

A REVISION OF *PANICUM*
SUBGENUS *PHANOPYRUM*
SECTION *LAXA* (POACEAE:
PANICOIDEAE: PANICEAE)¹

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ABSTRACT

Panicum subg. *Phanopyrum* sect. *Laxa* is revised. Twelve American and one Asian species are treated in this work, in which exomorphological and anatomical characters are considered. Section *Laxa* is defined mainly as perennial plants of humid places, with membranous ligules, spikelets unilaterally disposed on the inflorescences, upper antheria membranous to indurate, with silica bodies and simple papillae, a basic chromosome number of $x = 10$, and conspicuous fusoid cells in the leaves. Possible relationships of *Laxa* to other sections of subgenus *Phanopyrum* and subgenus *Steinchisma*, as well as with other genera of the Paniceae such as *Homolepis* and *Hymenachne*, are discussed. A key to the species as well as an anatomical description of the section and photomicrographs of six species, morphological descriptions of the species, and distribution maps are presented. The taxonomic position of *Panicum scabridum* and *Panicum grande* are also discussed.

The group *Laxa* was informally established within *Panicum* by Hitchcock & Chase (1910); these authors initially included seven species in the group: *Panicum polygonatum* Schrader, *P. longum* A. Hitchc. & Chase, *P. pilosum* Sw., *P. laxum* Sw., *P. cupreum* A. Hitchc. & Chase, *P. hians* Elliott, and *P. exiguiiflorum* Griseb. In 1915, Hitchcock & Chase validly published the group, adding to *Laxa* *P. stevensianum* A. Hitchc. & Chase and *P. milleflorum* A. Hitchc. & Chase, defining the group mainly by the inflorescence type, with spikelets unilaterally disposed on short pedicels. Hitchcock & Chase (1915) also described *P. stagnatile* and *P. grande*, not grouping these species within *Panicum*.

Pilger (1931) raised the *Laxa* group to sectional level and in 1940 characterized the section by the inflorescence type, considering approximately 20 species as belonging to the section. Examples are *P. grumosum* Nees, *P. pernambucense* (Sprengel) Mez ex Pilger, and *P. gynerioides* (Griseb.) Pilger (= *P. prionitis* Nees).

Hsu (1965) differentiated *Laxa* as having 3-nerved lodicules, membranous ligules, papillose upper antherium, and a basic chromosome number of $x = 10$. Hsu noted relationships between *Laxa* and sections *Tenera* and *Verrucosa* and stated that *Laxa* should be excluded from subgenus *Panicum*

and included in subgenus *Megathyrsus*, because of the ornamentation of the upper antherium.

The classification of *Panicum* has undergone many changes in recent years, due mainly to the study of the Kranz syndrome (Brown, 1977). These new anatomical and physiological characters showed that section *Laxa* sensu lato included species differing markedly in exomorphological and photosynthetic characteristics. Brown & Brown (1975) cited *P. milioides* Nees ex Trin. (= *P. hians*) as a species with physiological characters intermediate between Kranz and non-Kranz species, as is the case in other species such as *P. spathellosum* Doell and *P. decipiens* Nees ex Trin. (Ku et al., 1976; Ku & Edwards, 1978; Morgan & Brown, 1979; Morgan et al., 1980). Brown (1977) placed these three species in a separate genus *Steinchisma* Raf., with intermediate C_3/C_4 photosynthesis, spikelets not unilaterally disposed on the inflorescences, upper antherium entirely papillose, and lower palea expanded at spikelet maturity. Brown (1977) included eight species of the *Laxa* group within subgenus *Sarmentosum*, whereas he placed others in the *Grandia* group. The *Grandia* group in the sense of Brown is a complex of Kranz species, i.e., *P. petersonii* A. Hitchc. & E. Ekman and *P. prionitis*, and non-Kranz species, such as *P. grumosum*, *P. pernambucense*, and *P. stagnatile*.

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Zuloaga (1987) defined section *Laxa* by the inflorescence type, nervation of the spikelet, and upper antheria ornamentation. He included approximately 15 species in the section, which he placed in the non-Kranz subgenus *Phanopyrum* of *Panicum*. *Panicum prionitis* and *P. petersonii* were excluded and placed in section *Prionitia* of subgenus *Agrostoides*, and *P. grande* was ungrouped within subgenus *Phanopyrum*. *Steinchisma* was considered as a separate subgenus of *Panicum*.

In the present treatment, section *Laxa* is defined and diagnosed by its exomorphological and anatomical characters. In addition, the systematic position of *P. scabridum* Doell, *P. condensatum* Bertol., *P. auritum* J. S. Presl ex Nees, and *P. grande* is discussed in relation to this definition of section *Laxa*.

MATERIALS AND METHODS

Procedures of classical taxonomy were used in this study. Specimens were examined from the following herbaria: B, BAA, BAF, BLA, CEN, CEP, COL, F, G, GH, HB, IAN, IBGE, K, LE, LIL, M, MO, MY, NY, P, PORT, R, RB, SI, SP, UB, US, VEN, W. Field methods included collection and drying of specimens for herbaria, preserving leaves, spikelets, and other structures in FAA (formalin-ethanol-acetic acid) and transferring them to 70% ethanol in the laboratory.

Laboratory studies were made using a Wild M5 dissecting microscope. For the scanning electron microscope (SEM), antheria were removed from herbarium specimens, secured on stubs, carbon coated in a vacuum evaporator, and coated with a gold-palladium alloy. These specimens were then viewed in a Cambridge S4-10 or Cambridge Stereoscan 259 Mk2 scanning electron microscope operating at 10–20 kV.

Transverse sections of leaf blade material, 10 μm thick, were sectioned after desilicification in 30% hydrofluoric acid, dehydration in a methyl cellosolve series and infiltration and embedding in Tissue Prep (Fisher Scientific). The sections were stained in safranin and fast green. For abaxial epidermis scrapes, the mesophyll and vascular tissue was removed with a scalpel and camel's hair paintbrush. These were stained in safranin.

The standardized terminology of Ellis (1976, 1979) was used for the anatomical descriptions. The following abbreviations are used: vb/s—vascular bundles; 1'vb/s—first order vascular bundle/s; 3'vb/s—third order vascular bundle/s; ibs—

inner bundle sheath; mestome sheath; obs—outer bundle sheath; parenchyma sheath.

Freshly fixed material of the following taxa was studied: *Panicum grumosum* (3 accessions), *P. hylaeicum* (4 accessions), *P. laxum* (13 accessions), *P. pernambucense* (6 accessions), *P. pilosum* (9 accessions), *P. polygonatum* (7 accessions), and the sectional anatomical description is based on this material. This sample was augmented by herbarium material of *P. auritum* (2 accessions), *P. bresolinii* (1 accession), *P. condensatum* (2 accessions), *P. leptachne* (2 accessions), *P. stagnatile* (2 accessions), *P. stevensianum* (6 accessions), *P. grande* (3 accessions), *P. scabridum* (6 accessions) and *P. longum* (1 accession), but anatomical detail was difficult to ascertain in much of this material.

Vouchers for this study are marked with an asterisk (*) in the specimens examined section of the taxonomic treatment.

EXOMORPHOLOGICAL CHARACTERS

Species of section *Laxa* grow in humid places, either along the borders of woods or forming dense colonies on the banks of streams and rivers. Examples are *Panicum pernambucense*, *P. grumosum*, and *P. stagnatile*. *Panicum laxum* and *P. pilosum*, on the other hand, are pioneer species and usually invade modified habitats.

The plants are short-rhizomatous or stoloniferous, decumbent and rooting and branching at the lower nodes, with hollow internodes and leaf blades flat, linear to ovate-lanceolate. The ligules are membranous, shortly lacinate or occasionally ciliate at the apex, commonly absent in *P. pilosum*.

INFLORESCENCE

The inflorescence type is one of the most distinguishing characters of this section, the spikelets being arranged unilaterally on first- or second-order racemose branches. All included species possess this feature.

First-order branches are alternate, subopposite, or whorled toward the base, diverging in all directions in relation to the main axis. A small membranous bract is usually present at the first node of the panicle. This bract has pilose margins or sometimes is reduced to a small arc of papillose hairs.

There is a gradient in the degree of ramification of the inflorescence. Paired spikelets are present on the ventral side of first-order branches in species such as *P. pilosum*, *P. leptachne* Doell, *P. condensatum*, and *P. longum*. In the other species

spikelets are paired on second-order branches, with these branches unilaterally disposed in relation to the first-order ones; the second-order branches are appressed or divergent from the axis of first-order branches, and there is variation in the length of the second-order branches, which gives the inflorescence a more or less lax appearance.

SPIKELET

The spikelet in section *Laxa* has the typical structure of the Paniceae, with two glumes and two antheia, the lower one with a lemma and with or without a palea, the flower present or absent, being male when present; the upper antheium is hermaphrodite, with a lemma and palea enclosing it. Internodes of the rachilla are inconspicuous between glumes, lower and upper flower.

The spikelets are biconvex, the lower glume reaching $\frac{1}{3}$ to $\frac{3}{4}$ the length of the spikelet, 1–3-nerved; the upper glume and lower lemma are subequal, or the upper glume is slightly shorter and not covering the apex of the upper antheium, 5(–7)-nerved; the lower palea may be conspicuous and either the same length as the lower lemma, or reduced to completely absent; the lower flower is occasionally present, with two lodicules and three stamens, but is usually absent; the upper antheium encloses a perfect flower, with two cuneiform, conduplicate lodicules, which embrace the lower borders of the palea; the caryopsis has a punctiform to oblong hilum, with the embryo reaching $\frac{1}{3}$ to $\frac{1}{2}$ the length of the caryopsis.

The lower lemma is commonly membranous but occasionally indurate at maturity in specimens of *P. polygonatum*, e.g., *Idrobo & Cuatrecasas* 2665, and *P. laxum*, e.g., *Cuatrecasas & Llanos* 24054. Bisexual flowers occur in the lower antheium of specimens of *P. stevensianum*, with two lodicules, three stamens and a conspicuous gynoeium, with two styles and a plumose stigma; in this case there is no variation in the consistency of the lower lemma, it being similar to the upper glume; no caryopsis was found in these bisexual lower flowers. The presence of bisexual flowers in the lower antheium of *Panicum* was previously reported by Palacios (1968), Pohl (1980), and Zuolaga & Sendulsky (1988).

Three-flowered spikelets were occasionally observed in specimens of *P. grumosum*, e.g., *Quarín et al.* 2745 and *Millán* 568, with antheium I neuter, while antheium II and upper antheium were bisexual, the two latter with the lemma and palea indurate.

UPPER ANTHECIUM TEXTURE AND ORNAMENTATION (FIG. 1)

The epidermis of the lemma and palea has rectangular long cells arranged in longitudinal rows, with longitudinal and transverse anticlinal walls strongly undulated. Stomata, simple papillae, prickly hairs, and silica bodies are present in species of this section.

The presence of stomata is variable among the different species, being located, when present, toward the apex of the lemma and palea.

Simple papillae are regularly distributed in longitudinal rows. They are associated with the periclinal, external wall of the long cells, eccentric, and near the anticlinal transversal distal wall.

Prickly hairs are frequent toward the apex of the lemma and palea, being retrorse in *P. bresolinii*, *P. polygonatum*, and *P. pilosum*, antrorse in *P. stagnatile*, *P. longum*, *P. laxum*, and *P. hylaeicum* Mez, or with both dispositions in *P. grumosum*, *P. stevensianum*, and *P. leptachne*.

Silica bodies are exfoliate, more or less cross-shaped to nodular.

The upper antheium varies from membranous at maturity, in such species as *P. grumosum*, *P. pernambucense*, *P. bresolinii* L. B. Smith & Wasshausen, *P. leptachne*, *P. longum*, *P. condensatum*, *P. stevensianum*, and *P. stagnatile*, to more or less indurate in *P. polygonatum*, *P. laxum*, *P. hylaeicum*, and *P. pilosum*.

Antheial ornamentation varies in relation to the texture of the antheium, with simple papillae, prickly hairs, and silica bodies abundant in species with membranous antheia. In the rest of the species with indurate upper antheia, such as *P. polygonatum*, *P. pilosum*, *P. hylaeicum*, and *P. laxum*, stomata, simple papillae, and prickly hairs are only present toward the apex, and silica bodies are occasionally present at the tip of the lemma.

Verrucose papillae, similar to the ones found in

FIGURE 1. Scanning electron photomicrographs of female florets of species of *Panicum*. —A. *Panicum longum*, $\times 100$ (from type specimen). —B. *Panicum grumosum*, $\times 500$ (*Smith & Klein* 15723). C, D. *Panicum auritum*. —C. Upper portion, $\times 50$. —D. Tip of the lemma, $\times 250$ (*Merrill* 101). E, F. *Panicum grande*. —E. Dorsal side, $\times 100$. —F. Upper portion of the lemma, $\times 250$ (*Black* 15352). G, H. *Panicum scabridum*. —G. Dorsal side, $\times 100$. —H. Ventral side, $\times 100$ (*Wurdack & Adderley* 42986).

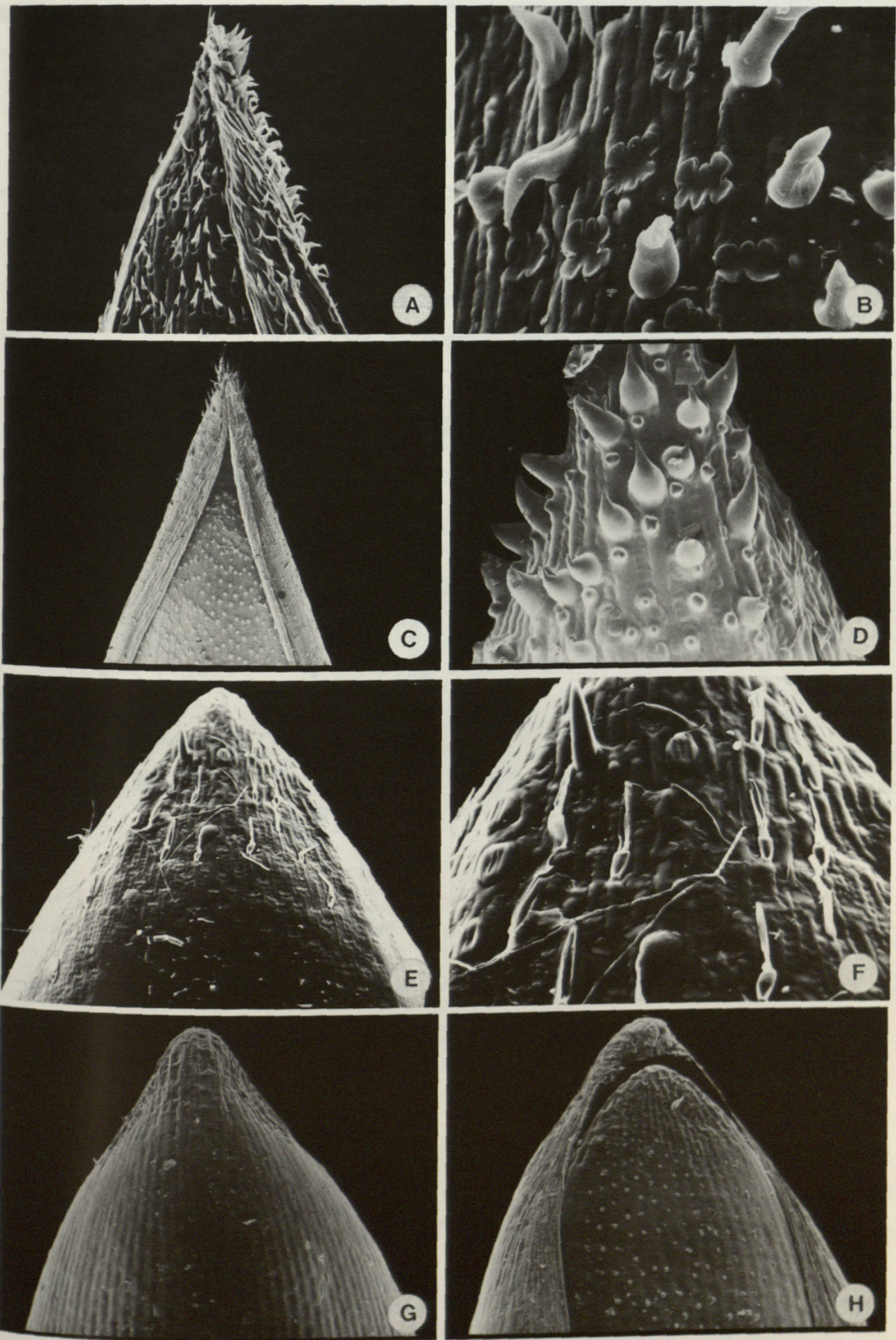




FIGURE 2. Distribution of *Panicum bresolinii*, *P. longum*, and *P. pilosum*.

species of subgenus *Steinchisma*, are sometimes present in specimens of *P. laxum*.

CHROMOSOME NUMBERS

There are few karyological studies on taxa belonging to section *Laxa*, with data of the cytology of only six species being available. A basic chromosome number of $x = 10$ characterizes the section. *Panicum auritum*: $n = 15$ (Mehra, 1982); $2n = 30$ (Christopher & Abraham, 1976; Mehra & Chaudhary, 1981; Mehra, 1982); $2n = 36$

(Mehra & Chaudhary, 1976, 1981). *Panicum grumosum*: $2n = 40$ (Núñez, 1952). *Panicum hylaeicum*: $2n = 40$ (Bouton et al., 1981). *Panicum laxum*: $n = 20$ (Davidse & Pohl, 1972b, 1974, 1978); $2n = 36$ (Gould & Soderstrom, 1967; Tateoka, 1962); $2n = 40$ (Pohl & Davidse, 1971; Gould & Soderstrom, 1967). *Panicum pilosum*: $n = 10$ (Davidse & Pohl, 1972a, 1974, 1978); $2n = 20$ (Pohl & Davidse, 1971, under *P. milleflorum*). *Panicum pernambucense*: $2n = 40$ (Bouton et al., 1981, under *P. rivulare*). *Pan-*



FIGURE 3. Distribution of *P. grumosum*, *P. hylaeicum*, and *P. polygonatum*.

icum polygonatum: $2n = 40$ (Pohl & Davidse, 1971, under *P. boliviense* Hackel; Pohl & Davidse, 1971).

LEAF ANATOMY (FIGS. 6–17)

The section *Laxa*, as constituted here, exhibits variable leaf blade anatomy, and two slightly different species groupings are evident. These two groups intergrade in their leaf anatomy, and the taxonomic significance of the differences between

them will only become apparent once additional species of section *Laxa* are collected and fixed in the field. The anatomical description of the section will, nevertheless, only be based on the following species: *Panicum hylaeicum*, *P. laxum*, *P. pilosum*, *P. bresolinii*, *P. longum*, *P. leptachne*, *P. stagnatile*, *P. stevensianum*, *P. auritum*, *P. condensatum*, and *P. polygonatum*. These species constitute a homogeneous anatomical group in which the leaf anatomy is remarkably uniform, as illustrated in Figures 8–11, 13–16. For convenience,



FIGURE 4. Distribution of *P. laxum* and *P. leptachne*.

this will be called the Laxa species group. The anatomy of *P. grumosum* and *P. pernambucense* will be treated separately, as their anatomy differs somewhat from that of the Laxa group (Figs. 7, 12). This will be informally called the Grumosum species group.

