. obtusiflora Stapf
- E. rotundiflora Clayton
  - [Brachiaria obtusiflora (Hochst. ex A. Rich) Stapf]

Eriochloa H.B.K.

- E. australiensis Stapf ex Thellung
- E. borumensis Hack.
  - [E. meyerana (Nees) Pilg.
- E. crebra S.T. Blake
- E. grandiflora (Trin.) Benth.
- E. nubica (Steud.) Stapf
- E. polystachya H.B.K.

Urochloa Beauv.

- U. brachyura (Hack.) Stapf
  - [U. geniculata Hubbard]
  - [U. novemneriva Hubbard]

TABLE 1 Continued. Species and nomenclature used in this study.

<u>Urochloa</u> Beauv.	<u>U</u>. <u>reptans</u> (L.) Stapf
<u>U</u>. <u>echinolaenoides</u> Stapf.	[<u>Panicum</u> <u>reptans</u> L.]
<u>U</u>. <u>gilesii</u> (Benth.) Hughes	[<u>Brachiaria</u> <u>reptans</u> (L.) Gardn. & Hubbard]
[<u>Brachiaria</u> <u>gilesii</u> (Benth.) Chase]	<u>U</u>. <u>rudis</u> Stapf
<u>U</u>. <u>mosambicensis</u> (Hack.) Dandy	[<u>U</u>. <u>gorinii</u> Chiov.]
[<u>U</u>. <u>pullulans</u> Stapf]	<u>U</u>. <u>sclerochlaena</u> Chiov.
[<u>U</u>. <u>rhodesiensis</u> Stent.]	<u>U</u>. <u>setigera</u> (Retz.) Stapf
[<u>U</u>. <u>stolonifera</u> (Goossen) Chippind.]	[<u>Brachiaria</u> <u>setigera</u> (Retz.) Hubbard]
<u>U</u>. <u>oligotricha</u> (Fig. & DeNot.) Henr.	<u>U</u>. <u>trichopus</u> (Hochst.) Stapf
[<u>U</u>. <u>bolbodes</u> (Steud.) Stapf]	[<u>U</u>. <u>engerleri</u> Pilger]
<u>U</u>. <u>panicoides</u> Beauv.	[<u>U</u>. <u>brachyphylla</u> Gilli]
<u>U</u>. <u>platyrhachis</u> Hubbard	
[<u>B</u>. <u>platyrhachis</u> (Hubbard) Chiov.]	

APPENDIX A

SPECIMENS EXAMINED FOR CHAPTERS III AND IV

Brachiaria adspersa (Trin.) Parodi

Examined anthecia, leaf anatomy,and leaf epidermis

Mrs. Rev. J. J. Ricksecker	384	5-24-1897
St. Croix, Danish West Indies		MO
Hervey Roberts	MB19	6-1-1966
Captiva, Florida		MO

Brachiaria arizonica (Scribn. & Merr.) S.T. Blake

Examined anthecia, leaf anatomy, and leaf epidermis

O. B. Metcalfe	1294	9-6-1904
Hillsboro, New Mexico		MO
O. B. Metcalfe	768	9-22-1903
Socorro Co., New Mexico		MO

Brachiaria breviglumis Clayton

Examined anthecia, leaf anatomy, and leaf epidermis

Bovdet	38073	11-30-1972
Dahar, Ethiopia		K

Brachiaria deflexa (Schumach.) Hubbard

Examined anthecia, leaf anatomy, and leaf epidermis

Thomas B. Croat	31179	----
----		MO

Jacques-Georges Adam	1498	6-27-1948
Hann, Senegal		MO

Examined anthecia

M. Reekmans	4023	6-12-1974
Gitaza, Brundi		MO
A. Gholson	s.n.	----
Florida		NCU

Examined leaf anatomy and leaf epidermis

Grown from seeds provided by the U.S.D.A. PI 364406

Brachiaria fasiculata (Swartz.) Parodi

Examined anthecia, leaf anatomy, and leaf epidermis

Edwin Anderson	1305	9-25-1950
Port-au-Prince, Hati		MO
Stephan L. Hatch	1092	8-11-1972
Burleson Co., Texas		MO
R. Romero-Castaneda	6383	7-15-1957
Riosucio, Colombia		MO

Examined anthecia

H. Leon	229	4-7-1976
Riosucio, Columbia		MO

Brachiaria longiflora Clayton

Examined anthecia, leaf anatomy, and leaf epidermis

J. B. Gillespie	s.n.	1961
Kiunga, Lamu, Kenya		K

Brachiaria pungipes Clayton

Examined anthecia, leaf anatomy, and leaf epidermis

Arne Strid	2603	11-22-1972
Mwinilunga, Zambia		K

Brachiaria subulifolia (Mez) Clayton

Examined anthecia, leaf anatomy, and leaf epidermis

Jean Pawek	10332	10-26-75
Vipya Plateau, Malawi		K
Jean Pawek	10332	10-26-75
Vipya Plateau, Malawi		MO

Brachiaria texana (Buckl.) S.T. Blake

Examined anthecia, leaf anatomy, and leaf epidermis

R. K. Godfrey	67536	11-3-1965
Quincy, Florida		MO
F. S. Earle & C. F. Baker	s.n.	10-12-1897
Auburn, Alabama		MO

Brachiaria umbellata (Trin.) Clayton

Examined anthecia, leaf anatomy, and leaf epidermis

P. O. Wiehe	s.n.	8-21-50
Nyassland, Zambia		K

Echinochloa callopus (Pilger) Clayton

Examined anthecia, leaf anatomy, and leaf epidermis

Jacques-Georges Adam	18136	12-30-61
Mali		K
Jacques-Georges Adam	15494	-----
Senegal		MO

Jacques-Georges Adam	28203	9-25-1963
Lyndiane, Senegal		MO

<u>Echinochloa</u> <u>rotundiflora</u> Clayton

Examined anthecia, leaf anatomy, and leaf epidermis

L. P. White	23	11-1968
Gaya, Niger		K
A. Pappi	s.n.	----
-----		MO

<u>Urochloa</u> <u>brachyura</u> (Hack.) Stapf

Examined anthecia, leaf anatomy, and leaf epidermis

W. Giess	10357	4-20-1968
Karibib, South Africa		MO

Examined anthecia

J. B. Phipps	2541	----
-----		MO

Examined leaf anatomy and leaf epidermis

B. deWinter & W. Giess	6815	2-4-1959
Ovamboland Native Reserve, South Africa		MO

<u>Urochloa</u> <u>echinolaenoides</u> Stapf

Examined anthecia, leaf anatomy, and leaf epidermis

M. McCallum Webster	T9	3-10-1959
Ufipa District, Tanganyika		MO
R. Wingfield	580	3-22-1970
Igurusi, Tanzania		MO

<u>Urochloa</u> <u>gilesii</u> (Benth.) Hughes

Examined anthecia, leaf anatomy, and leaf epidermis

C. E. Hubbard & C. W. Winders	7051	2-1-1931
Mitchell District, Queensland, Australia		MO

<u>Urochloa</u> <u>mosambicensis</u> (Hack.) Dandy

Examined anthecia, leaf anatomy, and leaf epidermis

Adele Lewis Grant	s.n.	3-1930
Lourenco Marques, Portuguese East Africa		MO

<u>Urochloa</u> <u>panicoides</u> Beauv.

Examined anthecia, leaf anatomy, and leaf epidermis

J. C. Scheepers	520	6-12-58
Letaba, Transvaal, South Africa		MO
J. J. F. E. de Wilde	5911	11-28-1969
Ogaden, Ethiopia		MO

<u>Urochloa</u> <u>pullulans</u> Stapf

Examined anthecia, leaf anatomy, and leaf epidermis

A. O. Crook	2074	3-3-75
Fairbridge Park, Rhodesia		MO
P. J. Greenway & Kanuri	15,413	10-7-1973
Mikumi, Tanganyika		MO

Examined leaf anatomy and leaf epidermis

P. Taylor	210	12-30-1971
Hippo Valley Estates, Chiredzi, Rhodesia		MO

Urochloa reptans (L.) Stapf

Examined anthecia

J. Reverchon	4170	9-20-1903
Sheldon, Texas, U.S.A.		MO
E. J. Palmer	6606	9-21-1914
Wharton, Texas, U.S.A.		MO

Examined leaf anatomy and leaf epidermis

Alfred E. Ricksecker	77	11-15-1895
St. Croix, Danish West Indies		MO
J. W. Ash	2589	9-8-1974
Arussi, Shoa, Ethiopia		MO

Urochloa rhodesiensis Stent.