LEAF BLADE IN TRANSVERSE SECTION

Outline: expanded, either flat or very broadly V-shaped; the arms of the lamina either straight or outwardly bowed; the two halves often not sym-

metrical on either side of the median vb, with one half being slightly wider, with more vbs; this asymmetry not pronounced being due to an extra 1'vb with an additional 3'vb between successive 1'vbs in one half of lamina; this can result in a maximum of an extra 20 vbs in one half out of a total of 52 (up to 99 in some specimens of *P. hylaeicum*) in the entire section. Thickness at mid-lamina 150–230 μm . *Ribs and furrows*: rounded adaxial ribs always present over all vbs; all ribs of similar size and shape; size of ribs differs between specimens; adjacent ribs separated by wide, open furrows; depth



FIGURE 5. Distribution of *P. pernambucense*, *P. stagnatile*, *P. stevensianum*, and *P. condensatum*.

varies from very shallow to medium furrows on different specimens of all species. Slight abaxial ribs usually distinguishable; vary from slight undulations associated with the vbs to ribs the same size as the adaxial ribs, resulting in a $\pm$ moniliform outline. *Keel*: always present, but size and amount of associated colorless parenchyma variable; varies from a simple median vb with small amount of adaxial colorless parenchyma to well-developed V-shaped keel incorporating 5 vbs, including 3 1'vbs; the vbs all abaxially located; no lacunae; this structure abruptly separated from the lamina

by bulliform cell groups; this type of keel differs considerably from that present in the Grumosum group of this section, where the keel intergrades with the lamina. *Vascular bundle arrangement*: (8-)9-13(-18) 1'vbs in entire blade, usually with an additional 1'vb in one half of lamina; 3, 4, 5, or 6 3'vbs between consecutive 1'vbs; this number differs by one in each half of the lamina; no 2'vbs. All vbs centrally located in the blade thickness, although 3'vbs may be slightly abaxially displaced. *Vascular bundle description*: 3'vbs angular with xylem and phloem distinguishable, 1'vbs circular

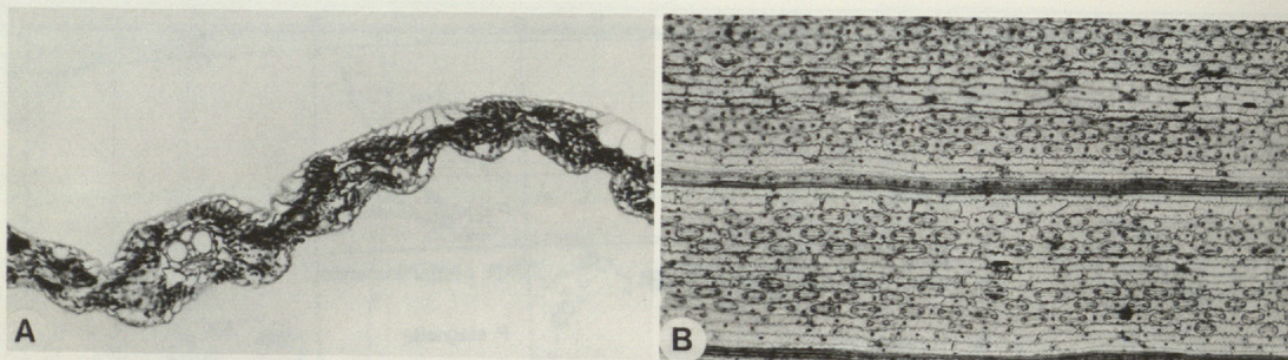


FIGURE 6. Leaf blade anatomy of *P. condensatum*.—A. Transverse section of poorly reconstituted herbarium specimen; fusoid cells and pallisadelike adaxial chlorenchyma are present.—B. Abaxial epidermis with narrow costal zones with dumbbell silica bodies and the intercostal zones clearly divided into lateral stomatal bands, and central files without stomata but with microhairs; epidermal cells nucleate ($\times 250$, based on *Davidse et al.* 11494).

to slightly elliptical in outline; phloem adjoins the ibs; lysigenous cavities and protoxylem present; circular metaxylem vessels narrower than the obs cells as seen in section. *Vascular bundle sheaths*: obs of 3'vbs conspicuous, entire, round, without extensions, although an additional adaxial cell is sometimes evident, consisting of 5 or 6 inflated, rounded cells, but up to 8 in some specimens of *P. hylaeicum*, *P. auritum*, *P. stevensianum*, *P. stagnatile*, and *P. bresolinii*, especially toward the midnerve; adaxial cells tend to be largest; chloroplast presence and type variable: either absent, or rarely, relatively small, centripetal specialized chloroplasts occur with few, small plastids; ibs absent. Obs of 1'vbs round or slightly elliptical, with slight abaxial interruption, without extensions, comprised of 8–11 cells; cells smaller than those of 3'vbs, inflated, rounded, usually all similar in shape, but extreme abaxial cells tend to be smallest. Chloroplasts as in obs of 3'vbs. Ibs present, complete, of small cells with uniformly thickened walls. *Sclerenchyma*: minute, inconspicuous adaxial and abaxial girders associated with all vbs; fibers lignified, secondary thickening variable. Small sclerenchyma cap in margin. *Mesophyll*: chlorenchyma not radiate but adaxial cells tend to a pallisade-type of arrangement; these cells tabular whereas the abaxially located chlorenchyma cells are very irregular in shape; more than 8 chlorenchyma cells between consecutive vbs; the cells, particularly those located abaxially, with definite invaginations of the walls, resembling arm cells very closely. Fusoid cells present in mesophyll: elongate, narrow, and inclined downward and present on either side of each vb. Very little reduction evident except near the margin where the lateral fusoid cells may be absent. No colorless cells. *Adaxial epidermal cells*: bulliform cells present in adaxial furrows between all vbs; in restricted groups, generally with a large, fan-shaped, inflated central cell or cells; occupy

up to $\frac{1}{2}$ leaf thickness. Epidermal cells small, regular in size, with a distinct continuous cuticle; no macrohairs, prickles, or papillae. *Abaxial epidermal cells*: no bulliform cells; thickened cuticle, no epidermal projections.

ABAXIAL EPIDERMIS IN SURFACE VIEW

Intercostal long cells: elongated, up to $3\times$ longer than wide; parallel side walls; vertical or angled end walls; unthickened, moderately undulating anticlinal walls; this sinuosity conspicuous. Cell shape consistent across intercostal zones except that interstomatal long cells are shorter, long cells in a file either adjoin one another or are separated by short cells—either a single tall and narrow cell or cork-silica cell pairs. Conspicuous nuclei usually present in intercostal long and short cells. *Stomata*: low dome-shaped or ovoid but may tend to low triangular; subsidiary cells with conspicuous nucleus often contained within a slight evagination at the apex. Common with 6–10 files of stomata per intercostal zone, with only the 3–6 central long cell files without stomata—these cells more elongate than the interstomatals and may stain less intensely. Stomatal rows in adjoining files of cells; usually one interstomatal cell between successive stomata in a file but this arrangement variable. Stomata files separated from the costal files by 1–2 intercostal files without stomata. *Intercostal short cells*: either absent, on solitary and tall and narrow or paired with both cork and silica cells and tall and narrow. Distribution irregular, but most common in central files of intercostal zones. *Papillae*: absent except in single specimen of *P. stevensianum* (Chase 6616). *Prickle hairs*: absent except for small intercostal hooks on one specimen of *P. pilosum* (Davidse 21866). Small angular prickles with short barbs present on the leaf margin. *Microhairs*: elongated, fingerlike, with distal and basal

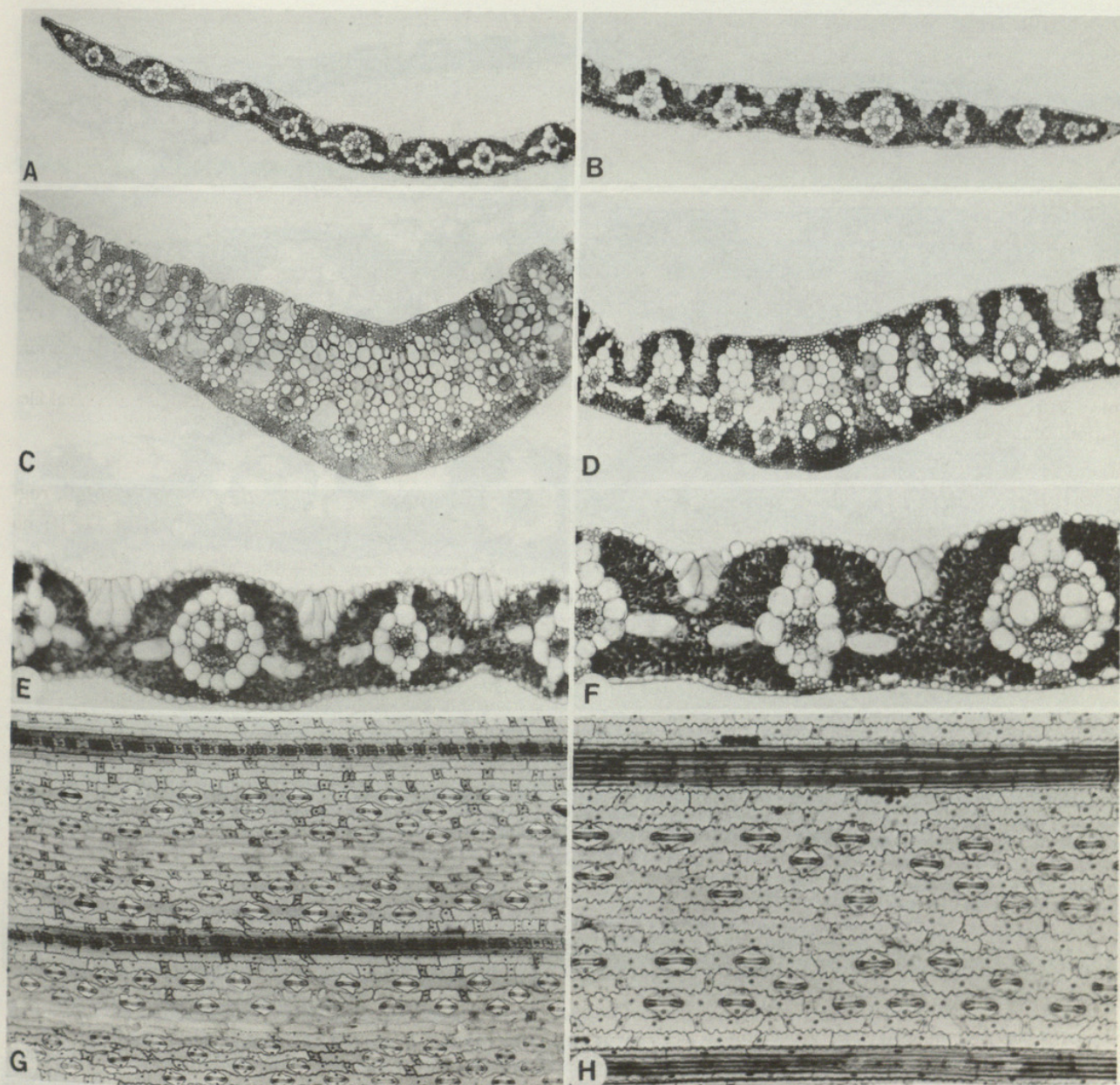


FIGURE 7. Leaf blade anatomy of *Panicum grumosum*. A-F, transectional anatomy.—A. Gently tapering leaf blade margin; note rather irregular occurrence of fusoid cells near margin.—B. Slightly acute margin with small sclerenchyma cap; fusoid not associated with three most lateral bundles and presence irregular, with other bundles situated near the margin.—C. Keel consisting of many vascular bundles (more than 12), all with adaxial bundle sheath extensions and gradually intergrading into the lamina; fusoid cavities in this region of the leaf resemble lacunae, as only a single cavity is present in the mesophyll between successive bundles.—D. Specimen in which keel is less developed but incorporates at least seven bundles; note lacunae intergrading laterally into typical fusoid cavities.—E. Detail of mesophyll at mid-lamina; note regular occurrence of fusoids and much shorter bundle sheath extensions than nearer the center of the blade.—F. Irregular occurrence of fusoid cells and extension of the outer bundle sheaths of the third-order vascular bundles in particular. G, H. Abaxial epidermal structure.—G. Nucleate intercostal long and short cells and narrow costal zones with irregularly dumbbell-shaped silica bodies; central files in intercostal zones without stomata.—H. Detail of nucleate intercostal long, short, and triangular subsidiary cells (A, E, based on Zuloaga 3087; B, D, F, H, Zuloaga s.n.; C, G, Zuloaga 3073; A-D $\times 50$; E-G $\times 125$; H $\times 200$).

cells of equal length; distal cell deciduous with very thin walls; common in the center of the intercostal zones. *Macro-hairs*: absent except for new cushion-based hairs on single specimen of *P. pilosum* (Davidse 21866). *Silica bodies*: vertically elongated dumbbell- or cross-shaped, or equidimensional dumbbell-shaped to elongated nodular (more

rarely and only overlying the 3'vbs). Alternate regularly with similar shaped or shorter costal short cells along central costal file; only 3 (rarely 5) files of cells per costal zone. Each costal zone therefore only has a single file of cells with silica bodies bounded on either side by a file of costal long cells.

This description is based only on the anatomy

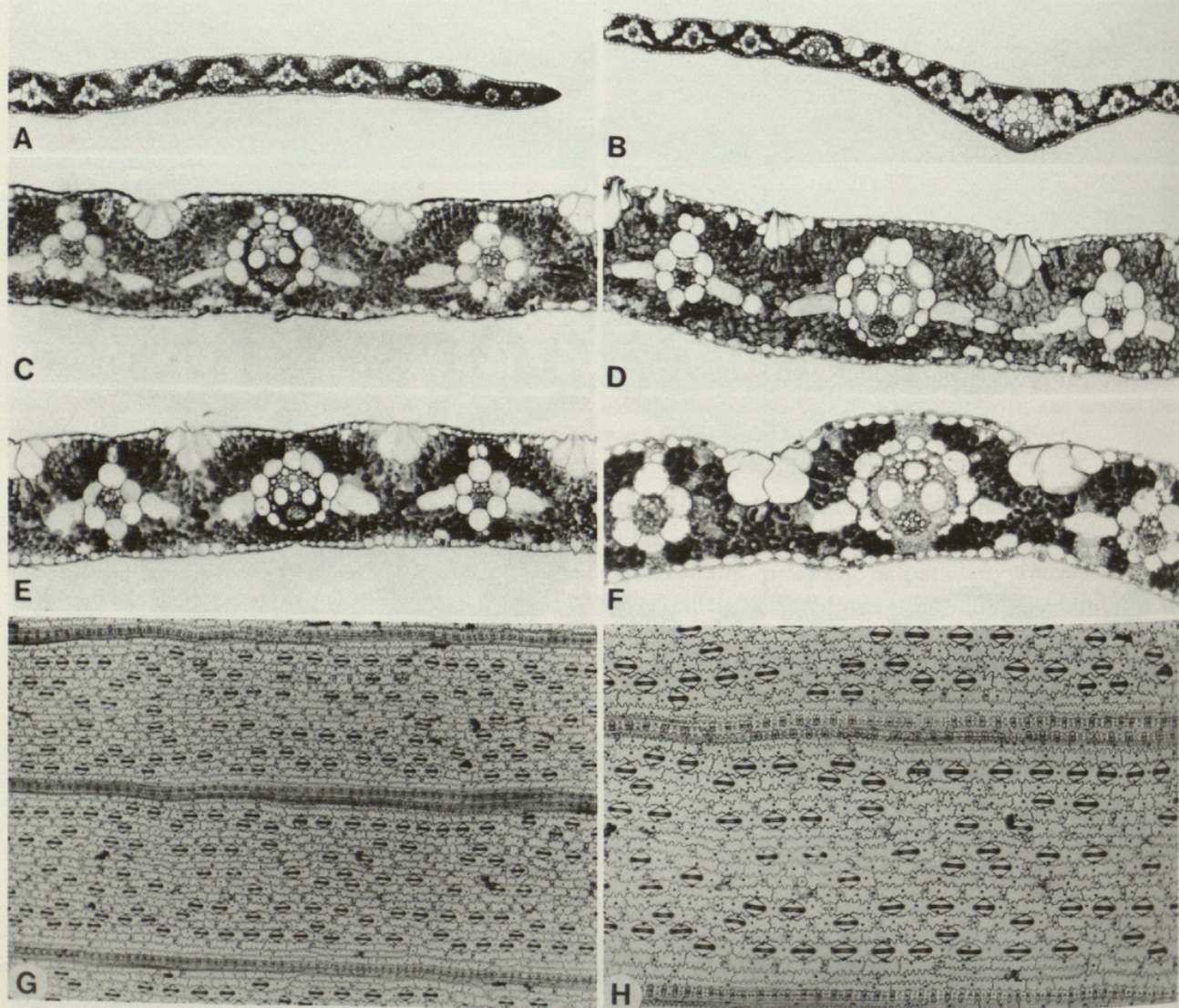


FIGURE 8. Leaf blade anatomy of *Panicum hylaeicum*. A-F, transectional anatomy. —A. Lateral part of lamina showing tapering margin with small cap of sclerenchyma; note regular presence of fusoid cells associated with all vascular bundles except for penultimate and ultimate lateral bundles in the margin. —B. Restricted keel comprising three vascular bundles; adaxial parenchyma developed in association with median first-order vascular bundle and adjacent third-order bundle on either side with bundle sheath extensions; regular fusoid cells not associated with these bundles. —C. Outer bundle sheath cells without chloroplasts, fusoids narrow and inclined toward the abaxial surface, adaxial chlorenchyma with pallisade arrangement. —D. Detail of arm cell-like chlorenchyma cells, particularly those located abaxially and adjacent to the fusoid cells; note the fusoid cavities appear to be bounded by the thin walls of the fusoid cells. —E. Regular occurrence of a fusoid cell on either side of most vascular bundles. —F. Specimen with small, unspecialized chloroplasts in the outer bundle sheath cells. G, H. Abaxial epidermis. —G. Narrow costal zones (3–5 files wide) and wide intercostal zones (16–19 files wide). —H. Low triangular stomata in files throughout intercostal zones, in all horizontal cell files, but tend to be less concentrated in the central files of the zones; subsidiary and intercostal long cells with characteristic persistent nuclei; note irregular dumbbell-shaped costal silica bodies alternating with similar shaped cork cells along costal cells files (A, B, E, F, Zuloaga *et al.* 2293; C, Zuloaga 2218; D, G, H, Zuloaga 3197; A, B $\times 50$; G $\times 80$; C–F, H $\times 125$).

of the Laxa species group, *P. hylaeicum*, *P. laxum*, *P. pilosum*, and *P. polygonatum*, as well as *P. leptachne*, *P. longum*, *P. condensatum*, *P. auritum*, *P. stagnatile*, *P. stevensianum*, and *P. bresolinii*. The Grumosum group, *P. grumosum* and *P. pernambucense*, differs in several respects: lamina width generally wider, although *P. hylaeicum*, *P. stagnatile*, and *P. leptachne* sometimes have blades as wide as those of *P. grumosum*,

a maximum of 105 vbs versus 52 in the Laxa group (although up to 99 can occur in *P. hylaeicum*); asymmetry less marked (48 versus 57 vbs); thickness at mid-lamina generally greater; keel well developed, incorporating 7–12 vbs (1–5 in Laxa group), wide and expanded and intergrading into the lamina (not abrupt as in Laxa group); lacunae present in the colorless parenchyma of the keel (absent in Laxa group); metaxylem vessel

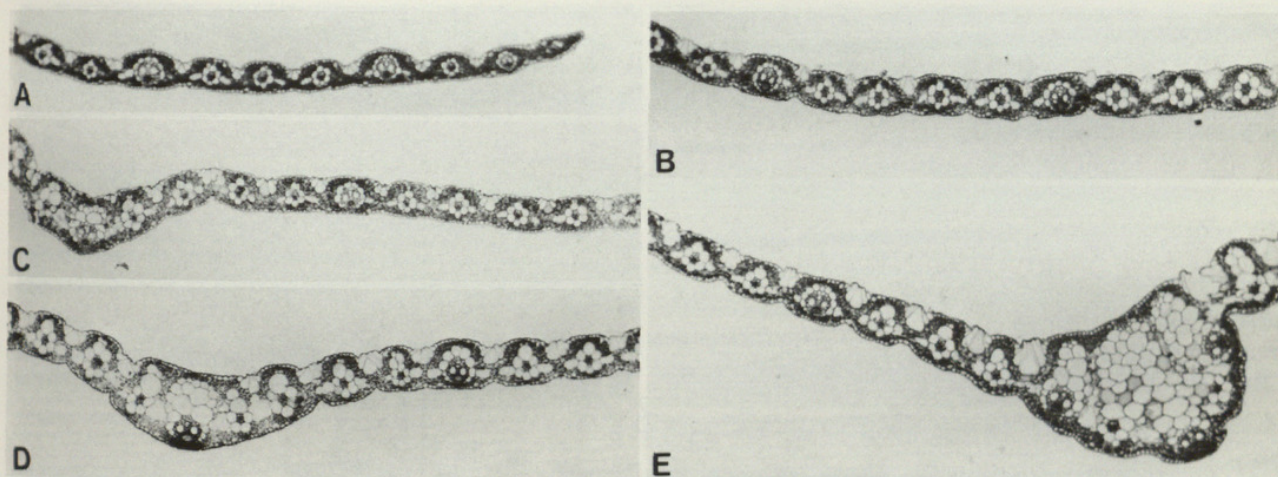


FIGURE 9. Transectional anatomy of the leaf blade outline of *Panicum laxum*.—A. Gently tapering margin with only the most laterally situated vascular bundles without associated fusoid cells.—B. Mid-lamina region showing four third-order vascular bundles located between successive first-order bundles; note fusoid cavities on either side of all bundles. C–E. Variation in the structure of the keel.—C. Insignificant keel incorporating only the median vascular bundle; this first-order bundle with small amount of adaxial colorless cell tissue.—D. Most common intermediate keel type incorporating 3 vascular bundles and adaxial colorless tissue.—E. Unusual elaborate V-shaped keel with 5 vascular bundles and extensive colorless parenchyma; note abrupt delimitation from lamina by bulliform cell groups (A, based on Zuloaga 3290; B, Stevens 25354; C, Zuloaga 2337; D, Davidse 30703; E, Zuloaga et al. 4330; A–E $\times 50$).

diameters greater than in Laxa group (often wider than obs cells); *outer bundle sheath* with 8–10 cells around 3'vbs (5–6(–8) in Laxa group); 16–20 cells in obs of 1'vbs (8–11 in Laxa group);

bundle sheath extensions always present (variable, from 1–4 cells deep); adaxial; uniseriate to biseriate; longest extensions closer to keel; *chlorenchyma cells* smaller and more compact, adaxial cells

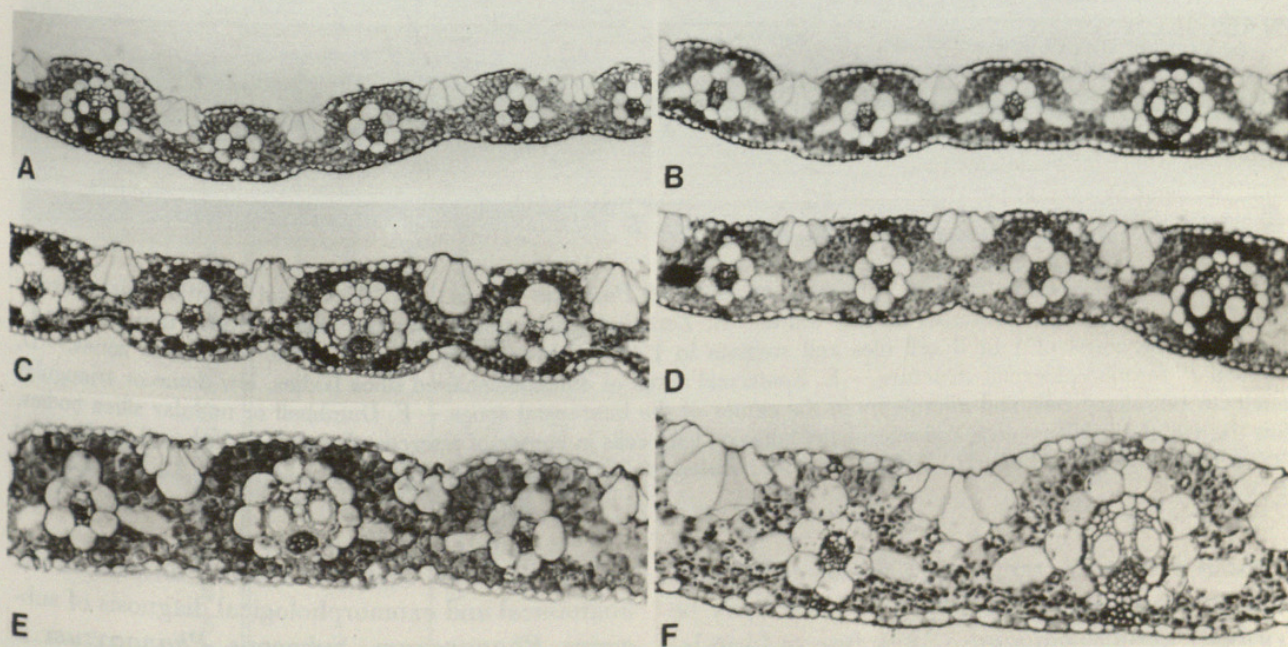


FIGURE 10. Detail of transectional leaf anatomy of *Panicum laxum*.—A. Thinner lateral part of lamina where fusoid cell occurrence is less regular; outer sheath cells without chloroplasts.—B. Specimen with typical anatomy of the Laxa group: regular fusoid cell presence and parenchyma sheath cells without chloroplasts.—C. Typical Laxa-type anatomy, but note well-developed adaxial ribs and furrows, very similar to those of *P. pilosum*.—D. Fusoid and bundle sheath cell structure.—E. Adaxial chlorenchyma tissue palisadelike, particularly above the fusoid cavities, whereas the abaxial chlorenchyma cells are equidimensional with discernible cell wall invaginations.—F. Specimen with anatomy tending to the intermediate C_3/C_4 type with a few, centripetally located chloroplasts, which differ structurally from those of the chlorenchyma; note the presence of fusoid cavities and that this leaf is thicker than other *P. laxum* specimens (A, based on Stevens 25275; B, Zuloaga 3290; C, Zuloaga et al. 4330; D, Zuloaga et al. 4367; E, Zuloaga 2337; F, Brown 19; A–D $\times 125$; E, F $\times 200$).