Examined anthecia, leaf anatomy, and leaf epidermis

P. Taylor	227	11-15-1977
Hippo Valley Estates, Chiredzi, Rhodesia		MO

Urochloa setigera (Retz.) Stapf

Examined leaf anatomy and leaf epidermis

M. Gilbert, M. Thulin, & G. Aweke	270	8-30-1975
Arba Minch, Gamu-Gofa, Ethiopia		MO

Urochloa stolonifera (Goossen) Chippind.

Examined anthecia, leaf anatomy, and leaf epidermis

E. Buitendag	1053	5-16-74
Lydenburg, Transvaal, South Africa		MO
J. N. Pienaar	259	1-8-74
Waterpcort, Transvaal, South Africa		MO

Urochloa trichopus (Hochst.) Stapf

Examined anthecia

J. J. F. E. de Wilde	6918	9-1-1970	
Kembolocha, Wollo, Ethiopia			MO
Smith	3145	3-13-1980	
Kuke, Botswana			MO

Examined leaf anatomy and leaf epidermis

W. Giess	7785	3-3-1964	
Tsumeb, South West Africa, South Africa			MO
Jean Pawek	11019	4-14-76	
Karonga, Malawi			MO

APPENDIX B

SPECIMENS EXAMINED FOR CHAPTER V

<u>Brachiaria</u> <u>adspersa</u> (Trin.) Parodi			
Mrs. Rev. J.J. Ricksecker	384	5-24-1897	
St. Croix, Danish West Indies			MO
[illegible] Roberts	MB19	6-1-1966	
Captiva, Florida			MO
<u>Brachiaria</u> <u>advena</u> J. Vickery			
*A. Noble	8475	2-13-1948	
Glen Innes, New South Wales			K
<u>Brachiaria</u> <u>arizonica</u> (Scribn. & Merr.) S. T. Blake			
O.B. Metcalfe	1294	9-6-1904	
Hillsboro, New Mexico			MO
O.B. Metcalfe	768	9-22-1903	
Socorro Co., New Mexico			MO
<u>Brachiaria</u> <u>arrecta</u> (Th. Dur. & Schinz) Stent			
Ecklon & Zeyhes	13	2-2-80	
South Africa		2100965	MO
P.A. Smith	1391	5-17-1975	
Xakue, Botswana		2624926	MO
Ecklon & Zeyhes	s.n.	2-2-80	
South Africa		2100966	MO

P.A. Smith	1989	4-20-1977	
Brigg's Camp, Botswana		2648859	MO
P.A. Smith	1979	4-16-1977	
Boro River, Botswana		2202569	MO
B.K. Simon	2311	1-16-1973	
Mbheleli Dam		2202569	MO
Brachiaria bovonei (Chiov.) Robyns			
Jean Pawek	8948	1-11-75	
Vipya Link Road, Malawi		2440783	MO
W.B. Cleghoan	1170	11-25-1965	
Sinoia		1903595	MO
P.C.V. du Toit	1011	12-13-15	
Sabie		2414738	MO
D.L. Barnes	41933	11-22-52	
Gwebi District, Southern Rhodesia		-------	MO
P.J. Greenway & Kanuri	13,412	4-4-1968	
Arusha National Park		1995817	MO
G. Quarre	3215	6-1933	
Dembo de Katubo, Belgian Congo		1603396	MO
Brachiaria breviglumis Clayton			
Bovdet	38073	11-30-1972	
Dahar, Ethiopia			K
Brahciaria chusqueoides (Hack.) Clayton			
*Rehman	8648	12-1875	
Africae Australis			K

C.J. Ward	5292	2-3-66	
Isipingo North, Natal			K
Col. A. Balsinhas	260	11-14-1960	
Lowenco Marques, Mosambique			K
E.J. Moll	4806	1-29-69	
Natal			K
A.O.D. Mogg	27263	7-17-1957	
Inhaca Island			K
A.O.D. Moog	28493	10/20-11/7-58	
[illegible]and, Mozambique		-----	
P.C.V. du Toit	1314	8-22-76	
Natal		2770593	MO
P.H. & T.E. Raven	26118	7-11-1973	
Natal		2473667	MO

<u>Brachiaria</u> <u>ciliatissima</u> (Buckl.) Chase

Dr. W.L. Tolstead	7529	6-26-1943	
Abilene, Texas		1270834	MO
S.M. Tracy	8294	5-14-1902	
Big Springs, Texas		2876656	MO
Gustav Jermy	53	1800's	
Sandy Creek, Texas		2876658	MO
S.M. Tracy	7955	5-20-1902	
Abilene, Texas		2876660	MO
A.S. Hitchcock	200	6-24-1910	
San Antonio, Texas		742624	MO

B.C. Tharp & Ecology Class	s.n.	11-1930	
Austin, Texas		1274653	MO
B.C. Tharp	s.n.	6-15-28	
Hebbronville, Texas		1271973	MO
B.C. Tharp	s.n.	4-21-38	
Austin, Texas		1272020	MO
J. Reverchon	4150	3-25-1903	
Laredo, Texas		2876667	MO
E.J. Palmer	9750	5-16-1916	
as		814222	MO

Brachiaria deflexa (Schumach.) C. E. Hubb.

Thomas B. Croat	31179	----	
----			MO
Jacques-Georges Adam	1498	6-27-1948	
Hann, Senegal			MO
M. Reekmans	4023	6-12-1974	
Gitaza, Brundi			MO
A. Gholson	s.n.	----	
Florida			NCU

Brachiaria dictyoneura (Fig. & DeNot.) Stapf

M. Reekmans	7740	4-4-1979	
Cibitoke, Burundi		2655934	MO
G. Bouxin & M. Radoux	1644	3-27-1970	
Bugesera, Rwanda		2671003	MO
G. Bouxin & M. Radoux	2035	5-12-1970	
Bugesera, Rwanda		2671005	MO

M. Reekmans	3224	3-3-1974
Bujumbura, Burundi		2193899 MO
R.P. Ellis	2763	3-23-1976
Nata, Botswana		2392109 MO
P. Auquier	2844	3-12-1972
Bugesera, Rwanda		2677516 MO
[illegible] lan	505	11-16-1948
Kwale-Tiwi Road, Kenya		1777652 MO
H.V. Lely	405	7-1930
Bauchi Plateau, Nigeria		1755766 MO
S.A. Robertson	2030	3-9-1974
Tebere Cotton Research Stn.		2269733 MO
B. deWinter & W. Giess	7002	2-15-59
Etomba, South Africa		1827683 MO

<u>Brachiaria</u> <u>erucaeformis</u> Griseb.

L. Smook	5155	3-20-1984
Namutoni, South West Africa		343992 RSA
L. Smook	2143AC	3-17-1980
Thaba Phatshwa Mt., Orange Free State		2895251 MO
L. Smook	2730AC	1-7-1980
Wakkerstroom, Natal		2895197 MO
A. Pappi	1255	9-15-1902
West Africa		1605282 MO
O. West	2668	2-3-1978
Matsbo District, South Rhodesia		1662294 MO

Schimperi	1868	1-1844	
Abyssinia		2100961	MO
C. Sandwith	24	9-1929	
Quien Lake, North Rhodesia		1712175	MO
J.J.F.E. de Wilde	6010	12-13-1969	
Neghelli, Ethiopia		2700775	MO
P.A. Smith	3072	2-17-1980	
Toromoja-Mopipi, Botswana		2832870	MO
<u>Brachiaria</u> <u>fasiculata</u> (Swartz.) Parodi			
Edwin Anderson	1305	9-25-1950	
Port-au-Prince, Hati			MO
Stephan L. Hatch	1092	8-11-1972	
Burleson Co., Texas			MO
R. Romero-Castaneda	6383	7-15-1957	
Riosucio, Colombia			MO
H. Leon	229	4-7-1976	
Riosucio, Columbia			MO
<u>Brachiaria</u> <u>foliosa</u> (R. Br.) Hughes			
C.T. White	71076	4-1937	
Gooviegen, Queensland			K
H. Tryson	AQ415589	4-1937	
Brisbane, Queensland			K
N.H. Speck	1900	5-20-1963	
Moura, Queensland			K
F.W. Higgins	s.n.	11-10-1933	
Derra Mundubbera, Queensland			K