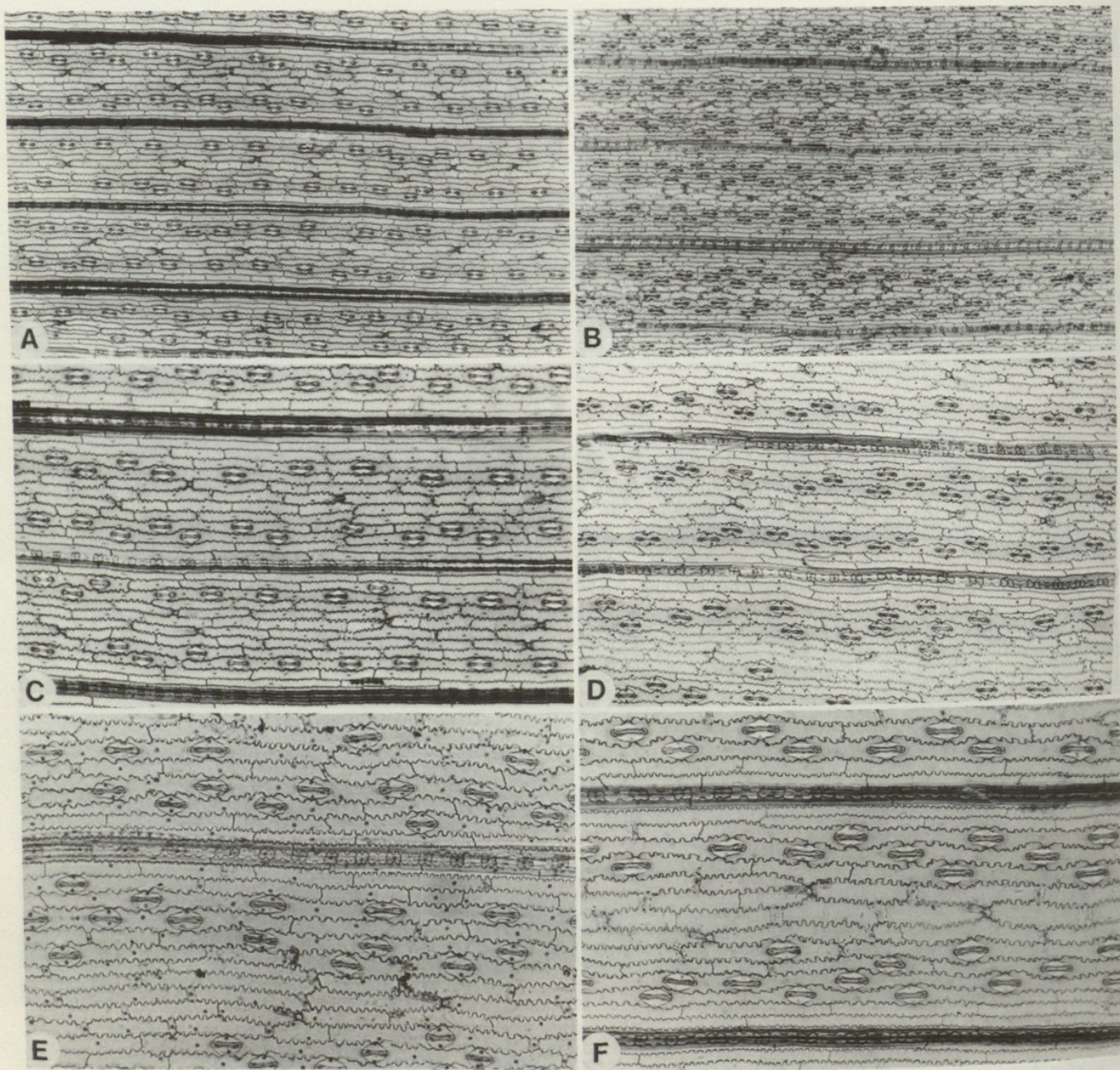


FIGURE 11. Consistent abaxial epidermis structure of *Panicum laxum*.—A. Epidermal zonation with narrow costal zones evenly spaced across lamina width.—B. Zonation with intercostal zones slightly wider than in A.—C. Narrow costal zones of 1 or 3 cell files and stomata in 1 or 2 files laterally situated in the intercostal zones.—D. Typical *P. laxum* epidermal structure.—E. Epidermal detail of dumbbell-shaped silica bodies, low dome or triangular nucleate subsidiary cells and microhairs in the center of the intercostal zones.—F. Dumbbell or nodular silica bodies, low triangular subsidiary cells and microhairs between long cells in center of intercostal zones (A, C, based on Davidse 32998; B, Zuloaga 3290; D, Zuloaga s.n.; E, Zuloaga 2571; F, Davidse 30703; A, B $\times 80$; C, D $\times 125$; E, F $\times 200$).

without palisade arrangement; *fusoid cells* irregular in occurrence, particularly laterally; may be virtually absent (Zuloaga 3232); fuse to form lacunae in keel; *intercostal long cells* short, generally less than $3 \times$ longer than wide; *interstomatal cells* often very short.

DISCUSSION

The possible affinities of section *Laxa* with other sections of *Panicum* and other genera of the Paniceae are summarized in Table 1.

Section *Laxa* conforms within *Panicum* to the anatomical and exomorphological diagnosis of subgenus *Phanopyrum*. Subgenus *Phanopyrum* is characterized anatomically by the presence of a double bundle sheath, the inner mesotome sheath with thick-walled cells and the outer sheath parenchymatous, with slightly thickened walls, and completely devoid of, or with few, nonspecialized chloroplasts (Zuloaga, 1987). The number of mesophyll cells between the vascular bundles varies between 5 and 12, and the mesophyll tissue is irregularly arranged; this is typical of non-Kranz anatomy. All

TABLE 1. Comparison of section *Laxa* with other sections of *Panicum*, *P. grande*, and genera *Homolepis* and *Hymenachne*.

	Genus <i>Homolepis</i>	Genus <i>Panicum</i>					
		Subg. <i>Steinchisma</i> sect. <i>Steinchisma</i>	Subg. <i>Phanopyrum</i> sect. <i>Laxa</i>		Subg. <i>Phanopyrum</i> <i>P. grande</i>	Subg. <i>Phanopyrum</i> sect. <i>Phanopyrum</i>	Genus <i>Hymenachne</i>
			Group <i>Laxa</i>	Group <i>Grumosum</i>			
Photosynthetic type	C ₃ (rarely C ₃ /C ₄ intermediate)	C ₃ /C ₄ intermediate	C ₃ (rarely C ₃ /C ₄ intermediate)	C ₃	C ₃	C ₃	C ₃
Fusoid cells present	+	—	+	+	—	—	—
Lacunae present	—	—	—	Present in keel only	Present in keel and mesophyll	Present in keel and mesophyll	Present in keel and mesophyll
Superposed bundles present	—	—	—	—	+	+	—
Upper anthecium consistency	Indurate	Indurate	Indurate to membranous	Membranous	Indurate	Indurate	Membranous
Palea covered at its apex by the lemma	+	+	+	+	+	+	—
Prickle hairs and papillae present	—	—	+	+	—	—	+
Inflorescence with unilateral branches	—	—	+	+	—	+	+
Lower palea expanded; compound papillae present	—	+	— (rarely present in <i>P. laxum</i>)	—	—	—	—

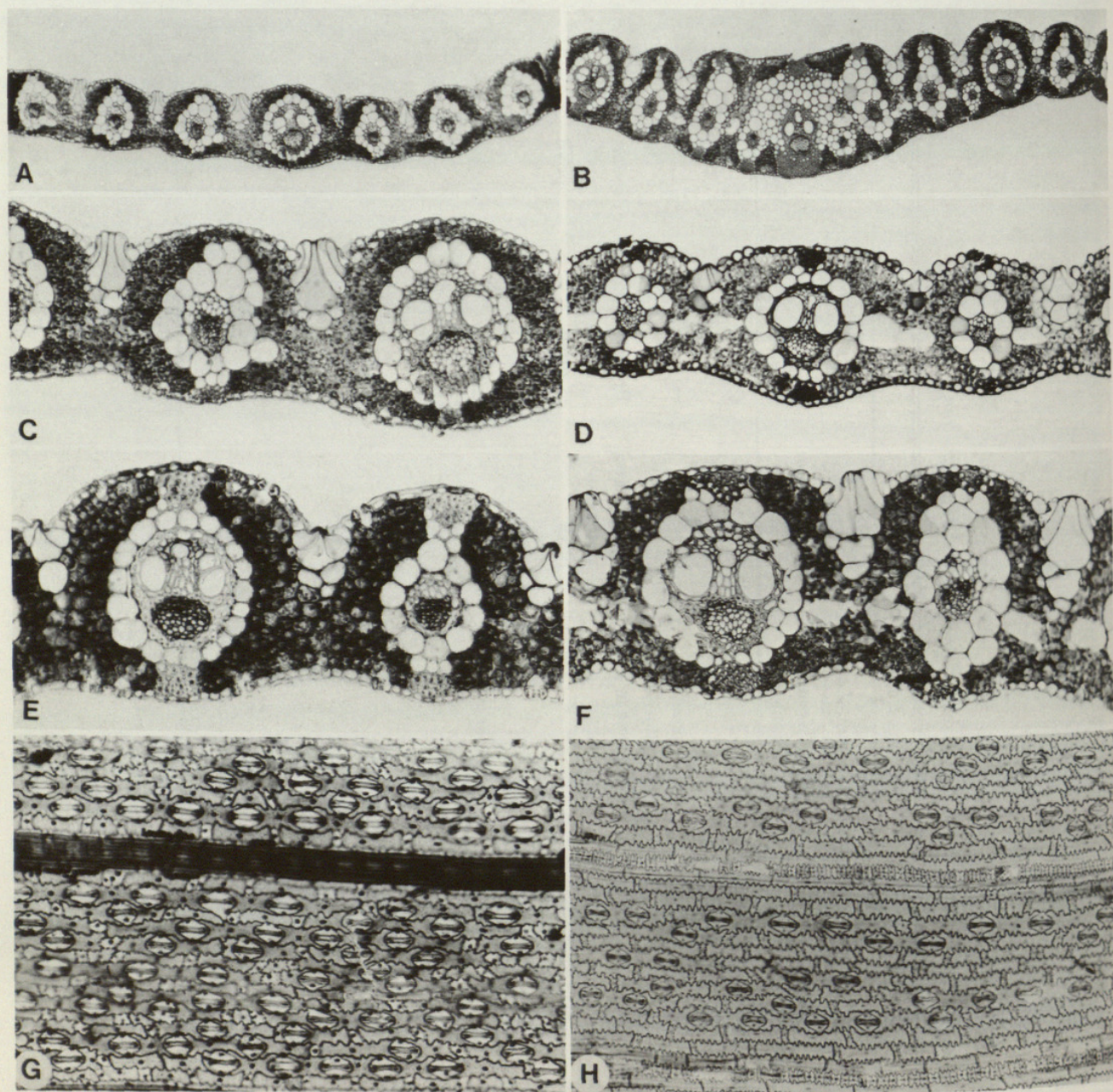


FIGURE 12. Leaf blade anatomy of *Panicum pernambucense*. A-F. Transectional anatomy. —A. Mid-lamina with first- and third-order bundles; note absence of fusoid cavities. —B. Keel with five bundles gradually intergrading with lamina; few lacunae present. —C. Anatomical detail showing virtual absence of fusoids and short adaxial bundle sheath extensions associated with the third-order bundles. —D. Specimen with irregular fusoid cell presence. —E. Detail of compact mesophyll without palisadelike tissue; no fusoid cells. —F. Irregular fusoid occurrence and compact mesophyll of arm cells. G, H. Abaxial epidermal structure. —G. Thickened long cell walls with stomata regularly distributed throughout intercostal zone; note nucleate nature of all intercostal cells. —H. All cells shorter than in *Laxa* type, particularly the intercostal long cells and the silica bodies (A, C, based on Zuloaga *et al.* 3232; B, E, G, Zuloaga 2235; D, Zuloaga *et al.* 3323; F, H, Zuloaga 2494; A, B $\times 50$; G, H $\times 200$; C-F $\times 125$).

taxa in this subgenus possess the C_3 photosynthetic pathway. Plants of subgenus *Phanopyrum* are commonly found in humid and shady habitats and have membranous, small ligules; the inflorescences vary in this subgenus from spikelets disposed unilaterally in racemose branches (as in sections *Stolonifera*, *Phanopyrum*, and *Laxa*), to spikelets dispersed in lax or contracted panicles; spikelet nervation is constant, the lower glume 1–3-nerved and the upper glume and lower lemma 5-nerved,

occasionally 7-nerved (Zuloaga, 1987). Zuloaga (1987) suggested two subgroups could be distinguished in subgenus *Phanopyrum*: one with a basic chromosome number of $x = 10$, spikelets disposed unilaterally on the branches, and upper antherium smooth, without papillae and bicellular microhairs, which includes sections *Phanopyrum*, *Laxa*, and *Stolonifera*; the other one with $x = 9$, spikelets in open or contracted panicles, not unilaterally disposed, and upper antherium papillate and with

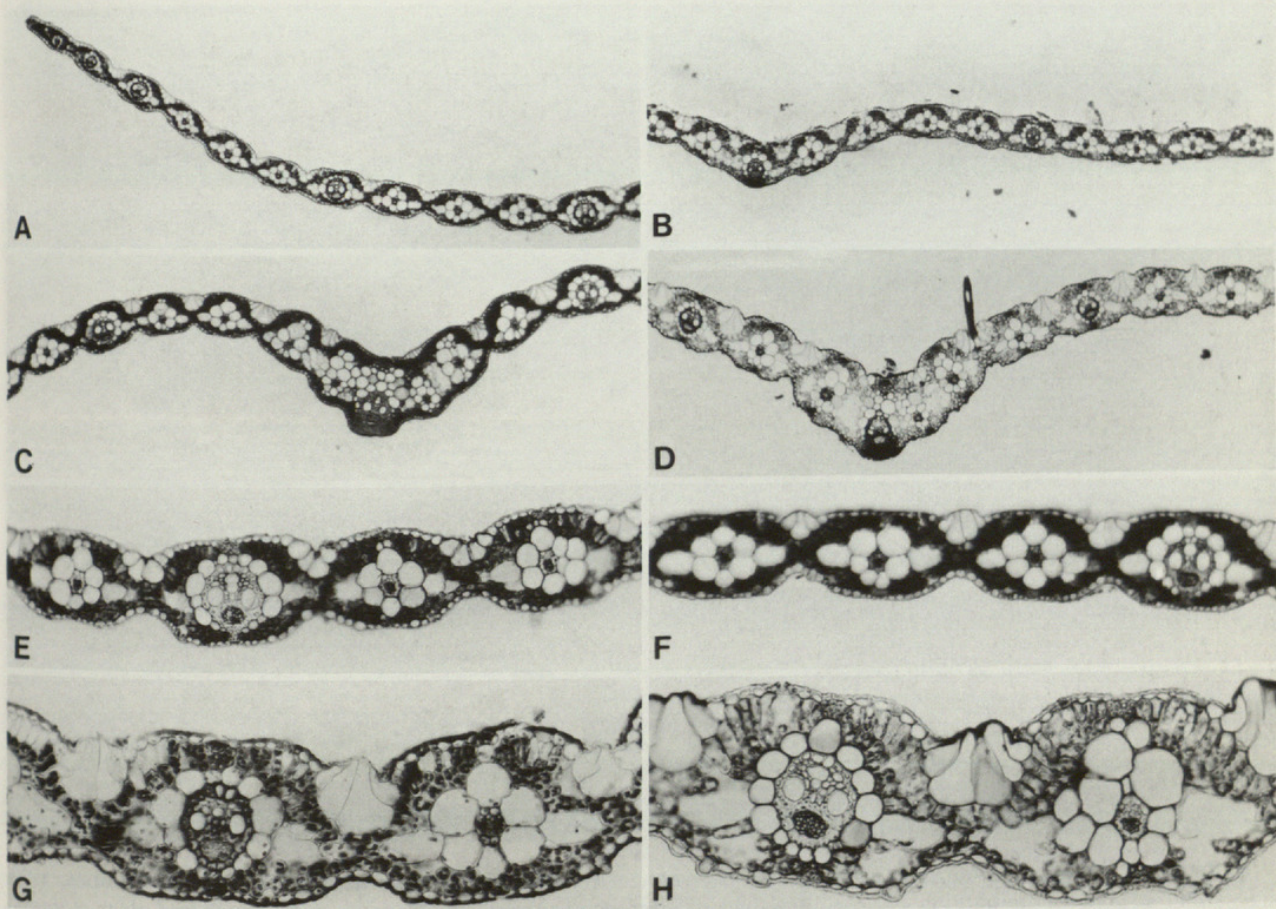


FIGURE 13. *Panicum pilosum* leaf blade in transverse section.—A. Margin showing fusoids associated with all vascular bundles except the most lateral ones. B–D. Structure of keel.—B. Median vascular bundle only, without associated colorless cell development.—C. Typical keel including three vascular bundles and with colorless parenchyma; median bundle with additional sclerenchyma girder development.—D. Typical keel but note lacunae in keel; unusual adaxial macrohair base evident.—E. Typical *Laxa* anatomy with palisadelike mesophyll, regular fusoid cell presence and parenchyma sheath cells without chloroplasts; presence of abaxial ribs and furrows characteristic.—F. Note that abaxial ribs and furrows larger than those of adaxial surface.—G. Few chloroplasts in outer sheath cells; note thick cuticle with evidence of abaxial epidermal hooks.—H. Typical palisade adaxial chlorenchyma; note breakdown of fusoid cavities to form lacunae (A, E, based on Zuloaga 3289; B, G, Stevens 25219; C, F, Zuloaga 2303; D, H, Davidse 21866; A–D $\times 50$; E, F $\times 125$; G, H $\times 200$).

bicellular microhairs, with sections *Parviglumia*, *Parvifolia*, *Monticola*, and *Verrucosa* within this group. Section *Lorea*, originally placed by Zuloaga (1987) in this second group, is more closely related to the first one, with a similar upper anthesis ornamentation and a basic chromosome number of $x = 10$, although spikelets are scattered on the panicles.

Section *Laxa* is distinct from the other sections of *Phanopyrum* as well as from sections of *Dichanthelium*, the other C_3 subgenus, in that all representatives possess translucent fusoid cells in the mesophyll. The presence of these fusoidlike cells in section *Laxa* has been reported by Killeen & Clark (1986), who suggest that their presence lends support to Brown's (1977) revised evolutionary scheme for the Paniceae based on leaf anatomy and photosynthetic pathway. Fusoid cells in species of section *Laxa* are illustrated for *P. hylaeicum*

(as *P. boliviense*) (Brown et al., 1985) and *P. pernambucense* (= *P. rivulare*) (Morgan & Brown, 1979; Wilson et al., 1983).

Fusoid cells are a distinguishing feature of the Bambusoideae and the peripheral bambusoid groups (Ellis, 1987) but have also been recorded in *Homo-lepis* (Watson et al., 1985) and *Streptostachys* (Clayton & Renvoize, 1986), in addition to section *Laxa* (Killeen & Clark, 1986). In all these non-bambusoid, panicoid taxa, the fusoid cavities are seen to be cellular in paradermal section, the cells being inflated and not constricted and girderlike as in most of the Bambusoideae. These structures therefore conform to the definition of fusoid cells and are not to be confused with lacunae, which are noncellular cavities in the mesophyll and which also occur in the Grumosum group of section *Laxa*.