C.E. Hubbard	5308	11-28-1930
Laidley, Queensland		K
R.W. Johnson	2618	4-24-1963
Brigalow Research Station		K
C.E. Collins	46642	1-20-1959
Grafton Experiment Farm, New South Wales		K
Brachiaria holosericea (R. Br.) Hughes		
*R. Brown	6094	5-1802
Australia		K
C.E. Hubbard & C.W. Winders	6945	1-28-1931
Mount St. John, Queensland		K
C.E. Hubbard	7834	2-21-1931
Jericho, Queensland		K
C.J. White	8739	3-19-1933
Torrens Creek, North Queensland		K
R.L. Specht	339	4-30-1948
Hemple Bay, Northern Australia		K
Brachiaria jubata (Fig & De Not) Stapf		
J.G. Adam	14409	6-15-1958
Niokolo-koba, Senegal		2449749 MO
M. Reekmans	9783	3-5-1981
Gihofi, Burundi		2835424 MO
P.O. Ekman	319	6-9-76
Pankshin, Nigeria		27006943 MO
E.A. Robinson	4815	12-30-61
Sumbawange, Tanganyika		1819074 MO

P.O. Wiehe	391	12-22-1949	
Tung Station, Nyasaland			MO
J.E.Au. Stephens	S.4.	----	
Soroti, Uganda		1702274	MO
A.J.M. Leeuwenberg	1959	9-11-1958	
Dabow, Ivory Coast		1791973	MO
s Geesteranus	4925	4-14-1949	
Tinderet Forest Reserve, Kenya		1716202	MO
Adjanohoun	410A	6-14-1962	
Dabon, Ivory Coast		1837983	MO
P.R. Guy	2198	1-7-1975	
Sengwa Research Station		2285377	MO
Brachiaria longiflora Clayton			
*R. Pohill and S. Paulo	674	4-28-61	
Kurawa, Kenya			K
R.B. & A.J. Faden	74/1080	7-15/16-1974	
Kitwa Pembe Hill, Kenya			K
J.B. Gillespie	s.n.	1961	
Kiunga, Lamu, Kenya			K
Brachiaria platynota (K. Schum.) Robyns.			
Portase K. Rwaburindore	Rwab.554	1-14-1971	
Rugongo, Uganda		2445026	MO
G. Bouxin & M. Radoux	1513	3-2-1970	
Kizibaziba, Rwanda		2680533	MO

lost label, but probably:

J. Lebrun	----	----	
Congo Belgica		1717668	MO
M. Reekmans	4653	12-25-1975	
INRS, Rwanda		2437790	MO
G. Bouxin & M. Radoux	1721	4-13-1970	
Nyamabuye, Rwanda		2781983	MO
G. Bouxin & M. Radoux	1780	4-17-1970	
Vallee de la Nyabrongo		2783058	MO
<u>Brachiaria poaeoides</u> Stapf			
*H.H.W. Pearson	2849	4-29-09	
S. Angola			K
H.G. Schweickerdi	2074	3-29-50	
Gootfontein, South West Africa			K
Dr. R. Seydel	3141	5-11-1962	
Fann Okingara, South West Africa			K
E.B. Schoenfelder	S.810	5-1934	
Grootfontein, South West Africa			K
<u>Brachiaria pungipes</u> Clayton			
Arne Strid	2603	11-22-1972	
Mwinilunga, Zambia			K
<u>Brachiaria mutica</u> (Forssk.) Stapf			
Gerrit Davidse & Ed Conroy	3269	11-26-1971	
Central Valley, Jamaica		2141872	MO
Otto Degener & Felix Salucop	11,501	11-4-1937	
Mokuleia, Oahu		1128698	MO

W.J.J.O. & J.J.F.E. de Wilde &		
B.E.E. de Wilde-Duyfjes	5167	1-3-1965
Fort Lamy, Chad		2252428 MO
G. Vieira	2270	1-13-1978
Aracuai, Brasil		2659699 MO
Jacques-Georges Adam	349	1-23-1948
Dakar, Senegal		2291098 MO
A.A. Heller	6293	12-15-1902
Yauco, Puerto Rico		2100984 MO
A.H. Curtiss	115	3-11-1903
Nassau, Bahamas		2100985 MO
Harold N. Moldenke	589	2-10-1930
Hollywood, Florida		1001779 MO
W.G. D'Arcy	9208	4-26-1975
Kartoum, Sudan		2281281 MO
Jacques-Georges Adam	2039	9-27-1948
Hahn, Senegal		2291097 MO
Brachiaria occidentalis Gardner & Hubbard		
*C.A. Gardner	----	8-29-1932
Wandagee Station, West Australia		K
Brachiaria subulifolia (Mez) Clayton		
Jean Pawek	10332	10-26-75
Vipya Plateau, Malawi		K
Jean Pawek	10332	10-26-75
Vipya Plateau, Malawi		2438925 MO