Fusoid cells are, therefore, diagnostic for section *Laxa* within *Panicum* but are not restricted to

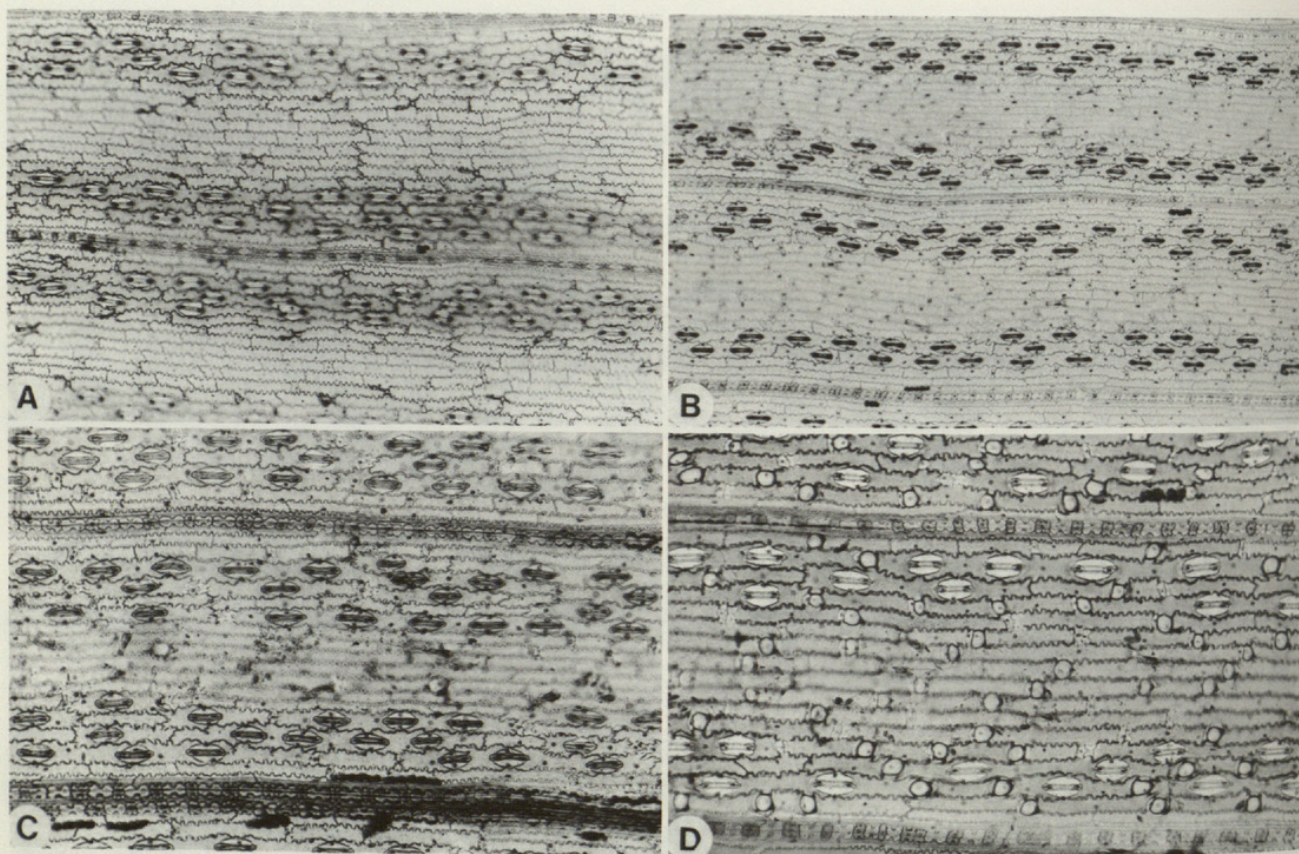


FIGURE 14. Abaxial epidermis of *Panicum pilosum*.—A. Typical zonation with wide intercostal zones; note differential staining of stomata files and central files of intercostal zones.—B. Narrow costal zones and clear stomatal bands.—C. Detail of dumbbell-shaped silica bodies and low triangular stomata; note microhairs and few hooks in center of intercostal zone.—D. Epidermis resembling *Homolepis glutinosa* with numerous small intercostal hooks (A, based on Zuloaga et al. 4513; B, Zuloaga 3289; C, Zuloaga 2303; D, Davidse 21866; A, B $\times 125$; C, D $\times 200$).

these taxa in the Paniceae, as they also occur in *Homolepis* and *Streptostachys*. The leaf anatomy of *Homolepis aturensis* (Kunth) Chase, *H. glutinosa* (Sw.) Zuloaga & Soderstrom, *H. isocalycia* (Meyer) Chase, and *H. villaricensis* (Mez) Zuloaga & Soderstrom, but not *H. longispicula* (Doell) Chase, closely resembles that of the Laxa group of section *Laxa* in most other respects as well. The only discernible anatomical difference between the Laxa group and *Homolepis* is that *Homolepis glutinosa*, in particular, often has numerous intercostal hooks, and macrohairs are sometimes present. These features, although rare, are not unknown in section *Laxa* and were observed on a specimen of *Panicum pilosum* (Davidse 21866), which is indistinguishable from most specimens of *H. glutinosa* on the basis of leaf anatomy.

Although the anatomy of section *Laxa* and *Homolepis* is similar, the exomorphological evidence does not suggest close affinities between these two taxa. In *Homolepis* spikelets are arranged in open, lax panicles; the lower glume reaches the same length and has the same nervation as the upper glume; the lower lemma has conspicuous bi- or tricellular secretory microhairs, which contain

a resin that is secreted when the spikelets mature; the upper anthecium in *Homolepis* is covered with dumbbell-shaped silica bodies, bicellular microhairs toward the apex, and it lacks simple, evenly distributed papillae; and the hilum is linear, reaching one half to the entire length of the caryopsis.

Fusoid cells are also present in the leaf blades of the Grumosum group of section *Laxa*, although in these species they may be absent, particularly near the margin. In some specimens this reduction is extensive, with most vascular bundles without associated fusoid cells (Fig. 12A, C, E). Specimens of *P. pernambucense* in which the fusoid cells are rare or absent closely resemble those of *P. rude* Nees, of section *Stolonifera*, and *P. mertensii* Roth, of section *Megista*, in transectional leaf anatomy. The epidermal structure is also similar, and this may indicate affinity. *Panicum rude* has a similar mesophyll to species of the Laxa group, the adaxial cells tending to a palisade-type of arrangement, with 6–8 cells in 3'vbs; metaxylem vessels are narrower than the obs cells as seen in cross section. *Panicum mertensii* has a similar mesophyll to that of *P. rude* and 6(–8) cells in 3'vbs. The keel is similar to that of *P. grumosum*. *Panicum rude*,

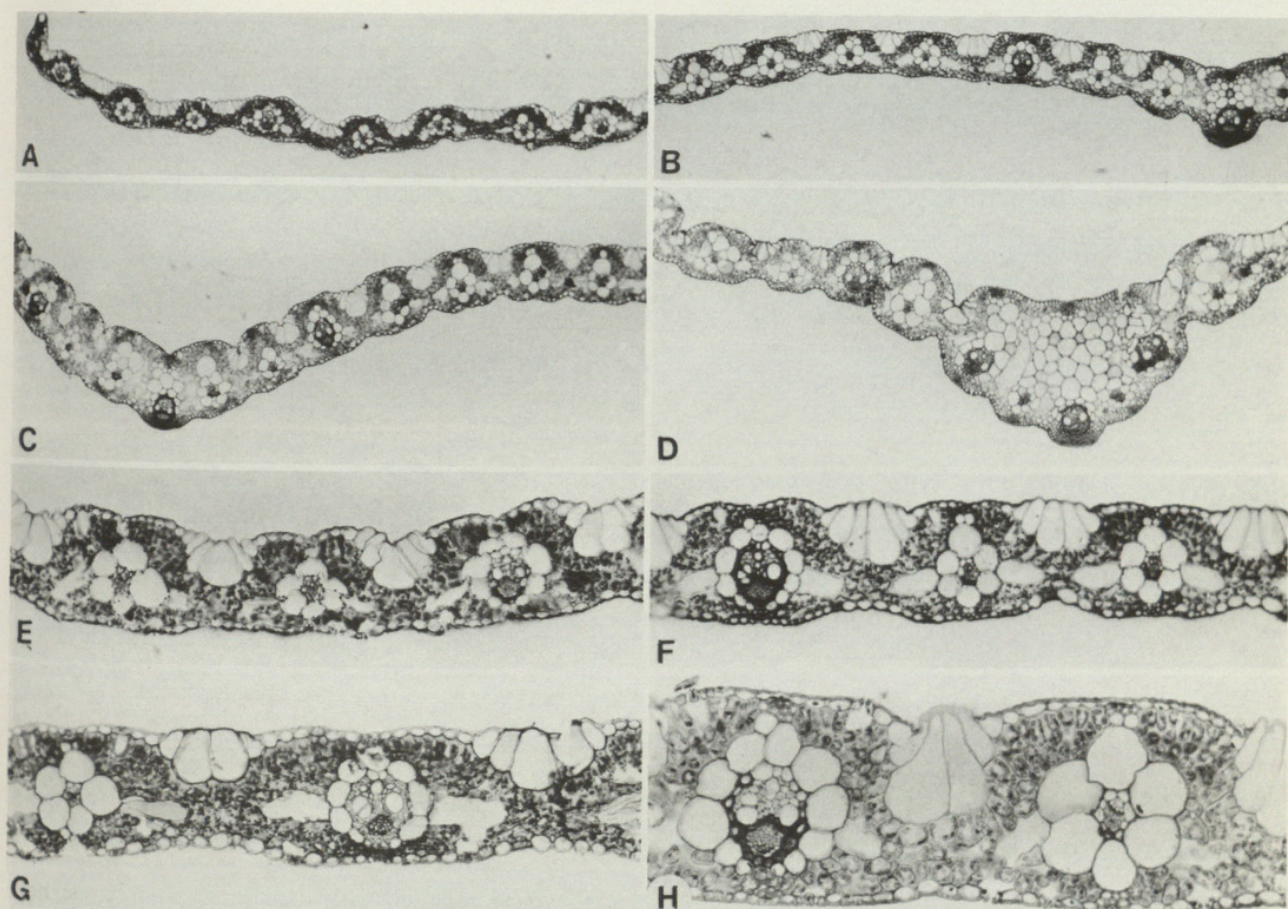


FIGURE 15. Transectional leaf anatomy of *Panicum polygonatum*.—A. Tapering leaf margin. B–D. Variation in structure of keel.—B. Keel with three vascular bundles; note that third-order bundles on either side of median bundle have additional colorless parenchyma cells associated with the outer bundle sheath.—C. Typical Laxa-type keel incorporating three vascular bundles.—D. Large keel of 3 first-order and 2 third-order vascular bundles and colorless parenchyma tissue.—E. Detail of parenchyma sheath cells with few, very small chloroplasts.—F. Conspicuous fusoid cavities present on either side of all vascular bundles.—G. Typical Laxa-type anatomy.—H. Detail of palisadelike adaxial chlorenchyma, fusoid cavities and parenchyma sheath cells devoid of chloroplasts (A, E, based on Zuloaga 3913; B, F, Davidse 30413; C, Davidse 26917; D, Zuloaga & Londoño 4238; G, Stevens 25879; H, Davidse 21844; A–D $\times 50$; E–G $\times 125$; H $\times 200$).

together with other species of section *Stolonifera*, shares with section *Laxa* a similar inflorescence type and basic chromosome number. Section *Stolonifera* is differentiated by its stipitate, smooth, and glabrous upper antherium and lower lemma with or without crateriform glands on the middle portion (Zuloaga & Sendulsky, 1988). Section *Megista* differs from section *Laxa* by the inflorescence type and spikelet outline and nervation, with branches of the inflorescence whorled and spikelets obovate, globose, with the upper glume and lower lemma 7–9-nerved (Zuloaga, 1987). Species of sections *Laxa*, *Stolonifera*, and *Megista* share a similar humid habitat, which may explain this superficial similarity in leaf anatomy.

Lacunae occur in the Grumosum group of section *Laxa* in the same location as fusoid cells in the mesophyll between the vascular bundles (Figs. 7D, 12D, F). Lacunae consist of a single lysigenous cavity between successive vascular bundles as seen

in transection (and not two inflated cells as in fusoids) and are not cellular. In *P. grumosum* and *P. pernambucense* these lacunae are often only associated with the keel and intergrade into normal fusoid cavities in the mid-lamina.

The Grumosum group resembles *Hymenachne* rather closely on the basis of the lacunae, as well as leaf anatomy in general, a trend that is not shared by the Laxa group of species. This relationship between *Hymenachne* and species of section *Laxa* was emphasized by Zuloaga & Soderstrom (1985), who suggested that species of *Laxa* could be congeneric with *Hymenachne*. These authors pointed out that *Hymenachne* differs from *Panicum* by having the upper palea free at its apex. Pohl & Lersten (1975) considered that the presence of aerenchyma is a good character to separate *Hymenachne* from related genera, such as *Sacciolepis* and *Panicum*. Species of *Laxa*, including the Grumosum group, have the upper

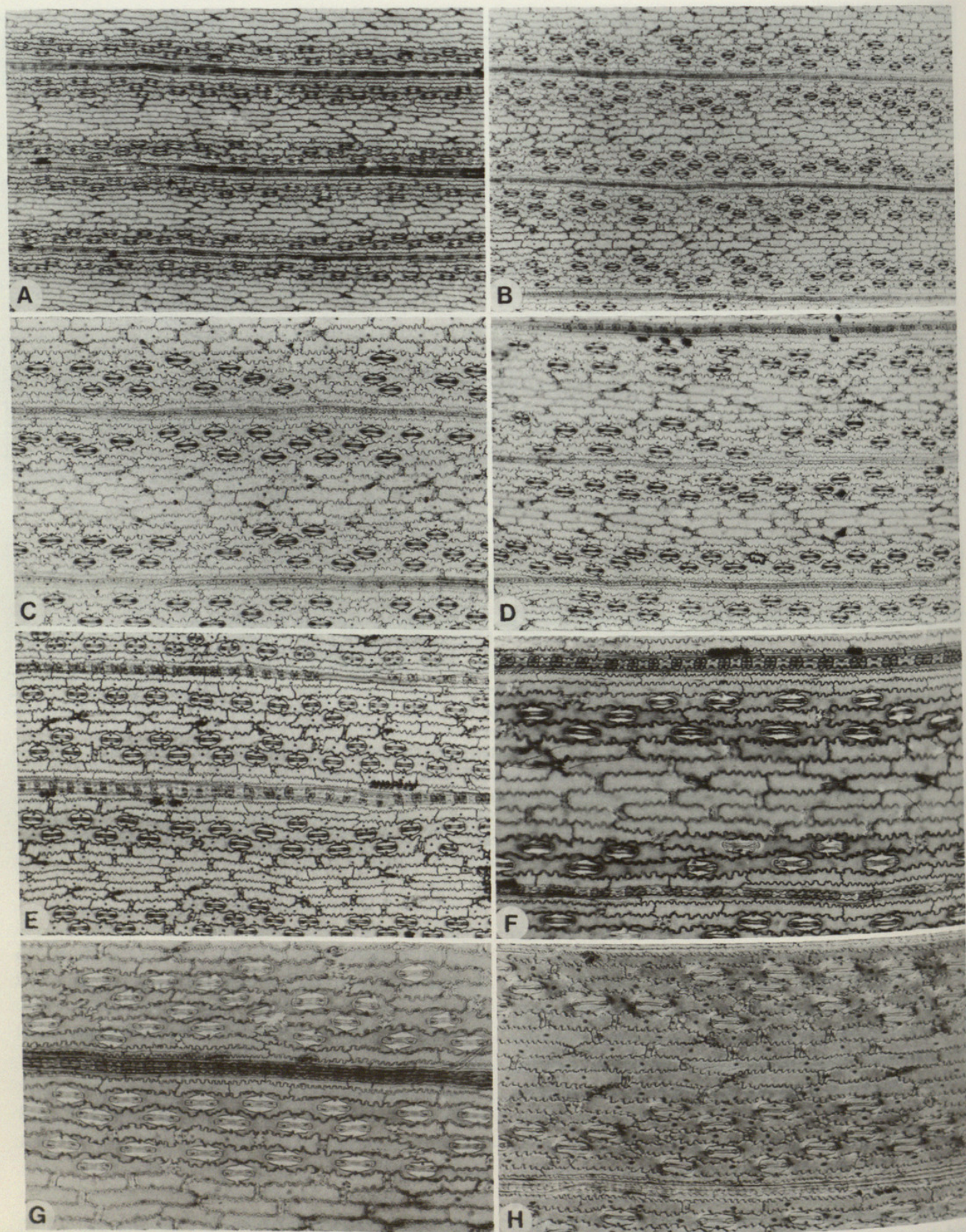


FIGURE 16. Typical Laxa-type abaxial epidermal structure of *Panicum polygonatum*. —A. Epidermal zonation with regularly spaced, narrow costal zones; note absence of stomata in center of intercostal zones. —B. Abaxial cellular pattern. —C. Costal zones 3 cell files wide, sinuous intercostal long cells and stomatal bands adjacent to the costal zones. —D. Typical Laxa-type abaxial epidermal structure. —E. Short dumbbell- to cross-shaped silica bodies alternating with darkly staining but similar shaped cork cells; stomata low dome-shaped; note that most epidermal cells have persistent nuclei. —F. Detail of dumbbell and nodular silica bodies and evaginations of subsidiary cells; note microhairs in center of intercostal zone. —G. Typical Laxa epidermal cellular structure and pattern; note differential staining of center of intercostal zone (without stomata) as compared to the stomatal files. —H. Interference contrast illumination showing nuclei in all long cells, short cells, and subsidiary cells; microhairs visible in center of intercostal zone (A, F, based on Davidse 30413; B, C, Zuloaga 4087; D, Zuloaga 3913; E, Stevens 25879; F, Davidse 21844; G, Davidse 26917; A, B $\times 80$; C-E $\times 125$; F-H $\times 200$).

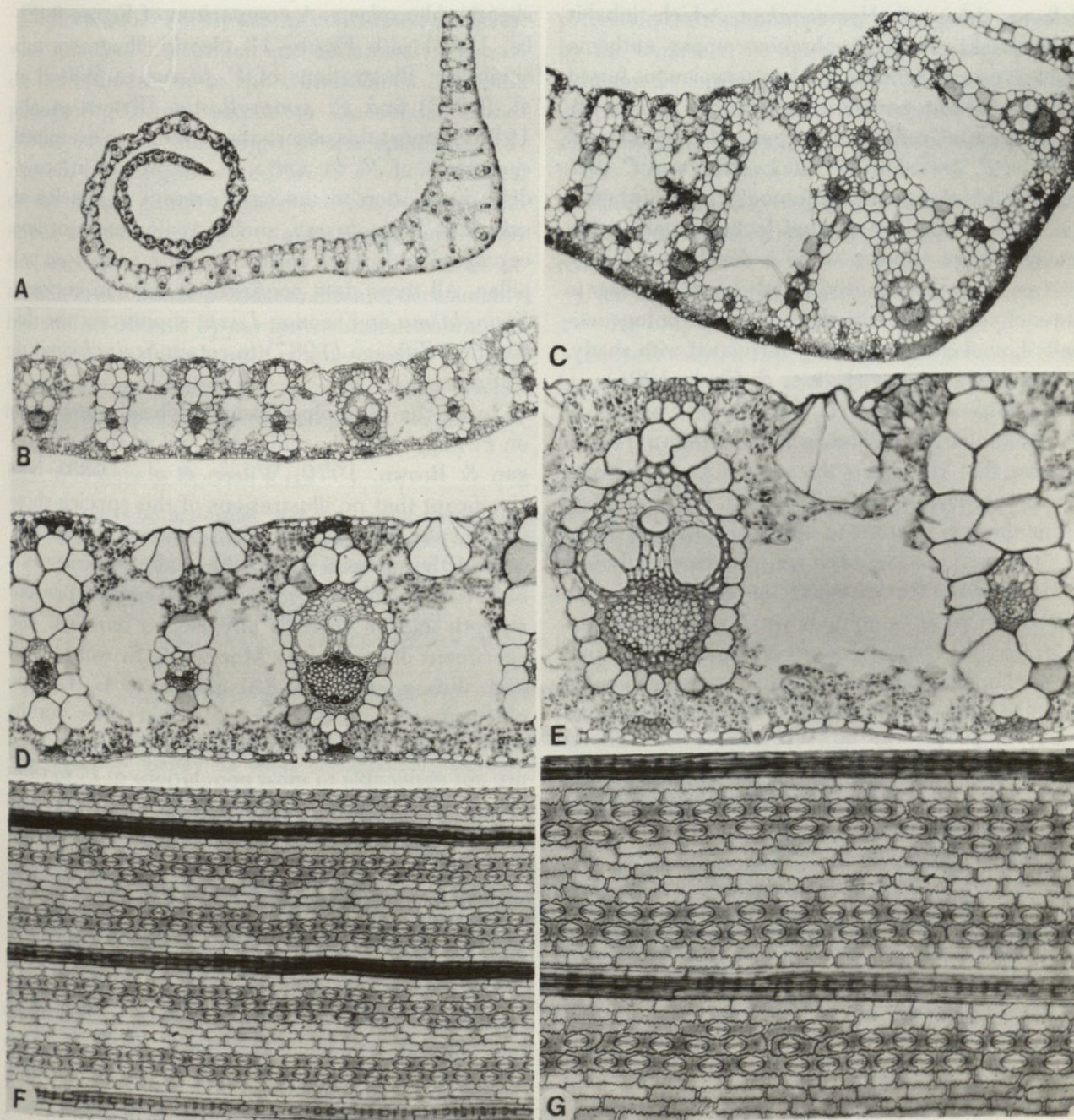


FIGURE 17. Atypical leaf blade anatomy of *Panicum grande*. A–E. Leaf anatomy as seen in transverse section. —A. Outline of blade as seen in cross section showing continuously decreasing thickness from median vascular bundle to margin. —B. Mid-lamina, showing arrangement of vascular bundles (3 third-order bundles between successive first-order bundles) and the presence of a single lacunal cavity in the mesophyll between all bundles. —C. Keel structure showing gradual integration into lamina, definite lacunae and the superposed vascular bundles located away from the abaxial surface. —D. Outer bundle sheath cells without chloroplasts and wide adaxial extensions present, particularly on the sheaths of smaller bundles. —E. Detail of bundles, sheaths, and mesophyll; note that the lacunae are not bounded by cell walls but are just cavities in the chlorenchyma. F, G. Abaxial epidermis. —F. Epidermal zonation with stomata clearly grouped into 2–3 files of cells on either side of 4–5 files of long cells located in the center of the intercostal zones. —G. Detail of relatively short long cells, particularly the interstomatal; all intercostal cells nucleate, although these rather indistinct (A–G, based on *Davidse 21867*; A $\times 125$; B, C $\times 50$; F $\times 80$; D, G $\times 125$; E $\times 200$).

palea covered at the apex by the lemma and lack stellate aerenchyma in culms, sheaths, and blades; they can also be separated by the presence of fusoid cells, although this can be controversial if reduction, or their replacement by lacunae has occurred. However, it could be argued that there has been a correlation with the presence of fusoid cells, upper

anthercia consistency, and habitat in these taxa. Species of drier habitats, usually found on edges of woods, have indurate upper anthercia with fewer silica bodies and papillae, are less robust, have conspicuous fusoid cells, and lack lacunae in transverse section of the blade. By contrast, species such as *P. grumosum* and *P. pernambucense*, as

well as those of *Hymenachne*, which inhabit streambanks, have membranous upper anthercia and leaves with lacunae and less conspicuous fusoid cells. There are, however, intermediate species between groups Grumosum and Laxa of section *Laxa*, such as *P. bresolinii*, *P. stagnatile*, and *P. leptachne*, which have membranous upper anthercia, conspicuous fusoid cells and lack lacunae in the leaves. There appears to be a developmental sequence from fusoid cavities through lacunae to aerenchyma: these structures may be ontogenetically homologous or merely correlated with shady, wet tropical habitats (Killeen & Clark, 1986).

Lacunae also occur in the keel and lamina of *P. gymnocarpon* Elliott, section *Phanopyrum*, a species that resembles the section *Laxa* in some respects of leaf anatomy. However, the keel differs from the one present in species of section *Laxa* by its superposed bundles and conspicuous lysigenous cavities. The midnerve has conspicuous pith aerenchyma, as is common in *Hymenachne amplexicaulis*. Taking into consideration the superposed bundles, pith aerenchyma, and conspicuous lacunae, this species seems to be more closely related to *P. grande* and *Hymenachne*. Alternatively, the presence of lacunae in these taxa may represent a convergence or similar adaptation to an aquatic habitat.

Subgenus *Steinchisma* is characterized by possessing an intermediate C_3 - C_4 photosynthetic pathway in which the anatomy is Kranz but with fewer centripetal chloroplasts in the outer bundle sheath cells than is usual. The vascular bundles are also farther apart than in normal Kranz sections, with 5 to 7 chlorenchyma cells between bundles (Zuloaga, 1987). Fusoid cells are absent in all species of this subgenus. Physiologically these species are intermediate between C_3 and typical C_4 plants (Brown & Brown, 1975; Morgan & Brown, 1979; Brown et al., 1985) but all have carbon isotope ratios in the C_3 range. Exomorphologically, species of *Steinchisma* can be distinguished by open panicles, with spikelets not unilaterally disposed, lower palea expanded at maturity, and upper anthercium covered by verrucose papillae.

Section *Laxa* generally has typical C_3 leaf anatomy with very few or no chloroplasts in the outer bundle sheath cells. However, in a few specimens of *P. laxum* specialized chloroplasts are present in these cells, and the anatomy tends toward the C_3 / C_4 intermediate type. Examples are Stevens 25354, Zuloaga et al. 4330 and, in particular, Brown 19 (Fig. 10F), which closely resembles *P. decipiens* Nees ex Trin. and *P. spathellosum* Doell, of subgenus *Steinchisma*, in the structure of the bundle

sheath chloroplasts. A comparison of Figure 8 (Ellis, 1988) with Figure 10 clearly illustrates this similarity. Illustrations of *P. laxum* in Wilson et al. (1983) and *P. spathellosum* (Brown et al., 1985) support this observation. We have examined specimens of *P. laxum* with characters intermediate in relation to the ones present in species of subgenus *Steinchisma*, such as palea more or less expanded and upper anthercium with verrucose papillae. All these data confirm the relation between *Steinchisma* and section *Laxa*, supporting the decision of Zuloaga (1987) to retain *Steinchisma* in *Panicum*.

In all the physiological and hybridization work on *P. laxum* that has included leaf anatomy (Morgan & Brown, 1979; Wilson et al., 1983), it is significant that no illustrations of this species show fusoid cells. This is in marked contrast to the findings of the present study where all 14 accessions of *P. laxum* had conspicuous fusoid cavities present on both sides of virtually all vascular bundles. The specimens illustrated by Morgan & Brown (1979) and Wilson et al. (1983) also have C_3 / C_4 -type chloroplasts, and it is possible that their results were based on incorrect identifications or at least are not applicable to most populations of *P. laxum*. However, *P. laxum* leaf blade material received from R. H. Brown did have fusoid as well as C_3 / C_4 -type anatomy (Fig. 10F), which appears to confirm their determination.

The decision to recognize two informal anatomical species groups in section *Laxa* for the purpose of the anatomical description appears to be supported by this discussion of character distributions and possible affinities. Thus, the *Laxa* group shows links to *Homolepis* on the basis of fusoid cells and such characters as keel structure, but not morphological characters, and even to *Steinchisma*, on the basis of the photosynthetic anatomy and the keel structure. Similarly, the Grumosum group tends toward *Hymenachne* and other taxa in subgenus *Phanopyrum* because of similar reduction of fusoid cells and presence of lacunae, C_3 anatomy, and the possession of wide keels with lacunae.

TAXONOMIC TREATMENT

Panicum* section *Laxa (A. Hitchc. & Chase) Pilger. Notizbl. Bot. Gart. Berlin-Dahlem 104(11): 243. 1931. *Panicum* Group *Laxa* A. Hitchc. & Chase, Contr. U.S. Natl. Herb. 15: 110. 1910 (invalid name); A. Hitchc. & Chase, Contr. U.S. Natl. Herb. 17(6): 201. 1915. TYPE SPECIES: *Panicum laxum* Sw.

Inflorescences with lax to contracted panicles, with spikelets $\pm$ crowded and unilaterally disposed on the branches or in short branchlets. *Spikelets* pilose or glabrous, elliptic to lanceolate. *Lower glume* $\frac{1}{3}$ to $\frac{3}{4}$ the length of the spikelet, 1–3-nerved. *Upper glume and lower lemma* subequal or the upper glume shorter and not covering the upper antherium. *Lower palea* conspicuous, with the same length of the lower lemma, to small or absent; lower flower present and male, occasionally bisexual, or absent. *Upper antherium* membranous to indurate, papillose, with simple papillae all over its surface or toward the apex and with prickly hairs at the apex of lemma and palea; silica bodies

present in the membranous antheria, palea covered by the lemma at its apex; upper flower bisexual, lodicules 2, conduplicate; stamens 3, styles 2, stigma plumose. *Blades* lanceolate to ovate-lanceolate. *Ligules* membranous, with or without short hairs at the distal portion.

Plants perennial, usually growing in wet places at edges of woods or margins of ponds, streams or rivers.

Non-Kranz anatomy, basic chromosome number $x = 10$.

Section with 12 American species, growing from Mexico to Argentina, and with one Asiatic species.

KEY TO SPECIES OF SECTION *LAXA*

- 1a. Spikelets on first-order branches, second-order branchlets absent, occasionally present toward the base of the inflorescence; main axis and branches usually long-pilose to scabrous.
 - 2a. Spikelets 1.9–3.2 mm long; ligules present.
 - 3a. Blades narrowed at base; Mexico 8. *P. longum*
 - 3b. Blades cordate at base; Brazil.
 - 4a. Branches of inflorescences glabrous; panicles 13–24 cm long; spikelets 1.9–2.4 mm long 3. *P. condensatum*
 - 4b. Branches of inflorescences papillose-pilose; panicles 25–40 cm long; spikelets 2.1–3.2 mm long 7. *P. leptachne*
 - 2b. Spikelets 1.3–1.5 mm long; ligules usually absent, occasionally present 10. *P. pilosum*
- 1b. Spikelets mainly on short second-order branchlets; main axis and branches scabrous to short-pilose, occasionally long-pilose.
 - 5a. Blades amplexicaulous, cordate.
 - 6a. Spikelets 1.4–1.7 mm long, lower palea present, the culms rigid; Mexico to Argentina 5. *P. hylaeicum*
 - 6b. Spikelets 2.1–2.3 mm long, lower palea absent, the culms herbaceous; Santa Catarina, Brazil 2. *P. bresolinii*
 - 5b. Blades not amplexicaulous, rounded to subcordate, occasionally cordate in specimens of *P. stagnatile*, *P. stevensianum*, and *P. polygonatum*.
 - 7a. Spikelets pointed at apex, without lower flower; lower palea absent to reduced.
 - 8a. Plants 0.15–0.50(–1) m tall; blades 4–17 cm long; panicles 8–20 cm long; spikelets 1.3–1.6 mm long 11. *P. polygonatum*
 - 8b. Plants 1–3 m tall; blades 17–60 cm long; panicles 20–40 cm long; spikelets 1.6–2.2(–3) mm long.
 - 9a. Spikelets (2.2–)2.5–3 mm long. Asia 1. *P. auritum*
 - 9b. Spikelets 1.6–2.2(–2.5) mm long; America.
 - 10a. Panicles slender, with spikelets not crowded on second-order branches; Mexico to Panama 12. *P. stagnatile*
 - 10b. Panicles congested, with spikelets crowded on second-order branches; north-eastern Brazil to Paraguay, Uruguay, and Argentina 9. *P. pernambucense*
 - 7b. Spikelets not pointed at apex, with a male lower flower, bisexual in specimens of *P. stevensianum*, occasionally absent; lower palea present.
 - 11a. Upper flower with two stamens, occasionally three; spikelets 1–1.7 mm long 6. *P. laxum*
 - 11b. Upper flower with three stamens; spikelets 1.9–3 mm long.
 - 12a. Culms spreading, decumbent at the base, 0.20–1 m tall; spikelets 1.9–2.6 mm long; lower flower bisexual, occasionally male or absent; West Indies and northern South America 13. *P. stevensianum*
 - 12b. Culms erect, 1.30–2 m tall; spikelets 2.3–3 mm long; lower flower male; eastern Brazil to Argentina 4. *P. grumosum*

1. ***Panicum auritum*** J. S. Presl ex Nees, *Agrost. Bras.*: 176. 1829. *Hymenachne aurita* (J. S. Presl ex Nees) Bal., *Cat. Indo-China Française*, Journ. de Bot. 4: 30. 1890. *Sacciolepis aurita* (J. S. Presl) A. Camus, in Lecomte, *Fl. Gen. Indo-Chine* 7: 459. 1922. TYPE: Phil-

ippines. “in Luzon insula” (holotype, PR? not seen; isotype, W).

Perennials, with erect culms 1.1–1.3 m tall, simple; internodes 5–17 cm long, terete, hollow, glabrous; nodes brownish, glabrous. *Sheaths* 4–10

cm long, shorter than the internodes, striate, glabrous, the margins membranous, ciliate or not at the upper portion. *Ligules* membranous, 0.4–1 mm long, lacinate or not, brownish. *Blades* lanceolate, 17–30 cm long, 0.8–1.6 cm wide, flat, cordate to subcordate at base, attenuate at the apex, short pilose on both surfaces to glabrous, the margins scabrous, the lower ones ciliate or not. *Inflorescence* exserted, peduncle 8–20 cm long, glabrous, smooth; panicles lax, 16–45 cm long, 3–15 cm wide; *main axis* wavy, scaberulous, pulvini pilose, with whitish hairs, to glabrous, first-order branches alternate, divergent, axis of the branches triquetrous, scabrous, spikelets short-pedicelled, appressed and paired on short second-order branchlets, pedicels triquetrous, scabrous. *Spikelets* narrowly ovate, (2.2–)2.5–3 mm long, 0.8–0.9 mm wide, glabrous, greenish and tinged with purple, upper glume and lower lemma subequal, acute, 5-nerved. *Lower glume* ovate, acute, 0.9–1.2 mm long, less than $\frac{1}{3}$ the length of the spikelet, 3-nerved, midnerve scaberulous toward the apex. *Lower palea* elliptic, small, 1–1.4 mm long, 0.3 mm wide, hyaline, glabrous, the borders ciliate or not; lower flower absent. *Upper antherium* narrowly elliptic, 1.9–2.6 mm long, 0.6–0.8 mm wide, acuminate, membranous at maturity, brownish, glabrous, with simple papillae and prickles toward the apex. *Caryopsis* ovate, 1–1.3 mm long, 0.5–0.8 mm wide, brownish; hilum oblong, embryo less than $\frac{1}{2}$ the length of the caryopsis.

Distribution and ecology. Found at edge of forest in humid places or in open, wet sites, from sea level to 1,200 m, in Southeast Asia, India, Sri Lanka, and southern China, in tropical Asia. It is a weed in plantations of rubber, tea, teak, and *Cinchona* (Lazarides, 1980).

Additional specimens examined. BORNEO. Sandakan and vicinity, *Ramos* 1597 (P). MALAYSIA. Singapur, Park of the broadcasting Station Jureng, *Sinclair* 9828 (M). PHILIPPINES. LUZON: Manila, *Merrill* 101 (M, P, SI*), 238 (W); Prov. of Sorsogon, Irosin, *Elmer* 14344 (P), 16398 (P, W); Prov. of Rizal, Morong, *Ramos* s.n. (W); San Francisco del Monte, *Loher* 1719 (M); Luzón central, *Loher* 1718 (P*). MINDANAO: Zamboanga district, Malangao, *Ramos & Edaño* s.n. (P). CEYLON [SRI LANKA]. Ratnapoora, *Thwaites* 3242 (P, W). THAILAND. Khw-Yau National Park, *Larsen et al.* 68 (W); Bangkok, *Kerr* 7044 (P); Bangkok, Wat Lum, *Kerr* 6952 (P). VIETNAM. Van-Yeu, *Balansa* 4914 (P, W); Hue, Annam, *Hitchcock* 19378 (P); Annam, Tourane, *Clemens* 4045 (P); Tupper, *Balansa* 1630 (P).

Panicum auritum, the only non-American species of the section, was included in *Laxa* by Pilger (1940). It is related to *P. laxum*, differing by

having spikelets pointed, with the lower palea reduced and lower flower absent.

2. *P. bresolinii* L. B. Smith & Wasshausen, *Bradea* 2(35): 245, fig. 2, A–D, 1978. TYPE: Brazil. Santa Catarina: Florianópolis, Morro Costa da Lagoa, 200 m, 19 Apr. 1967, *Klein & Bresolin* 7360 (holotype, US 2536896). Figures 2, 18.

Plants of indefinite duration, probably perennials, the *culms* decumbent, rooting and branching at the lower nodes, then becoming erect, ca. 90 cm tall, internodes compressed, hollow, glabrous, nodes dark, densely pilose with whitish hairs. Leaves with *sheaths* usually shorter than the internodes, short-hirsute with stiff papillose-pilose hairs, one margin membranous, the other short-ciliate. *Ligules* small, 0.5 mm long, membranous with a short fringe of hairs at the apex. *Blades* lanceolate, 15–26 cm long, 2.2–3 cm wide, flat, shortly pseudopetiolate, pseudopetiole brownish, ca. 0.2 cm long, pilose, blades cordate at the base, amplexicaulous, acuminate, short-pilose and with long hairs toward the base on the adaxial surface, the abaxial surface glabrous with anastomosed nerves. *Inflorescence* a lax panicle 26 cm long, 10–13 cm wide; *main axis* wavy, scabrous, spikelets unilaterally disposed on short secondary branchlets, paired or solitary, axis of the branches, branchlets and pedicels triquetrous, scabrous, axils of the branches pilose. *Spikelets* narrowly elliptic, 2.1–2.3 mm long, 0.5–0.6 mm wide, acute, glabrous, upper glume and lower lemma subequal. *Lower glume* ovate, 1.1–1.4 mm long, $\frac{1}{2}$ or more the length of the spikelet, 3-nerved, the nerves anastomosed toward the apex, the keel scabrous. *Upper glume* acute, 5-nerved, the nerves anastomosed, the keel scabrous. *Lower lemma* acute, 3-nerved, the keel scabrous. *Lower palea* absent; lower flower absent. *Upper antherium* lanceolate, 1.7–2 mm long, 0.5 mm wide, membranous at maturity, whitish, smooth, with simple papillae and conspicuous, retrorse prickles at the apex of lemma and palea, rachilla prolonged beyond the upper antherium as a short mucro. *Caryopsis* not seen.

Distribution and ecology. Known from Santa Catarina, Brazil, where it grows in swamp forest. In flower from March to April.

Additional specimens examined. BRAZIL. SANTA CATARINA: 5 km NE of Papanduva along highway BR-116 to Curitiba, 780 m, *Davidse et al.* 11056 (MO, SI*, SP).

Related to *P. hylaeicum* Mez, it differs by the spikelet size, 1.4–1.7 mm long in *P. hylaeicum*,



FIGURE 18. *Panicum bresolinii* (based on Davidse et al. 11056).—a. Habit, with panicle included.—b. Detail of ligule and lower portion of the blade.—c. Racemose branch.—d. Spikelet, lower glume view.—e. Spikelet, upper glume view.—f. Spikelet, lateral view.—g. Upper antherium, lemma view.—h. Upper antherium, palea view.—i. Upper portion of the upper lemma showing prickly hairs.

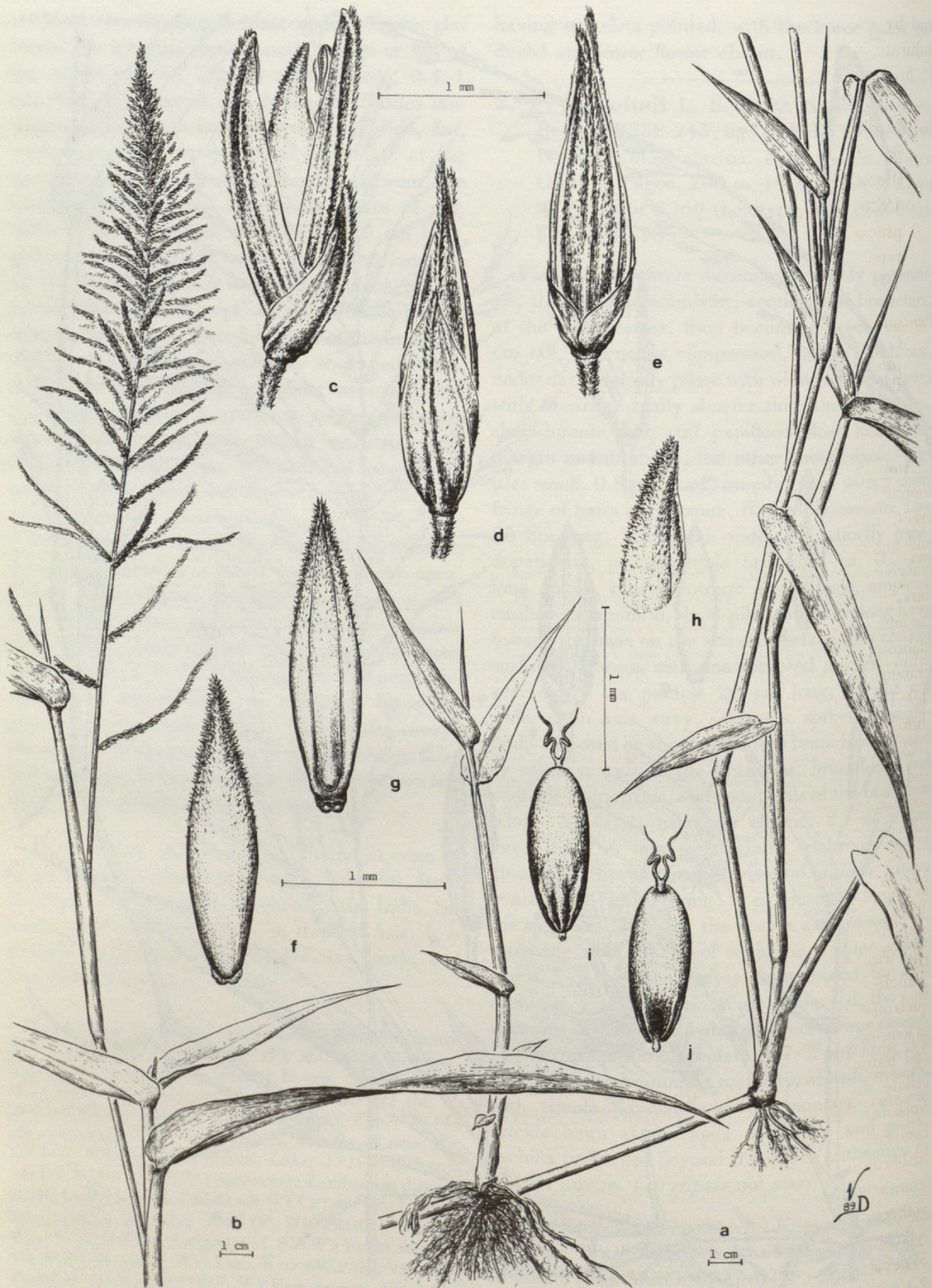


FIGURE 19. *Panicum condensatum* (a, based on Chase 8101; b-h, Chase 12127; i-j, Davidse 11494).—a. Habit.—b. Upper portion of a culm with panicle.—c. Spikelet, lateral view.—d. Spikelet, upper glume view.—e. Spikelet, upper glume view.—f. Upper anthecium, lemma view.—g. Upper anthecium, palea view.—h. Upper portion of the upper lemma showing prickly hairs.—i. Caryopsis, embryo view.—j. Caryopsis, hilum view.

and by the consistency of the upper antheridium, indurate in the latter species and membranous in *P. bresolinii*.

3. ***Panicum condensatum*** Bertol., Opusc. Sci. 3: 408. 1819. *Hymenachne condensata* (Bertol.) Chase, J. Wash. Acad. Sci. 13: 177. 1923. TYPE: Brazil. Rio de Janeiro: without precise locality, *Raddi s.n.* (holotype, PI; isotype, K, fragment, US 80598). Figures 5, 6, 19.