A. Balsinhas	2794	10-7-1975
Graskop, Transvaal		2575079 MO
L. Smook	2596	12-2-1980
Farm Groothoek, Transvaal		2895125 MO
N.C. Chase	3629	1-17-51
Inyanga Dist., Southern Rhodesia		1639554 MO
D.I. Field	3038	4-1974
Hubusanuko, Botswana		2346436 MO
E.A. Robinson	1885	11-13-1956
odesia		2154862 MO
A.O. Crook	2032	1-10-74
Salibury, Rhodesia		MO
<u>Brachiaria</u> <u>texana</u> (Buckl.) S.T. Blake		
R. K. Godfrey	67536	11-3-1965
Quincy, Florida		MO
F.S. Earle & C.F. Baker	s.n.	10-12-1897
Auburn, Alabama		MO
<u>Brachiaria</u> <u>umbellata</u> (Trin.) Clayton		
P. O. Wiehe	s.n.	8-21-50
Nyassland, Zambia		K
Mrs. S.A. Robertson	2486	11-24-77
Mahe, Seychelles		265671 MO
Thomas B. Croat	32405	2-27-1975
Tamatave, Madagascar		26110033 MO
Thomas B. Croat	32344	2-26-1975
Tanarive, Madagascar		2611002 MO

<u>Brachiaria</u> <u>whiteana</u> (Domin) Hubbard			
S.T. Blake	7799	3-2-1935	
Rockhampton, Australia			K
H.D. Stephens	s.n.	4-1968	
Gympie, Queensland			K
C.E. Hubbard	2035	4-6-1930	
Mt. Coot-tha, Queensland			K
C.E. Hubbard	2749	5-24-1930	
Mt. Gravatt, Queensland		2892761	MO
C.E. Hubbard	2749	5-24-1930	
Mt. Gravatt, Queensland		281518	RSA
<u>Echinochloa</u> <u>callopus</u> (Pilger) Clayton			
*G. Schweinfurth	2151	7-17-69	
Bongoland, Central Africa			K
*A. Chevalier	34598	9-13-1930	
Manou a Dalaba, French Guinea			K
L. Ake Assi	8295	11-2-1905	
Boundiali, Ivory Coast			K
L. Ake Assi	8284	11-1-1905	
Boundiali, Ivory Coast			K
R. Germain	4287	11-1945	
Bangendze, Belgium Congo			K
Jacques-Georges Adam	18136	12-30-61	
Mali			K
Jacques-Georges Adam	15494	----	
Senegal			MO

Jacques-Georges Adam	28203	9-25-1963	
Lyndiane, Senegal		2295210	MO
Jacques-Georges Adam	12439	----	
Lyudiane, Senegal		244566	RSA
<u>Echinochloa</u> <u>rotundiflora</u> Clayton			
*Schimper	1553	8-5-1941	
Absyssia	Herbarium Hookerianum		K
*Schimper	1553	8-5-1941	
	Herbarium Benthanianum		K
L. P. White	23	11-1968	
Gaya, Niger			K
F.W. Andrews	3284	8/9-1948	
Karadis, A.E. Sudan			K
E. Evans Pritchard	20	9-12/16-1935	
Sobat, Nile, A.E. Sudan			K
A. Pappi	s.n.	----	
----			MO
<u>Echinochloa</u> <u>obtusiflora</u> Stapf			
Comm. Dept. Agric.	1677/1946	9-3-1946	
Northern Nigeria			K
Musa Daggash	24881	10-13-49	
Filca Nigeria			K
H.B. Johnston	61	9-2-1950	
Gajibo, Northern Nigeria			K
C. Parker	2055	----	
Kaduna, Nigeria			K

<u>Urochloa</u> <u>brachyura</u> (Hack.) Stapf

Robert J. Rodin	9210	4-4-1973	
Oshikango, Ovamboland		2219815	MO
W. Giess	10357	4-20-1968	
Farm Aneib, South West Africa		2820483	MO
B. deWinter & W. Giess	6815	2-4-1959	
Ovamboland Native Reserve, South Africa			MO
	124	3-13-1980	
Barbersapn Nature Reserve, Transvaal		2343216	MO
P.A. Smith	3203	3-16-1980	
Groot Laagte Valley, Botswana		2832887	MO
G. Davidse & A. Loxton	6390	2-5-1974	
Gochas, Southwest Africa		2315001	MO
B. deWinter	7339	2-17-1960	
Muramosh, Bechuanaland Protectorate			MO