Panicum auriculatum Willd. var. *fasciculosum* Doell, in C. Martius, Fl. Bras. 2(2): 238. 1877. *Panicum januarium* Mez, in Engler, Bot. Jahrb. Syst. 56, Beibl. 125: 4. 1921. TYPE: Brazil. Rio de Janeiro: Rio de Janeiro, *Gaudichaud 288* (isotypes, P, W, fragment US 80476).

Annuals or perennials?, the culms decumbent, rooting and branching at the lower nodes, then erect, up to 100 cm tall, branching at the middle and upper nodes, internodes compressed, hollow, glabrous, (5-)10-23 cm long, nodes compressed, dark, glabrous. Leaves with sheaths shorter than the internodes, 4-10 cm long, with tessellate nerves, glabrous, the margins membranous. Ligules membranous at the base and shortly ciliate at the apex, 0.9-1.3 mm long; collar brownish, glabrous to shortly ciliate. Blades lanceolate, 7-17 cm long, 1-2 cm wide, flat, acuminate, cordate at the base and amplexicaulous, shortly pseudopetiolate, pseudopetiole brownish, short-pilose and sparingly papillose-pilose, blades glabrous, the margins scabrous, ciliate at the lower margins. Inflorescence 13-24 cm long, 1.5-6 cm wide, with approximately 50 unilateral, racemose branches, the branches verticillate, subopposite to alternate; main axis wavy, scabrous, lower branches 3-4 cm long, branches and pedicels scabrous, the branches triquetrous, flattened on one side, axils of the branches long-pilose, branchlets absent, the spikelets secund and paired, one subsessile, the other short-pedicellate on the branches, alternating in 2 rows. Spikelets lanceolate, brownish, somewhat laterally compressed, 1.9-2.4 mm long, 0.4-0.5 mm wide, scaberulous, acuminate, upper glume and lower lemma subequal, exceeding in length the upper antheridium. Lower glume ½ to ¾ the length of the spikelet, 1-1.6 mm long, ovate, acuminate, 3(-5)-nerved, the keel scabrous. Upper glume 1.8-2.1 mm long, 5-nerved, the keel scabrous. Lower lemma 1.7-2.1 mm long, 5-nerved, keel scabrous. Lower palea absent; lower flower absent. Upper antheridium lanceolate, 1.5-1.8 mm long, 0.5 mm wide, membranous at maturity, whitish, scabrous at the apex of lemma and palea and with simple

papillae all over its surface, the lemma 5-nerved. Caryopsis lanceolate, brownish, hilum elliptic, embryo ⅓ or less the length of the caryopsis.

Distribution and ecology. Brazil, from Bahia to Minas Gerais, Rio de Janeiro, São Paulo, and Santa Catarina, in wet places on margins of streams or in marshy areas, up to 500 m elevation. In flower from November to April.

Additional specimens examined. BRAZIL. BAHIA: Cachoeira, *Chase 8101* (US, W). MINAS GERAIS: ca. 1 km S of São Pedro do Suacui along highway MG-3, *Davidse et al. 11494* (MO, SI, US). RIO DE JANEIRO: Rio de Janeiro, Recreio dos Bandeirantes, *Casari 552* (MO); Furnas de Agassiz, *Chase 12127* (US*); Tijuca, *Schott 4845* (US, W); Jacarepagua, *Chase 8414, 8418* (US*); without locality, *Kuhlmann s.n.* (US). SANTA CATARINA: Pedra de Amolar, *Condim 1* (US); Florianópolis, *Klein & Bresolin 9966* (US). SAO PAULO: Pindorama, *Viegas s.n.* (US); without state and locality, *Riedel s.n.* (W).

Pohl & Lersten (1975) indicated that *Panicum condensatum* (as *Hymenachne condensata*) did not have aerenchyma in culms as is typical in other species of the genus *Hymenachne*. *Panicum condensatum* also has the apex of the palea covered by the lemma, and fusoid cells are present in transverse section of the blades. This species has spikelets disposed in first-order branches, as in *P. pilosum* and related species. Its habit is similar to that of *P. grumosum* and *P. pernambucense*.

4. ***Panicum grumosum*** Nees, Agrost. Bras.: 182. 1829. *Panicum rivulare* var. *grumosum* (Nees) Hackel, Repert Spec. Nov. Regni Veg. 6: 343. 1909. SYNTYPES: "Habitat in Monte Video et in confinibus Regni Paraguayani (*Sellow*)" (syntype of "Uruguay, *Sellow*," B; isosyntypes P, W, fragments BAA, US). Figures 3, 7.

Panicum pycnanthum Steudel, Syn. Pl. Glumac. 1: 70. 1853. TYPE: Uruguay. Montevideo: Montevideo, *Deloche s.n.* (holotype, P, fragments BAA, US 2903523).

Panicum pavonii Mez, Bot. Jahrb. Syst. 56, Beibl. 125: 5. 1921. TYPE: Peru. Without locality, *Pavon s.n.* (holotype, B, fragments, BAA, US; isotype, G).

Panicum knuthii Herter, Revista Sudamer. Bot. 6: 137, fig. 6, 1940. TYPE: Uruguay. Minas: Corrales, Feb. 1924, *Schroeder s.n.* (herb. Osten 16731) (fragment of the type, BAA).

Panicum schroederi Herter, Revista Sudamer. Bot. 6: 137, 138, fig. 7. 1940. TYPE: Uruguay. Barra del Santa Lucía, Jan. 1920, *Schroeder s.n.* (herb. Osten 15402). (fragment of the type, US 2903525).

Strongly rhizomatous perennials, culms erect, 1.3-2 m tall, freely branching at the upper nodes, internodes cylindric, hollow, glabrous, 8-30 cm long, nodes glabrous, purplish. Sheaths glabrous,

shorter than the internodes, 9–20 cm long, the margins membranous, collar glabrous, brownish. *Ligules* membranous, 1.2–2 mm long. *Blades* lanceolate, 14–44 cm long, 0.6–3 cm wide, subcor-date, glabrous, the margins scaberulous, midnerve conspicuous. *Inflorescence* a terminal panicle, 15–45 cm long, 3.5–13 cm wide; *main axis* scabrous, branches ascending, alternate or opposite, axis of the branches and pedicels scabrous, spikelets paired and densely crowded on short secondary branch-lets, pedicels short. *Spikelets* long-elliptic, 2.3–3 mm long, 0.5–1 mm wide, glabrous, greenish or tinged with purple. *Lower glume* 1–1.7 mm long, $\frac{1}{2}$ to $\frac{3}{4}$ the length of the spikelet, 3-nerved, the nerves anastomosed toward the apex, the keel sca-brous. *Upper glume* 1.8–2.5 mm long, slightly shorter than the lower lemma, 5-nerved, the keel finely scabrous toward the apex. *Lower lemma* 5-nerved, 2.2–2.7 mm long. *Lower palea* 2.2–2.6 mm long, 0.5–0.6 mm wide, membranous, ciliolate on the margins; lower flower male, anthers 3. *Upper antherium* long-elliptic, 2–2.6 mm long, 0.5–0.7 mm wide, membranous, scabrous toward the apex and with silica bodies and simple papillae; lemma 5-nerved. *Caryopsis* obovate, brownish, 1.1–1.3 mm long, 0.5–0.6 mm wide, plano-con-convex; hilum oblong, embryo approximately $\frac{1}{2}$ the length of the caryopsis.

Distribution and ecology. South America, from Brazil and Paraguay to Uruguay and Argen-tina. It is common at margins of rivers and streams, in inundated areas. In flower between October and January.

Selected specimens examined. ARGENTINA. BUENOS AIRES: Isla Santiago, *Cabrera* 3422 (F, NY, SI, SP, US); Punta Lara, *Zuloaga* 3357 (SI), 3073 (SI*). DISTRITO FEDERAL: Palermo, *Burkart* 238 (BAA). CORRIENTES: Isla Apipé Grande, Puerto Mora, *Krapovickas et al.* 24388 (CTES, SI). CHACO: Colonia Benítez, *Schulz* 1796 (BAB). ENTRE RIOS: Salto Grande, Casa de Piedra, *Renvoize et al.* 2975 (K, MO, NY, SI); Concepción del Uruguay, Arroyo La China, *Zuloaga et al.* 3087 (MO, SI*). MI-SIONES: Posadas, *Ekman* 622 (CORD, US). SANTA FE: Villa Guillermina, *Meyer* 3322 (BAA). BRAZIL. MINAS GERAIS: Caldas, *Regnell III*-1361 (P, US). PARANA: Rio Jordão, Aguas Sta. Clara, *Hatschbach* 10549 (US). RIO GRANDE DO SUL: Pelotas, *Sacco* 212 (NY, RB, US); 20 km from Porto Alegre, grown at Athens, Georgia, *Brown & Barreto* 107 (P). SANTA CATARINA: Mun. Caçador, 52 km west of Caçador near the eastern edge of the campos of Palmas, 1,000–1,200 m, *Smith & Reitz* 9132 (NY, US); Lages, wet ground, bank of stream and margin of banhado, *Fachinal, Swallen* 8126 (US). PARAGUAY. AMAMBAY: Sierra de Amambay, *Hassler* 10155 (G, K, LIL, NY, P, W). CAAZAPA: Tavai, Castor-Cué, 26°10'S, 55°20'W, *Mereles* 2188 (MO). CENTRAL: Capiatá, *Schini-ni* 4960 (G, MO, SI). CORDILLERA: Cordillera de Altos, *Fiebrig* 421 (F). GUAIRA: prope Villa Rica, in paludosis,

Hassler 8773a (G). PARAGUARI: Parque Nacional Ybicú, gallery forest along Arroyo Minas, on trail to Salto Guara-ní, 26°03'S, 56°50'W, *Zardini* 7474 (MO). PRESIDENTE HAYES: S de Villa Hayes, *Rosengurt* 5627 (BAA, US); Estancia de la "Copacar," El Milagro, *Ramírez* 223 (US). URUGUAY. CANELONES: Río Santa Lucía, Estancia Paso Cuello, *Gallinal et al.* PE-5571 (MO, P, US). COLONIA: bank of Arroyo de San Juan, *Bartlett* 21266 (NY). RIO NEGRO: San Javier, *Chebataroff s.n.* (LIL 57356). SAN JOSE: Río Santa Lucía, *Rosengurt* B-4956 (P, SI). TACUAREMBO: Arazatí, *Rosengurt* 1676 (US).

This species is related to *P. pernambucense*, from which it differs by being commonly smaller in overall size (2–3 m tall in *P. pernambucense*) and by having bigger spikelets (1.7–2.2(–2.5) mm long in *P. pernambucense*) with a conspicuous lower palea and lower flower. *Panicum grumosum* is common in Uruguay and northeastern Argentina, but becomes less common north of these areas. It ranges as far north as Minas Gerais, Brazil, but becomes quite rare. It is difficult to separate the two species in Paraguay.

There is a gradation in the pilosity of leaves and panicles. Some specimens have densely papillose-pilose sheaths covered with rigid, caducous hairs and inflorescences with papillose-pilose rachis and branches; others are glabrous.

Panicum pavonii was described by Mez on the basis of material presumably collected in Peru. We considered this to be an error on the label of the type specimen since the known geographical range of *P. grumosum* does not come close to Peru.

Three-flowered spikelets were found in *Quarín et al.* 2745, *Hunziker* 4614 (also with geminate spikelets), and *Millán* 568.

5. *Panicum hylaeicum* Mez, Notizbl. Bot. Gart. Berlin-Dahlem 7: 75. 1917. *Panicum laxum* Sw. var. *pubescens* Doell, in C. Martius, Fl. Bras. 2(2): 213. 1877, pro parte. TYPE: Brazil. Pará: in vicinibus Santarem, Aug 1850, *Spruce* 1061² (*Panicum* 26) (holotype, M, fragment, US; isotypes, K, P). Figures 3, 8, 20.

Panicum minutiflorum Doell, in C. Martius, Fl. Bras. 2(2): 253. 1877. Not *Panicum minutiflorum* Ras-pail, 1825. LECTOTYPE: Brazil. Pará: prope Santar-em, *Spruce* 720 (lectotype, here designated, P; iso-lectotype, K, fragment, US).

Panicum potamium Trin. var. *pubescens* Doell, in C. Martius, Fl. Bras. 2(2): 214. 1877, pro parte. TYPE: Brazil. "Ad Tocantins fluvium inter Porto Imperial et Funil," *Burchell* 8795 (holotype, K; isotype, W).

Panicum laxum Sw. var. *amplissimum* Hackel, Repert. Spec. Nov. Regni Veg. 6: 343. 1909. TYPE: Para-guay. "in reg. curs. inf. fl. Pilcomayo," *Rojas* 276 (holotype, W; isotypes, G, K, P, US, W; fragment of the type, BAA, US).

Panicum schiedeianum Mez, Bot. Jahrb. Syst. 56, Beibl.



FIGURE 20. *Panicum hylaeicum* (a, based on Guaglianone et al. 728; e-g, Spruce 26).—a. Habit.—e. Hispid spikelet, lateral view.—f. Hispid spikelet, upper glume view.—g. Hispid spikelet, lower glume view.—*Panicum polygonatum* (based on Buchtien 2501).—b. Spikelet, lateral view.—c. Spikelet, lower glume view.—d. Spikelet, upper glume view.—h. Upper antherium, palea view.—i. Caryopsis, hilum and embryo view.

125: 4. 1921. Not *Panicum schiedeianum* Trin. ex Beal, 1886. LECTOTYPE, here designated: Mexico. Without locality, *Schiede* 29 (lectotype, B; isolecotype, P, fragment and photo, US 2830931).

Panicum schaffneri Mez, Bot. Jahrb. Syst. 56, Beibl. 125: 4. 1921. Not *Panicum schaffneri* Kuntze, 1898. TYPE: Mexico. Without locality, *Schaffner* 156 (holotype, B, fragment, US 2830930).

Panicum doellii Mez, Bot. Jahrb. Syst. 56, Beibl. 125: 6. 1921. SYNTYPES: Brazil. Pará: Santarem, *Spruce* 347 (*Panicum* n. 18). Paraguay. Central: Asunción, Apr. 1874, *Balansa* 49; in regione cursus inferiores fluminis Pilcomayo, *Fiebrig* 4689; without locality, *Rojas* 276 (isosyntype of *Spruce* 347 (*Panicum* n. 18), P, fragments, BAA, US; isosyntype of *Balansa* 49, G, K, P, US; isosyntype of *Rojas* 276, G, P, US, fragments, BAA, US; fragment of the syntype *Fiebrig* 4689, US).

Panicum guianense A. Hitchc., Contr. U.S. Natl. Herb. 22: 487, f. 83. 1922. TYPE: Guyana. Rockstone, 1 Jan. 1920, *Hitchcock* 17313 (holotype, US 1038517; isotypes, BAA, F, G, K, NY, W).

Plants perennial, robust, 1–2(–3) m tall, culms cylindric, rooting and branching or not at the lower nodes, then erect, sprawling and clambering, many-noded, internodes 4–20 cm long, rigid, hollow, glabrous, tinged with purple, nodes glabrous, purplish. Leaves with sheaths equal to or shorter than the internodes, 3.5–10 cm long, stramineous to purplish, pilose to glabrescent, with papillose-pilose, caducous hairs on the upper margins, collar pilose, glabrous. Ligules membranous, lacinate to short pilose on the upper portion, 0.3–0.7 mm long. Blades ovate-lanceolate, flat, 7–26 cm long, 1–3 cm wide, cordate, clasping at base, shortly pseudopetiolate, attenuate at the apex, densely pilose to glabrescent on both surfaces, the lower margins long-ciliate, otherwise scabrous, the nerves tessellate. Inflorescence a terminal, diffuse to contracted panicle 10–32 cm long, 4.5–17.5 cm wide, included or not at the upper sheaths; main axis and branches and pedicels scabrous, pulvini short-pilose, first-order branches alternate to opposite, spreading, spikelets unilateral on short, second- or third-order appressed branches, paired on short pedicels 0.5–1.3 mm long. Spikelets narrowly elliptic, 1.4–1.7 mm long, 0.4–0.6 mm wide, greenish to purplish, hispid with caducous hairs, to glabrous. Lower glume 0.7–1 mm long, less than ½ the length of the spikelet, ovate, acute, amplexicaulous, 3-nerved, the keel scabrous on the upper portion. Upper glume 1–1.7 mm long, covering or not the upper antherium, 5-nerved, blunt. Lower lemma 5-nerved, acute. Lower palea elliptic, 0.9–1.3 mm long, 0.3–0.5 mm wide, membranous, small in some specimens; lower flower male or absent. Upper antherium elliptic, 1–1.4 mm long, 0.4–0.6 mm wide, scabrous at the apex,

otherwise smooth, glabrous, indurate. Caryopsis elliptic, 0.9 mm long, 0.5 mm wide, hilum punctiform, embryo less than half the length of the caryopsis.

Distribution and ecology. Mexico, Mesoamerica, Cuba, Dominica, and South America, from Colombia to Argentina. It is common at margins of rivers and swamps or at edge of forest in humid soils, usually scandent over the vegetation, from sea level to 1,500 m.

Selected specimens examined. ARGENTINA. CHACO: Puerto Vilelas, *Schulz* 3379 (BAA, CTES, SI). CORRIENTES: Ituzaingó, Puesto de Prefectura, 42 km al E de Ituzaingó, *Zuloaga et al.* 624, 2293* (MO, SI). FORMOSA: Estancia Bouvier, *Guaglianone et al.* 728 (SI). MISIONES: Santa Ana, camino al balneario Municipal, *Zuloaga et al.* 2218 (MO, SI*). BELIZE: Temash River, *Schipp* 1372 (G, US). BOLIVIA. BENI: Río Yata, 30 km W de Guayaquerín, camino a Riberalta, *Krapovickas & Schinini* 35086 (CTES, K). BRAZIL. ALAGOAS: without locality, *Gardner* 1435 (K). AMAPA: Igarapé do Lago, *Black & Froes* 51-12342 (IAN). AMAZONAS: Rio Solimoes, *Froes* 20549 (IAN, US). BAHIA: Rio Itapicuru, *Pinto* 687 (US). GOIAS: Santa Rita do Paranaíba, *Chase* 11622 (US). MARANHÃO: Caxias to Barra do Corda, *Swallen* 3595 (IAN, US). MATO GROSSO: bank of Rio S. Lourenço, Barça S. Lourenço, *Chase* 11966 (US). MATO GROSSO DO SUL: Porto Esperança, *Chase* 11073, 11099 (US). MINAS GERAIS: Capinópolis, Cachoeira Dourada, *Macedo* 4545 (US). PARA: Santarem, *Swallen* 3311 (US), *Spruce* 347 (P, US), 436 (US). PARANA: mouth of Rio Ivaí, *Lindeman & Haas* 4322 (K, NY, US). RONDONIA: Forte da Príncipe da Beira, *Rodriguez* 3490 (US). RORAIMA: Rio Mucajá, Colonia Fernando Costa, *Black & Magalhaes* 51-12877 (IAN, US). SÃO PAULO: Porto Pulador on the Rio Moji-Guaçu, 8.9 km NNE of RR Station at Santa Eudóxia, *Eiten & Campos* 3487 (MO, US). COLOMBIA. CASANARE: Río Casanare, barranco de Atahuarpa, *Cuatrecasas & García Barriga* 4238 (COL), 4284 (COL, US). META: Río Meta, Orocué, *Cuatrecasas & García-Barriga* 4432 (COL, US). COSTA RICA. ALAJUELA: Cariblanco, *Pohl & Davidse* 11024 (US). CUBA. ORIENTE: Sierra de Nipe, Río Pilabo, *Ekman* 15105 (G). PINAR DEL RIO: Baños de San Vicente, *Britton et al.* 7452 (US). SANTA CLARA: banks of Banao River, *León* 5460 (US). DOMINICAN REPUBLIC. Santo Domingo, Cuenca, *Ekman* 13305 (G). FRENCH GUIANA. Haut Itany, *Hook s.n.* (NY). GUATEMALA. ALTA VERAPAZ: Cobán, *von Tuerckheim* 1254 (US). ESCUINTLA: South of Río Burrión, northeast of Escuintla, 700 m, *Standley* 89612 (US). HUEHUETENANGO: entre Ixcán y Río Ixcán, Sierra de los Cuchumatanes, *Steyermark* 49333 (F). IZABAL: Chickasaw Farm of the United Fruit Company, about 15 km north of Quirguá, *Standley* 24623 (US). SANTA ROSA: plains north of Los Cerritos, on road between Chiquimulilla and El Ahumado, *Standley* 79566 (US). SOLOLA: around lake at Finca Mocá, slopes of Volcán Atitlán, 1,000 m, *Steyermark* 47887 (US). GUYANA. Crab Fall, Cuyuni River, *Tutin* G-69 (K, US). HONDURAS. COMAYAGUA: below Barranco Trincheras, *Williams & Williams* 18435 (US). COPAN: entre Acrópolis y Jaguarpete, *Molina* 26236 (F, US). MEXICO. CHIAPAS: 13 km south of Ocozocoautla, *Breedlove & Davidse* 54040 (US). SAN LUIS POTOSI: in a tropical forest along Mexico Highway

55 to Xilitla, *Sohns* 1449 (US). VERACRUZ: Córdoba, *Hitchcock* 6435 (BAA, LIL, P, US). PARAGUAY. AMAMBAY: Pedro Juan Caballero, *Fiebrig* 4760 (M). CONCEPCION: zwischen Río Apa und Río Aquidabán, Villa Sana, *Fiebrig* 4689 (G, K, US). NEEMBUCU: Alberdi, *Reales* 231 (LIL). PRESIDENTE HAYES: Colonia Inglesa, frente a Trinidad, *Sparre & Vervoorst* 898a (LIL). PERU. LORETO: Río Mamón near Río Nanay, *Croat* 19893 (MO). VENEZUELA. AMAZONAS: Dpto. Atures, terraplén y área de rebalse del Río Orinoco, en el muelle de Puerto Ayacucho, *Guánchez* 2357 (MO, VEN). APURE: Hato San Juan del Río Claro, a orillas del Río Claro, al S de Cunaviche, 1 Feb. 1956, *Borsotti s.n.* (VEN). BARINAS: en cercanías de Ciudad Nutrias, *Zuloaga et al.* 4315 (MO, SI*, VEN). GUARICO: at intersection of Río Orituco and road from Calabozo to Cazorla, along river bank, wet soil, semi-erect in shrubs, up to 2 m tall, *Davidse* 3716 (K, MO, VEN). ZULIA: Distrito Perijá, 14 airline km NE of the intersection of the Río Aricuaísa and the Maracaibo-La Fria Hwy, 9°26'N, 72°29'W, *Davidse et al.* 18411 (MO, NY, VEN).