<u>Urochloa</u> <u>echinolaenoides</u> Stapf

R. Wingfield	580	3-22-1970	
Igurusi, Tanzania		2108037	MO
Brynaert	375	1-14-1955	
Simauo sur Dikuluwe, Belgin Congo		17611334	MO

<u>Urochloa</u> <u>gilesii</u> (Benth.) Hughes

*Herb. F. Mueller	1077	----	
Central Australia			K
C.E. Hubbard & C.W. Winers	6011	12-31-1930	
Mungullala, Queensland			K

S.T. Blake 10265 11-27-35

Jericho, Australia K

L.S. Smith 03494 10-24-1947

Port Curtis Dist., Queensland K

C.E. Hubbard & C.W. Winders 7051 2-1-1931

Mitchell District, Queensland 2892747 MO

Urochloa mosambicensis (Hack.) Dandy

Adele Lewis Grant s.n. 3-1930

nco Marques, Portuguese East Africa 2204045 MO

G. Davidse & R. Ellis 5892 1-24-1974

Krager National Park, South Africa MO

K. Sturgeon 45320 2-1-54

Dandy Agriculture Experiment Station,

Southern Rhodesia 1702344 MO

Simon, Pope, & Biegel 2439 4-5-1973

Belingwe Dist., Rhodesia 2202563 MO

E.T. Kelaole A165 4-17-1973

Gaberone, Botswana 2200653 MO

J. Greenway & Kanuri 15,413 7-10-1973

Mikumi, Tanganyika 2248982 MO

A.O. Crook 2074 3-3-75

Fairbridge Park, Rhodesia 2318162 MO

P. Taylor 227 11-15-1971

Hippo Valley Estate, Rhodesia 2655362 MO

P. Taylor 210 12-30-1971

Hippo Valley Estate, Rhodesia 2200523 MO

H. Biegel, G. Pope & E. Rusell	4913	1-2-1975	
Mah Square, Rhodesia		2384841	MO
<u>Urochloa</u> <u>oligotricha</u> (Fig & De Not) Henr.			
D.C.H. Plowes	1673	1-15-54	
Pasture Research Station, Southern Rhodesia			K
D. Vesey-Fitzgerald	3104	3-6-1961	
Que Que, Southern Rhodesia			K
Dr. C.K. Brain	5139	1-15-1931	
Bulawayo, Southern Rhodesia			K
G. Norrgrunn	502	2-6-74	
Waterford, Rhodesia			MO
J.N. Piennaar	392	1-8-74	
Messina, Transvaal		2348337	MO
<u>Urochloa</u> <u>panicoides</u> Beauv.			
J.C. Scheepers	520	6-12-58	
Top House, Transvaal		1778064	MO
J.J.F.E. de Wilde	5911	11-28-1969	
Ogaden, Ethiopia		2694429	MO
M. Wilman	B.H.25515	1-1952	
Kimberley, Cape Province		2315280	MO
Smook & Gibbs Russell	2354	3-28-1980	
Bethulie, Orange Free State		2895430	MO
B. Trelawny	A.B.4489	3-31-1957	
Kongolai, Kenya		1824694	MO
M. Lazardies	4201	2-27-1954	
Conjuboy Station, Queensland		2536833	MO

Mrs. S.A. Robertson	1559	7-29-71	
Tebere, Kenya		2689440	MO
B. deWinter	7326	2-17-1960	
Luthle, Bechuanaland Protectorate		1827319	MO
W.J.J.G. de Wilde & B.E.E.			
De Wilde-Duyfijes	10602	4-6-1966	
Awash-Station, Ethiopia		2256718	MO
[illegible]yrhachis Hubbard			
*H.G. Mundy	5038	6-1931	
Sakania, Belgian Congo			K
E. Detilleux	853	4-19-1957	
Elisabethville, Congo			K
S. Lisowski	639	4-25-1971	
Lugumbasi, Congo-Kinshasa			K
Urochloa reptans (L.) Stapf			
J. Reverchon	4170	9-20-1903	
Sheldon, Texas			MO
E. J. Palmer	6606	9-21-1914	
Wharton, Texas			MO
Alfred E. Ricksecker	77	11-15-1895	
St. Croix, Danish West Indies			MO
J. W. Ash	2589	9-8-1974	
Arussi, Shoa, Ethiopia			MO
Urochloa rudis Stapf			
*Dr. R.E. Drake-Brockman	954	----	
Eharbrosni nr Obbia			K