Panicum hylaeicum is distinguished from *P. laxum* mainly by its cordate and amplexicaulous leaves, and the culms usually rigid. It differs from *P. polygonatum* also by its amplexicaulous leaves, and by having spikelets not pointed, with the lower palea well developed and a lower flower staminate.

Zuloaga (1981) considered this species to be a synonym of *P. boliviense* Hackel. A detailed study revealed that *P. boliviense* is a synonym of *P. polygonatum*, representing only a robust form of the latter species. There is in *P. hylaeicum* a gradation in the pilosity of the spikelet, from some specimens with spikelets densely pilose to others with spikelets completely glabrous.

6. *Panicum laxum* Sw., Prodr.: 23. 1788. TYPE: Jamaica. Without locality, *Swartz s.n.* (holotype, S, photo of the type, K; isotype, M). Figures 4, 9–11.

Panicum agrostidiforme Lam., Tabl. Encycl. 1: 172. 1791. TYPE: "Ex Amer. merid. Communic. A. D. Richard" (holotype, P, fragments, BAA, US 80537).

Panicum tenuiculmum G. Meyer, Prim. Fl. Esseq.: 58. 1818. TYPE: Guyana (holotype, LE, fragment, US).

Panicum leptomerum J. S. Presl, Reliq. Haenk. 1: 311. 1830. TYPE: Without locality, *Haenke s.n.* (holotype, PR, fragment, US 2903500).

Panicum diandrum Kunth, Revis. Gramin. 2: 393, pl. 110, 1831. TYPE: "Crescit in insula Guadelupae inque Brasilia" (type, B not seen, photo and fragment, US 80660).

Panicum ramuliflorum Hochst. ex Steudel, Syn. Pl. Glumac. 1: 65. 1853. TYPE: Surinam. Without locality, *Kappler* 1523 (holotype, P, fragment of the type, US 2830942; isotypes, G, M, W).

Panicum psilanthum Steudel, Syn. Pl. Glumac. 1: 66. 1853. TYPE: Uruguay. Without locality, *Deloche s.n.* (not seen).

Panicum laxum Sw. var. *pubescens* Doell, in C. Martius, Fl. Bras. 2(2): 213. 1877, pro parte. SYNTYPES: Brazil. Goiás: Porto Real, *Burchell* 8705. Pernam-

buco: Without locality, *Gardner* 1182. Without state and locality, *Riedel* 943, *Burchell* 3456 (syntype of *Burchell* 8705, W, fragment, US; of *Gardner* 1182, G, K, P, W; of *Riedel* 943, G, K, W; of *Burchell* 3456, W).

Panicum pilosum Sw. var. *epilosum* Fourn., Mexic. Pl. 2: 24. 1886.

Panicum luticola A. Hitchc., Contr. U.S. Natl. Herb. 22: 485, fig. 82, 1922. TYPE: Guyana. Mazaruni River, Penal Settlement, 5 Dec. 1920, *Hitchcock* 17313 (holotype, US; isotypes, F, G, K, NY, P, US, W).

Panicum hondurensis Swallen, Contr. U.S. Natl. Herb. 29: 270. 1949. TYPE: Honduras. Valle: San Lorenzo, 10 Sep. 1945, *Rodríguez* 3323 (holotype, US 1869140; isotypes, MO, US 1869141).

Panicum caroniense Lucas, Bol. Soc. Venez. Ci. Nat. 15: 26, f. 12. 1953. TYPE: Venezuela. Bolívar: cercanías de Santa Elena, 28 Mar. 1946, *Tamayo* 3209 (holotype, VEN; isotype, US 80558).

Panicum laxum Sw. var. *vestitum* L. B. Smith & Wasshausen, Bradea 2(35): 245. 1978. TYPE: Brazil. Santa Catarina: Joinville, Palacio Episcopal, 8 Nov. 1957, *Reitz & Klein* 5665 (holotype, US 2240919).

Plants perennial, culms decumbent and rooting at the lower nodes to stoloniferous, then ascending to erect, 0.15–0.80 m tall, simple or branching at the upper nodes, internodes 2–15 cm long, glabrous, nodes dark, pilose to glabrous. Leaves with sheaths 2–11 cm long, pilose with papillose-pilose, caducous hairs to glabrous, the margins ciliate with tuberculate hairs, more so toward the distal portion, collar pilose to glabrous. Ligules membranous, shortly lacinate or ciliate at the distal portion, 0.4–0.8 mm long. Blades lanceolate, 4–30 cm long, 0.3–1.4 cm wide, flat, rounded to occasionally subcordate at base, sparingly pilose to glabrous, the margins scabrous. Inflorescence terminal, lax to contracted, 6–29 cm long, 2–14 cm wide; main axis, branches and pedicels scabrous, axils of the branches short- to long-pilose, first-order branches alternate or occasionally opposite, ascending or spreading, spikelets crowded on short secondary branchlets, pedicels 0.5–1.4 mm long. Spikelets narrowly elliptic, 1–1.7 mm long, 0.4–0.6 mm wide, pilose, with caducous hairs, to glabrous, greenish or tinged with purple. Lower glume ovate, 0.6–1.1 mm long, $\frac{2}{5}$ to $\frac{1}{2}$ the length of the spikelet, 3-nerved, the keel scabrous on the upper portion. Upper glume 1–1.6 mm long, covering or not the upper antherium, 5-nerved, the keel scabrous. Lower lemma 0.9–1.6 mm long, 5-nerved. Lower palea oblong, 1.1–1.5 mm long, 0.4–0.6 mm wide, membranous, shortly ciliate on the margins, occasionally expanded or not at maturity; lower flower staminate, stamens 3, or occasionally absent. Upper antherium elliptic, 1–1.4 mm long, 0.4–0.5 mm wide, scabrous toward

the apex, papillose, indurate, shining; anthers 2, occasionally 3, 0.3–0.7 mm long. *Caryopsis* elliptic, 0.8–0.9 mm long, 0.4–0.6 mm wide; hilum oblong, embryo $\frac{1}{2}$ the length of the spikelet.

Distribution and ecology. Widely distributed in America, from Mexico to Argentina, and introduced in Africa. It is common in wet and open, disturbed places, in margins of roads, swamps, and rivers, between 0 and 1,500 m.

Selected specimens examined. ARGENTINA. BUENOS AIRES: Isla Martín García, *Parodi* 4662b (BAA). CHACO: Puerto Antequera, *Zuloaga et al.* 3319 (SI*). CORRIENTES: 42 km E de Ituzingó, puesto de Prefectura, *Zuloaga et al.* 593, 2298 (SI). ENTRE RIOS: Concepción del Uruguay, borde del Río Uruguay, *Zuloaga et al.* 2337 (MO, SI*). FORMOSA: Estancia Monteagudo, *Guaglianone et al.* 326 (MO, SI). JUJUY: Calilegua, toma del Río Zora, *Cabrera et al.* 30378 (SI). MISIONES: Santa Ana, camino al balneario municipal, *Zuloaga et al.* 3170*, 3178 (SI). SALTA: de Río Pescado a Orán, *Cabrera et al.* 26510 (SI). SANTA FE: Alto Verde, *Pensiero* 116 (SI). TUCUMAN: Acheral, *Venturi* 1635 (SI). ANTIGUA. Without locality, *Wulfschaege* 623bis (M). BELIZE. BELIZE: 41 mi. northwest of Belize along Northern Highway, *Croat* 23967 (MO). CAYO: 4 km W of Hattievill along the Western Highway to Belmopan, *Davidse & Brant* 32998 (MO*). TOLEDO: near border of Stann Creek along Southern Highway, *Croat* 24185 (MO). BOLIVIA. BENI: Prov. Balivián, Estancia El Porvenir, 50 km E of the Río Maniqui (San Borja) on the road to Trinidad, *Solomon* 14775 (MO). COCHABAMBA: Campamento Izarzama, *Beck* 1587 (LPB). LA PAZ: Zonga valley, below the dam at Lago Zongo, *Solomon* 12901 (MO, SI). PANDO: Prov. Manuripi, along Río Madre de Dios, 80 km (by air) downstream from and NE of Chibe, *Nee* 31529 (MO). SANTA CRUZ: Montero to Puerto Grether, *Renvoize & Cope* 3953 (K, MO, SI). TARIJA: camino a Bermejo, Río Seco, *Coro-Rojas* 1434 (LPB). BRAZIL. ACRE: NW of Cruzeiro do Sul, along road from Cruzeiro do Sul to Barao do Rio Branco, *Croat & Rosas* 62653 (SI). AMAPA: Campo Experimental do Cerrado, km 45 da rodovia BR-156, *Valls* 11644 (CEN). AMAZONAS: Fazenda Santa Terezinha, Costa da Terra Nova, Ilha do Careiro, *Prance & Ramos* 23298 (US). BAHIA: by Rio Cumbuca, ca. 3 km S of Mucugé, *Harley et al.* 15968 (CEPEC, K, MO). CEARA: Serra do Baturité, S. Inácio do Azevedo, *Eugenio* 267 (RB). DISTRITO FEDERAL: Taguatinga Norte, *Silva* 257 (IBGE, SP). ESPIRITO SANTO: Mirassol, *Mattos et al.* 10849 (SP). GOIAS: ca. 20 km W of Veadeiros, 1,000 m, *Irwin et al.* 12931 (MO, NY). MARANHÃO: Barra do Corda to Grajaú, *Swallen* 3625 (RB). MATO GROSSO: Poconé, Fazenda Ipiranga, *Allem & Vieira* 1011 (CEN). MATO GROSSO DO SUL: Fazenda Bodoquena, *Allem et al.* 2188 (CEN, MO). MINAS GERAIS: Serra do Espinhaço, 18 km W of Grão Mogol, *Irwin et al.* 23558 (MO, P, UB, US). PARA: Santarém, *Spruce Panicum* 5 (G, MO, P, M, W). PARANA: Parque Nacional de Sete Quedas, Ilhas dos Saltos, *Sendulsky* 1824 (SI, SP). PERNAMBUCO: Beberibe, vicinity of Recife, *Chase* 7760 (MO). PIAUI: between Floriano and Oeiras, *Swallen* 4166 (US). RIO DE JANEIRO: Leblon, near Lagoa Rodrigo de Freitas, Rio de Janeiro, *Chase* 8227 (MO). RIO GRANDE DO SUL: Tenente Portela, Reserva Florestal do Turvo, *Valls et al.* 1791 (CEN). RONDONIA: vicinity of Santa

Bárbara, 15 km east of km 117, *Prance & Ramos* 7168 (MO). RORAIMA: vicinity of Caracará, along BR-174 road, between Caracará and Rio Branco, *Coradin & Cordeiro* 1040 (CEN). SANTA CATARINA: 6 km N of Abelardo Luz, *Smith & Klein* 15617 (SI). SAO PAULO: 1 km NE of Juquitiba along Highway 116 to Curitiba, *Davidse et al.* 10914 (MO). COLOMBIA. AMAZONAS: Trapecio Amazónico, between Amazon and Putumayo water sheds, *Black & Schultes* 46-396 (COL). ANTIOQUIA: Medellín, *Archer* 351 (COL). ARAUCA: kilometro 13 al Sur de Arauca, Laguna El Venero, Hato de Tiberio Sosa, *Jorgenson* 28 (COL). BOYACA: Villa de Leyva, *Zuloaga et al.* 4181, 4183 (COL, MO, SI*). CALDAS: La Dorada, Hacienda "El Palmar," *Restrepo s.n.* (COL). CAQUETA: Florencia, Granja Macagual del I.C.A., *Echeverry* 2477 (COL). CASANARE: Río Casanare, Hato "El Mochuelo," *Jaramillo* 164 (COL). CAUCA: Guapi, Parque Nacional de Isla Gorgona, camino a Pablo Sexto, *Lozano & Rangel* 5218 (COL). CHOCO: Hoya del Río San Juan, Andagoya, *Forero et al.* 5120 (COL). GUAINIA: Río Inírida, Caranacoa, *Fernández et al.* 7091 (COL); MAGDALENA: Santa Marta, *Smith* 202 (COL, SI, W), 204 (COL, G, P). META: Puerto Gaitán, 4 km al W, borde de arroyo, *Zuloaga* 3983 (COL, MO, SI*). NARINO: El Pedregal y Pilcuan, *Mora* 2491 (COL). NORTE DE SANTANDER: Abrego, *García & Cabrales* 6 (COL). SANTANDER: Barrancabermeja, carretera a El Llanito, *Schmidt-Mumm* 450 (COL). TOLIMA: Ibagué, Planta Eléctrica de Mirolindo, 1,200 m, *Echeverry* 1188 (COL). VALLE: Cartago, Santa Ana de los Caballeros, *Cuatrecasas* 23036 (P). VAUPES: raudal de Yurupari, *Schultes & Cabrera* 19735 (US). VICHADA: 20 km NW of San José de Ocuté, *Hermán* 10944 (COL). COSTA RICA. ALAJUELA: Carrillos de Poas, *Brenes* 20172 (NY). GUANACASTE: Finca La Pacífica, 5 km NW of Cañas, *Pohl* 12959 (MO). HEREDIA: roadside in pasture, 10 km SSE of Puerto Viejo, E side of Río Puerto Viejo, *Pohl* 12819 (MO). LIMON: north shore or the mouth of the Río Colorado at Barra del Colorado, between the village and the Caribbean sea, *Davidse & Herrera* 30979 (SI). PUNTARENAS: along west side of Río Grande de Tarcoles, ca. 0.5 km S of mouth of Río Turrubares, *Grayum et al.* 5238 (MO). SAN JOSE: along Río Conejo in the valley of the Río Alumbre, *Pohl & Davidse* 11059 (MO). CUBA. CAMAGUEY: vicinity of La Gloria, *Shafer* 174 (US). ISLA DE LA JUVENTUD: San Pedro and vicinity, *Britton & Wilson* 14803 (US). HABANA: Laguna de Ariguanabo, *Ekman* 13092 (G). ORIENTE: Bayate, *Ekman* 6065 (G). PINAR DEL RIO: Sierra de los Organos, Grupo del Rosario, *Ekman* 12957 (US). SANTA CLARA: Minas de Motembo, *León et al.* 8613 (US). DOMINICAN REPUBLIC. LA VEGA: vicinity of Jarabacoa, 500–1,200 m, *Allard* 14513 (US). PACIFICADOR: Pimentel, near sea level, *Abbott* 687 (US). ECUADOR. GUAYAS: Milagro, *Asplund* 5761 (P). IMBABURA: Lita, *Acosta Solís* 12150 (F). LOS RIOS: 14 km SE of Quevedo, *MacBryde* 1119 (MO). NAPO: Carretera Hollín-Loreto, km 40–50, *Hurtado* 688 (MO). PASTAZA: Mera, *Asplund* 18340 (P). PICHINCHA: Puente Gloria de María, *Asplund* 7271 (G). EL SALVADOR. AHUACHAPAN: vicinity of Ahuachapán, *Standley* 19824 (US). LIBERTAD: Hwy. 2, ca. 20 km E of La Libertad, crossing of Río Tihuapa, *Pohl* 11856 (MO). FRENCH GUIANA. Passoura, *Black & Klein* 17230 (IAN, NY). GRENADA. Without locality, *Broadway* 1870 (M). GUADELOUPE. Montebello, *Questel* 503 (P, US). GUATEMALA. ALTA VERAPAZ: Panzos, along road to Hydrochulac and Cahabon from Tactic–El Estor road, *Stevens et al.* 25354 (MO*). IZABAL: between El Estor and plant of abandoned nickel mine, *Stevens & Martínez*

25275 (MO*). PETEN: Sabanas y bosque secundario de Santa Rita, 20 kms al sur de Santa Elena, *Molina* 15523 (MO). GUYANA. Rupununi, *Chan Choong* 25 (US). HAITI. Massif de la Hotte, western group, Dame-Marie, Etang-Dérémond, *Ekman* 10473 (US). HONDURAS. ATLANTIDA: Orillas del Río Piedras Gordas, Tela, *Ordóñez* 6 (MO). CHOLUTECA: Marcovia, 20 km NE de Choluteca, *Argenal* 33 (MO). COMAYAGUA: Vado Alto, orilla del Río Sulaco, *Nelson et al.* 7671 (MO). COPAN: Ocoteseco, 20 km NE de Santa Rosa de Copán, 1,300 m, *Portillo* 47 (MO). EL PARAISO: near Piedra Herrada, drainage of the Río Yeguare, *Williams* 15982 (MO). GRACIAS A DIOS: Alrededores del Río Platano, *Clewell & Cruz* 4167 (MO). FRANCISCO MORAZAN: Alrededor de Nueva Tatumbula, 20 km al SE de Tegucigalpa, *Maradiaga* 68 (MO). OLANCHO: Montaña de Chifringo, 20 km del campamento, *Izaguirre* 36 (MO). SANTA BARBARA: Trinidad, Finca Las Colmenas, *Salguero* 15 (MO). VALLE: 3 km E of San Lorenzo along the road to the new sea harbor, *Davidse & Pilz* 31687 (MO*). YORO: Victoria, orilla del Río Sulaco, *Nelson et al.* 7055 (MO). JAMAICA. Hope Grounds, *Harris* 11800 (P). MARTINIQUE. St. Pierre, *Hahn* 757, 1536 (G). MEXICO. CAMPECHE: about 9 miles W of Escarcega in calcareous soil, *Reeder & Reeder* 6101 (MO). QUINTANA ROO: 15 km SSW of Puerto Morelos on Hwy. 307 to Felipe Carrillo Puerto, *Davidse et al.* 20645 (MO). TABASCO: km 10.2 de Huimanguillo hacia Malpaso en carretera Huimanguillo-Malpaso, *Cowan et al.* 2574 (MO). TAMAULIPAS: Hacienda Santa En Gracia, *V. Chase* 7592 (MO). VERA-CRUZ: about 2 miles W of Minatitlán in area of tropical vegetation, *Reeder & Reeder* 6027 (MO). NICARAGUA. CHINANDEGA: Los Balcones, a 9 km de Somotillo, carretera a Cinco Pinos, *Moreno* 11511 (MO). CHONTALES: Hacienda Veracruz, including Cerro La Batea and Cerro Los Charcos, *Stevens* 22372 (MO). ESTELI: 1.5 km al N del valle San José de la Laguna, camino a San Nicolás, *Moreno* 11361 (MO). JINOTEGA: along road from Hwy. 3 through La Fundadora, between Las Camelias and La Salvadora, *Stevens & Grijalva* 15305 (MO). MATAGALPA: Ranchería, 11 km al NE de Muy muy, *Moreno* 24430 (MO). RIO SAN JUAN: meadow along Río San Juan, *Seymour* 5295 (MO). ZELAYA: Puerto Cabezas, ca. 14°01'N, 83°23'W, *Stevens* 17805 (MO). PANAMA. BOCAS DEL TORO: Alrededores de Quebrada Chica, *Correa et al.* 3830 (MO). CANAL ZONE: Cerro Gordo, near Culebra, *Standley* 25995 (MO). COLON: vicinity of San Miguel de La Borda, *Croat* 9878 (MO). DARIEN: vicinity of Campamento Buena Vista, Río Chucunaque above confluence with Río Tuquesa, *Stern et al.* 834 (MO). LOS SANTOS: one mile south of Pedasi, *Correa* 70 (F). PANAMA: between Pacora and Chepo, *Woodson et al.* 1632 (MO). VERAGUAS: roadside savanna 2-4 miles E of Santiago, *Duke* 12346 (MO). PARAGUAY. ALTO PARANA: Puerto Bertoni, *Bertoni* 4951, 3673, 3602, 5831, 5846 (W). AMAMBAY: Pedro Juan Caballero, *Fiebrig* 4776 (G, W). CAAGUAZU: Caaguazú, *Balansa* 56a (P). CAAZAPA: Tavaí, *Mereles* 2297 (MO). CENTRAL: Asunción, *Balansa* 57, 58 (G, P). CONCEPCION: Río Apa, *Hassler* 8189 (P). CORDILLERA: Cordillera de Altos, Cerro Tobatí, *Schinini* 24029 (G, MO). GUAIRA: Azucarera de Tebicuary, Río Tebicuary, *Schinini* 5907 (G, SI). MISIONES: Santiago, Estancia La Soledad, *Pedersen* 3260 (SI). PARAGUARI: Paraguarí, *Balansa* 57c (G, P). PRESIDENTE HAYES: Pilcomayo River, *Morong* 977 (G, MO). PERU. AMAZONAS: ridge above Cikan Ece Creek, *Berlin* 1643 (MO). CUZCO: entre Otalaya y Salvación, *Vargas* 16277 (US). HUANUCO: Tingo María, *Asplund* 13003 (P). JUNIN: Prov. Satipo, km 41 on road to Satipo,

1,000 m, *Smith et al.* 1438 (MO). LORETO: Prov. Alto Amazonas, Capahuari Sur (Campamento Petrolero), *Vásquez et al.* 3023 (MO). MADRE DE DIOS: Prov. Manú, Parque Nacional del Manú, Cocha Cashu Station, *Foster* 9864 (MO). PASCO: Oxapampa, Río Iscozacín, tributary of Río Palcazu, *Knapp et al.* 7830 (MO). SAN MARTIN: Quebrada de Canuto, *Schunke Vigo* 10661 (K, SI). PUERTO RICO. 8 km SW of Vega Baja, *Mac Kee* 10605 (P). SURINAME. Near Kayser Airstrip, *Irwin et al.* 57554 (MO, NY, P, US). TRINIDAD & TOBAGO. Piarco Savanna, south of Arouca, *Hitchcock* 10343 (US). URUGUAY. San José, Río Santa Lucía, Colonia Etchejare, *Rosengurt* B-4957 (P). VENEZUELA. AMAZONAS: Depto. Atabapo, Salto Yureba, Cerro Yureba, *Liesner* 18764 (MO). ANZOATEGUI: Morichal El Pinal, 3 km norte de San Diego de Cabrotica, *Montes* 1756 (MO). APURE: N de casa principal de UNELLEZ, en médano grande, *Zuloaga et al.* 4330 (MO, SI*, VEN). BARINAS: cercanías de Ciudad Nutrias, 8°5'N, 69°19'W, *Zuloaga et al.* 4313 (MO, SI, VEN). BOLIVAR: entre Piedra de la Virgen y la parte alta de la Escalera, carretera a la Gran Sabana, *Zuloaga et al.* 4401 (MO, SI, VEN). COJEDES: San Carlos, *Burkart* 16161 (SI). FALCON: Carretera Coro-Mirimire, cerca del Río Hueque, *Wingfield* 6227 (MO). GUARICO: 21 km SSE of Calabozo along road to Cazorla, 95 m, *Davidse* 3752 (MO, PORT). LARA: en potreros irrigados de Sicarigua, *Burkart* 16657 (SI). MIRANDA: Cerros del Bachiller, near east end, between Quebradas Corozal and Santa Cruz, south of Santa Cruz, *Steyermark & Davidse* 116468 (MO). MONAGAS: Alrededores de Laguna Grande, a unos 15 km, *Aristeguieta* 3909 (MO). PORTUGUESA: a 4 km al Oeste de Guanare hacia Ciudad Barinas, *Zuloaga et al.* 4302 (MO, SI, VEN). SUCRE: 8 km al N de Santa Fé, entre Barcelona y Cumaná, *Zuloaga et al.* 4367 (MO, SI*, VEN). TACHIRA: alluvial flats, at El Vado, along Río Lobatera, in Parcelamiento Guarumito, 5.5 km west of La Fría (by air), *Steyermark et al.* 120340 (MO). YARACUY: San Felipe, orilla del Río Yaracuy, *Burkart & Tamayo* 16430 (SI). ZULIA: Distrito Perijá, between the Ríos Yasa and Tucuco along the Machiques and Los Angeles de Tucuco road, *Davidse et al.* 18393 (MO).