R. Roselunes & E.C. Trump	RR/998	11-28-83	
Qunyo Barow, Southern Somialia			K
Urochloa sclerochlaena Chiov.			
J. Lewbould	3520	12-20-58	
Ol Doinyo Lengio, Kenya			K
A.D. Graham	33	5-28-63	
[illegible]ra, Kenya			K
Urochloa setigera (Retz.) Stapf			
*C. Holst	2844	6-1893	
Amboni, Ostafrika			K
M. Gilbert, M. Thulin, & G. Aweke	270	8-30-1975	
Arba Minch, Gamu-Gofa, Ethiopia		2397094	MO
Sir A.G. & Lady Bourne	s.n.	9-1898	
Saidapet Farm, Madras			K
J.D. Nusker	1298	9-15-1894	
Bengal			K
U Thein Lwin	355	10-26-1974	
Toungoo, Burma			K
Urochloa stolonifera (Goossen) Chippind.			
E. Buitendag	1053	5-16-74	
Lydenburg, Transvaal, South Africa			MO
J.N. Pienaar	259	1-8-74	
Waterpcort, Transvaal, South Africa			MO
Urochloa trichopus (Hochst.) Stapf			
J.J.F.E. de Wilde	6918	9-1-1970	
Kembolocha, Ethiopia		2693793	MO

P.A. Smith	3145	3-13-1980	
Kutegate, Botswana		2832874	MO
W. Giess	7785	3-3-1964	
Tsumeb, South West Africa		2701997	MO
Robert J. Rodin	9210	4-4-1973	
Oshikango, Ovamboland		2772464	MO
[illegible] Pienaar	351	1-8-74	
[illegible]svaal		2348335	MO
J.B. Gillett	13118	5-8-1952	
Kenya--Ethiopia Boundary		2867644	MO
J.W. Ash	2564	9-2-1974	
Afden, Ethiopia		2443392	MO
P.A. Smith	875	2-25-1974	
Maun, Botswana		2649941	MO

*A type specimen

VITA

Rahmona Ann James Thompson

Candidate for the Degree of

Doctor of Philosophy

Thesis: STUDIES IN THE PANICEAE: GENERIC BOUNDARIES IN THE BRACHIARIA COMPLEX (POACEAE)

Major Field: Botany

Biographical:

Personal Data: Born in Oklahoma City, Oklahoma, June 17, 1953, the eldest daughter of Rahmon D. James, Jr. and Marilyn F. Strong James. Married to Ronald K. Thompson on August 2, 1971.

Education: Graduated from Ada High School, Ada Oklahoma, in May, 1971; attended East Central State College from August, 1971, to May, 1972; dropped out of college; recieved Bachelor of Science Degree in Botany from The University of Oklahoma in May, 1978; received Master of Science in Botany from The University of Oklahoma in December, 1981; completed requirements for the Doctor of Philosophy degree in Botany at Oklahoma State University in July, 1988.

Professional Experience: Teaching Assistant, Department of Botany and Microbiology, The University of Oklahoma from August, 1979, to May, 1981; Research Assistant, Oklahoma Biological Survey, The University of Oklahoma for summers 1980, 1981; Teaching Assistant, Department of Botany and Microbiology, Oklahoma State Univeristy from August, 1981 to May, 1985; Herbarium Assistant, Robert Bebb Herbarium, The University of Oklahoma for summer 1984; Research Specialist, Department of Botany and Microbiology, The University of Oklahoma from May, 1985 to December, 1987; Postdoctoral Research Associate, Department of Botany and Microbiology, The University of Oklahoma from January, 1988, to present.

Grants, Awards and Fellowships: Scholarship from The University of Oklahoma Biological Station in 1977; Research Grant from the Graduate College, The University of Oklahoma in 1981; Regents Fee Waiver Scholarships from Oklahoma State University from August, 1981 to May, 1985; Fellowship from the McAlester Scottish Rite Foundation for 1985.

Professional Memberships and Societies: American Association for the Advancement of Science; American Society of Plant Taxonomists; Association of Women in Science; Botanical Society of America; Phi Sigma; Oklahoma Academy of Sciences; Oklahoma Society of Electron Microscopy; Sigma Xi.