This species has a wide distribution and a great amount of variability. There are small to medium specimens, some with contracted panicles, described as *P. laticola* and *P. caroniense*; others have open panicles, spikelets pilose or glabrous, and flowers with two (unusual in *Panicum*) or three anthers.

Specimens previously included in *Panicum hondurensis*, a species considered here as a synonym of *P. laxum*, are characterized by having the upper anthecium covered by verrucose papillae regularly distributed. This character links the species to subgenus *Steinchisma*. Also, there are other specimens of *P. laxum*, such as *Smith* 202, *Schunke Vigo* 10661, 10802, *Duke* 11684 (2), *Lewis & Pire* 808, and *Arbo et al.* 1348, that have the upper anthecium with verrucose papillae all over its surface; these specimens are intermediate in this character with species of subgenus *Steinchisma*.



FIGURE 21. *Panicum leptachne* (based on Chase 8803).—a. Habit.—b. Detail of ligule, sheath and blade.—c. Racemose unilateral branch.—d. Axis of a branch with hairs and pedicels.—e. Detail of paired, short pedicels on a branch.—f. Spikelet, lateral view.—g. Spikelet, lower glume view.—h. Spikelet, upper glume view.—i. Lower palea with lodicules and filaments of stamens.—j. Upper antherium, lemma view with prickly hairs at the upper portion.—k. Upper antherium, palea view.

7. *Panicum leptachne* Doell in C. Martius, Fl. Bras. 2(2): 195. 1877. TYPE: Brazil. Without locality, *Widgren 1157* (holotype, S, fragment US 80737). Figures 4, 21.

Panicum pilosum Sw. var. *polychaetum* Hackel, Ergeb. Bot. Exped. Akad. Wiss. Sudbras.: 9. 1906. TYPE: Brazil. São Paulo: prope Rio Grande inter Santos et Urbem São Paulo, 750–800 m, 1902, *Wacket s.n.* (holotype, W, fragment, US 2907505).

Plants of indefinite duration, probably perennial, the culms erect, ca. 100 cm tall, simple, internodes compressed, hollow, glabrous, nodes compressed, dark, densely pilose with appressed, whitish hairs to glabrous. *Sheaths* 11–14 cm long, longer than the internodes, with tessellate nerves, covered by short, appressed papillose-pilose hairs to glabrous, the margins short-ciliate with papillose-pilose hairs. *Ligule* membranous, 0.8–1 mm long, laciniate at apex. *Blades* lanceolate, 13–22 cm long, 1.8–2.5 cm wide, shortly pseudopetiolate, pseudopetiole sparingly pilose, brownish, blades flat, cordate, acuminate, glabrous. Peduncle ca. 10 cm long, glabrous. *Inflorescence* a terminal, ovate panicle 25–40 cm long; *main axis* wavy, scaberulous and sparingly pilose near the axils of branches, first-order branches ascending, numerous, axis triquetrous, with one side flattened, scabrous and covered with conspicuous, long papillose-pilose hairs; second-order branches absent; spikelets paired and secund on short, scabrous pedicels. *Spikelets* narrowly elliptic, 2.1–3.2 mm long, 0.5–0.8 mm wide, greenish or tinged with purple, scabrous on glumes and lower lemma. *Lower glume* 1–2 mm long, $\frac{2}{3}$ to $\frac{1}{2}$ or more the length of the spikelet, 3(–5)-nerved, the keel scabrous above, acute. *Upper glume* 5(–7)-nerved, not covering the apex of the upper anthecium, cucullate. *Lower lemma* 3(–5)-nerved, the keel scabrous above. *Lower palea* lanceolate, brownish, 1.7 mm long, 0.4 mm wide, hyaline, glabrous, to absent; lower flower present, with 2 lodicules and 3 anthers, or absent. *Upper anthecium* narrowly elliptic, 1.8–2.5 mm long, 0.6–0.7 mm wide, brownish, membranous, scabrous at the apex of lemma and palea; lemma 5-nerved. *Caryopsis* obovate, 1.2 mm long, 0.6 mm wide, plano-convex, brownish; hilum oblong, embryo $\frac{1}{3}$ the length of the caryopsis.

Distribution and ecology. This species grows in Brazil in the states of Minas Gerais, Rio de Janeiro, Paraná, and São Paulo, in wet places up to 650 m elevation.

Additional specimens examined. BRAZIL. MINAS GERAIS: Juiz de Fora, Faz. da Cachoeira, *Roth 1323* (RB, US); Lavras, *Chase 8771* (F, MO, RB, W), *8803* (US*);

Viçosa, *Bailey 1177* (US), *Chase 9432* (F, MO, US), *Kuhlmann 1936* (RB), *s.n.* (RB 110562, SI, US); Belo Horizonte, Ressaca, *Mello Barreto 3019* (R, US). PARANA: Serra do Mar, Ypiranga, *Dusén 3664* (R, SI, US, W); Gral. Carneiro, Rio Lajeado, *Hatschbach 13727* (K). RIO DE JANEIRO: Petrópolis, Caetité, *Goes & Dionisio 762* (RB). SANTA CATARINA: Canoinhas, campo, 17 km W of Canoinhas on the road to Pôrto Uniao, *Smith et al. 10701* (NY, US). SAO PAULO: Horto Botânico, *Edwall 3859* (SP, US*); Pirajussura, *Gehrt s.n.* (SP 30558); São Paulo, Mogi das Cruzes, *Pickel 5222* (US); without locality, *St. Hilaire 623* (P), *Burchell 4495-2* (K, W), *4355* (K).

Related to *P. pilosum*, *P. leptachne* has bigger spikelets, 2.1–3.2 mm long, and a membranous upper anthecium.

Renvoize (1988) regarded *P. leptachne* as similar to *Hymenachne donacifolia*, differing by having the upper palea enclosed by the lemma at the apex.

8. *Panicum longum* A. Hitchc. & Chase, Contr. U.S. Natl. Herb. 15: 111, fig. 106. 1910. *Panicum pilosum* Sw. var. *macranthum* Scribner, U.S.D.A. Div. Agrost. Circ. 19: 1. 1900. Not *P. macranthum* Trin. 1826. TYPE: Mexico. Veracruz: swamps near Jalapa, *Pringle 8195* (holotype, US* 354552; isotypes, M, NY, P, W). Figure 2.

Plants perennial, ascending or spreading from a $\pm$ geniculate base; culms 1 to 2 m long, many-noded, simple or sparingly branching from the lower nodes, internodes glabrous, compressed, hollow, nodes dark, compressed, glabrous. *Sheaths* shorter or longer than the internodes, papillose-pilose with long caducous hairs, the margins ciliate. *Ligule* 0.6 mm long, a membrane with a fringe of hairs at the upper portion. *Blades* lanceolate, 10–25 cm long, 0.6–1.2 cm wide, shortly pseudopetiolate, pseudopetiole dark, blades flat, narrowed at base, acuminate, sparsely papillose-pilose on the adaxial surface, glabrous beneath, margins scabrous, the midnerve manifest. *Inflorescence* a terminal panicle 18–25 cm long, 2–5 cm wide, short-exserted or included at base; *main axis* wavy, with long, stiff hairs toward the distal portion, first-order branches ascending, the lower alternate, middle and upper opposite or whorled, axis of the branches triquetrous, flattened on one side, densely papillose-pilose with hairs exceeding the length of the spikelets, second-order branches absent; spikelets secund and paired or occasionally singly on short, scabrous pedicels. *Spikelets* narrowly elliptic, 2.3–2.5 mm long, 0.6–0.7 mm wide, acuminate, scabrous, especially over the nerves of glumes and lower lemma. *Lower glume* 1.3–1.5 mm long, $\frac{1}{2}$ or more the length of the spikelet, acuminate, 3-nerved, nerves anastomosed toward the apex.

Upper glume shorter than the lower lemma, 5-nerved. *Lower lemma* exceeding the upper anthercium in length, 3(-5)-nerved. *Lower palea* absent; lower flower absent. *Upper anthercium* narrowly elliptic, 2-2.2 mm long, 0.6-0.7 mm wide, membranous, scabrous toward the apex and covered with silica bodies. *Caryopsis* unknown.

Distribution and ecology. Mexico, known only from the type collection, growing in swamps.

This species is related to *P. leptachne*, from which it differs slightly by having leaves narrow at their bases and spikelets usually smaller; the two species may be conspecific. However, due to the geographic distribution of *P. longum* and *P. leptachne*, both are maintained as separate species in the present treatment.

9. ***Panicum pernambucense*** (Sprengel) Mez ex Pilger in Engler, Nat. Pflanzenfam. (ed. 2) 14e: 15. 1940. *Agrostis pernambucensis* Sprengel, Syst. Veg. 1: 258. 1825. TYPE: Brazil. Pernambuco: Without locality and collector. Figures 5, 12, 22.

Panicum rivulare Trin., Gram. Panic.: 213. 1826. TYPE: Brazil. Rio de Janeiro: Serra dos Orgaos, Langsdorff s.n. (holotype, LE, fragments, BAA, US 974638, photo of type, K).

Panicum excelsum Nees, Agrost. Bras.: 180. 1829. TYPE: Brazil. "Habitat in Brasilia meridionale (Sellow)" (holotype, B; isotypes, K, US 1061585, fragments, BAA, NY, US 974640, 1061585, 2907336).

Panicum urticans L. B. Smith & Wasshausen, Bradea 2(35): 246, fig. 2 E-G, 1978. TYPE: Brazil. Paraná: Porto Vitoria, barranco do Rio Jangada, 7 Dec. 1971, Smith & Klein 15715 (holotype, US 2849460).

Robust rhizomatous perennial, 2-3 m tall, culms erect, branching at the middle and upper nodes; internodes 8-22 cm long, 0.8-1 cm diam., stramineous, hollow, hirsute to glabrous; nodes pilose to glabrous, dark. *Sheaths* 8.7-18 cm long, glabrous or densely papillose-pilose with caducous hairs. *Ligules* 0.5-1.3(1.8) mm long, membranous; collar brownish. *Blades* lanceolate, 17-60 cm long, 0.8-2 cm wide, subcordate, attenuate at the apex, the margins scaberulous, sparsely pilose to glabrescent, the midnerve conspicuous. *Inflorescence* a terminal, lax panicle 27-40 cm long, 8-12 cm wide; *main axis* scabrous, with or without short hairs, axils of the branches short-pilose, spikelets short-pedicelled, crowded on short, second-order branches, first-order branches ascending to spreading, distant, alternate to opposite, occasionally whorled, appressed, the branchlets short, appressed; pedicels scabrous, short, 0.4-2 mm long.

Spikelets narrowly elliptic, 1.7-2.2(-2.5) mm long, 0.4-0.8 mm wide, glabrous. *Lower glume* ovate, 0.8-1.2 mm long, ½ the length of the spikelet, 3-nerved, the keel scabrous toward the apex. *Upper glume* 1.4-2.1 mm long, shorter than the lower lemma, 3-5-nerved, the keel scaberulous. *Lower lemma* oblong, 1.7-2.2 mm long, 3-5-nerved, the keel scabrous. *Lower palea* usually absent, when present elliptic, hyaline; lower flower absent. *Upper anthercium* narrowly elliptic, 1.7-2.2 mm long, 0.4-0.8 mm wide, membranous, stramineous, scabrous at the apex of lemma and palea, the rest of its surface with simple papillae and silica bodies. *Caryopsis* elliptic, 0.9-1 mm long, 0.5-0.6 mm wide.

Distribution and ecology. South America, from northeastern Brazil, in the state of Paraíba, to Paraguay and Argentina. It is found at margins of streams and rivers, where it forms huge colonies. In flower between October and February.

Selected specimens examined. ARGENTINA. BUENOS AIRES: San Pedro, Isla del Recreo, Nicora 3610 (SI). CHACO: Puerto Antequera, Zuloaga et al. 3323 (SI*). CORRIENTES: ruta nacional 12, 5 km antes del Arroyo Itaembé, Zuloaga et al. 3232 (SI*). ENTRE RIOS: San Carlos, Meyer 10811 (LIL); ruta entre Concepción del Uruguay y Gualaguaychú, Zuloaga & Deginani 2494 (SI*). FORMOSA: Formosa, Jorgensen 2418 (SI, US). MISIONES: de Apóstoles a Concepción de la Sierra, Arroyo Las Tunas, 2 km de Concepción de la Sierra, Zuloaga et al. 3251 (SI*); Santa Ana, camino al balneario municipal, Zuloaga et al. 2235 (MO, SI*). SANTA FE: Reconquista, Isla Mascota, Job 956 (LP, NY). BRAZIL. BAHIA: Serra do Sincorá, on road to Cascavel, 3 km S of Mucugé, Harley et al. 15961 (CEPEC, K, MO, NY, P, US). ESPIRITO SANTO: Rodovia BR-101, Rio Santa Maria, Hatschbach 48776 (K). MATO GROSSO: Porto Frangeli, Hatschbach 40611 (MO, NY). MATO GROSSO DO SUL: vicinity of Dourados, Chase 10957 (MO, RB, US). MINAS GERAIS: 9 km NE of Camundacaia, Davidse & D'Arcy 10563 (K, MO, SP). PARAIBA: Soledade, Glaziou 16632 (F, P, US, W). PARANA: Pitanga, Borboleta, Hatschbach 46007 (K, NY, US). PERNAMBUCO: near Santa Esmeralda, Pires Furtado 119 (RB). RIO DE JANEIRO: Monte Serrat, below Serra de Itatiaia, near Campo Bello, Chase 8365 (MO, NY, RB, US). RIO GRANDE DO SUL: Vacaria, Vale do Rio Ibitirã, Valls et al. 1897 (CTES, US). SAO PAULO: city of São Paulo, 6-7 km SW of center of city, along the Rio Pinheiros, Skvortzov 90 (K, UB, US). PARAGUAY. ALTO PARANA: Puerto Bertoni, Bertoni 3889, 4177, 5134 (W). CAAGUAZU: Tacurú, Sparre & Vervoorst 2229 (LIL). CENTRAL: in regione lacus Ypacaraí, Hassler 11468 (G, NY, US). CORDILLERA: Cordillera de Altos, Cerro Tobati, Schinini 23974 (G, SI). GUAIRA: Itapé, Joergensen 4089 (F, MO, NY, SI, US). PARAGUARI: prope Sapucay, Hassler 12904 (G, US). SAN PEDRO: Puerto Antequera, Rojas 2326 (SI).

There is variation in the pilosity of culms and sheaths of this species. In *P. pernambucense* there are specimens with culms and sheaths with abun-



FIGURE 22. *Panicum pernambucense* (based on Joergensen 2418).—a. Upper portion of a culm with blade and terminal panicle.—b. Detail of membranous ligule and hairs at the lower portion of the blade.—c. Racemose unilateral branch with paired spikelets.—d. Spikelet, lower glume view.—e. Spikelet, upper glume view.—f. Spikelet, lateral view.—g. Upper anthecium, lemma view.—h. Upper anthecium, palea view.—i. Upper palea with lodicules and stigmas.—j. Caryopsis, embryo view.—k. Caryopsis, lateral view.—l. Caryopsis, hilum view.

dant rigid and caducous papillose-pilose hairs, while others are almost glabrous; the presence or absence of hairs is not correlated with any other character. For this reason, *P. urticans*, which is similar in other respects to *P. pernambucense*, has been included in synonymy.

Panicum pernambucense is similar to *P. grumosum*, and in some cases specimens are difficult to assign to one or the other species, as in several collections from Paraguay (e.g., Hassler 11468, Schinini & Bordas 25190). However, *P. pernambucense* can be distinguished by its usually smaller spikelets, lower palea absent or less commonly present, lower flower absent, and a wider range of distribution.

10. *Panicum pilosum* Sw., Prodr.: 22. 1788.

Setaria pilosa (Sw.) Kunth, Revis. Gramin. 1: 47. 1829. *Panicum distichum* Lam. var. *pilosum* (Sw.) Griseb., Fl. Brit. W. Ind.: 548. 1864. TYPE: Jamaica. Without locality, Swartz s.n. (holotype, S; isotype, M, fragment, US 80916). Figures 2, 13, 14.

Panicum distichum Lam., Encycl. 4: 731. 1798. *Setaria disticha* (Lam.) HBK, Nov. Gen. & Sp. 1: 112. 1816. TYPE: "Cette plante croit a la Jamaïque" (holotype, P, fragment, US 80650).

Panicum pilisparsum G. Meyer, Prim. Fl. Esseq.: 57. 1818. *Setaria meyeri* Kunth, Revis. Gramin. 1: 47. 1829. TYPE: Guyana. Essequibo: "in graminosis humidis plantationis Hamburg" (holotype, GOET not seen, fragment, US 2907509).

Panicum pennisetum Roth, Nov. Pl. Sp.: 55. 1821. TYPE: Guyana. Essequibo: *Mertens* s.n. (holotype, B not seen, photo of type, K).

Panicum trichophorum Schrad. ex Schultes, Mantissa 2: 247. 1824. *Setaria schraderi* (Schrad. ex Schultes) Kunth, Revis. Gramin. 1: 47. 1829. TYPE: Brazil: "In Brasilia, Princeps Sereniss. Maximil. Neowidens" (type not seen).

Panicum densiflorum Willd. ex Sprengel, Syst. Veg. 1: 320. 1825. TYPE: "*P. densiflorum* Willdenow. America merid. Humboldt" (holotype, B not seen, fragment, US 2903513, photo of type, SI).

Panicum distichum Lam. var. *luxurians* G. Meyer, Nova Acta Phys.-Med. Acad. Caes. Leop.-Carol. Nat. Cur. 12: 768. 1825.

Panicum distichum Lam. β *lancifolium* Griseb., Fl. Brit. W. I.: 548. 1864. *P. distichum* Lam. var. *lancifolium* (Griseb.) A. Hitchc., Man. Grasses W. Ind.: 267. 1936. *Panicum distichum* Lam. γ *lancifolium* Griseb., Fl. Brit. W. I.: 548. 1864. *Panicum pilosum* Sw. var. *lancifolium* (Griseb. ex A. Hitchc.) Pohl, Fieldiana, Bot. 4: 381. 1980. TYPE: Trinidad. Without locality, *Crueger* 84 (fragment and photo of the type, US 80649).

Panicum coenosum Doell, in C. Martius, Fl. Bras. 2(2): 191. 1877. TYPE: Brazil. Amazonas: Manaus, *Spruce* 1235 (*Panicum* 38) (isotypes, G, K, M, NY, P, US 1445789, W, fragment, US).

Panicum pilosum Sw. var. *latifolium* Doell, in C. Martius,

Fl. Bras. 2(2): 212. 1877. SYNTYPES: Brazil. Rio de Janeiro: Tijuca, 27 Feb. 1870, *Glaziou* 4300, *Raben* 169 (isosyntype of *Glaziou* 4300, P, fragment of *Raben* 169, US 80918).

Panicum milleflorum A. Hitchc. & Chase, Contr. U.S. Natl. Herb. 17: 494. 1915. TYPE: Panama. Canal Zone: Frijoles, *Hitchcock* 8387 (holotype, US 693327; isotypes, G, K, NY, P, US, W).

Plants of indefinite duration, probably perennial, stoloniferous, culms decumbent, rooting and branching at the lower nodes, then erect, 10–70 cm tall, internodes 1.5–13 cm long, compressed, glabrous, nodes brownish to purplish, glabrous to densely pilose with long, whitish hairs. Sheaths usually shorter than the internodes, 3–9 cm long, densely papillose-pilose to glabrous, the margins pilose, more so toward the distal portion, collar brownish, pilose to glabrous. Ligules small, membranous, to commonly absent. Blades lanceolate, 6–28 cm long, 0.5–2 cm wide, shortly pseudopetiolate, subcordate and asymmetric at the base, glabrous to sparsely covered with papillose-pilose hairs on both surfaces, the margins scabrous. Inflorescence lax, 9–20 cm long, 2–8 cm wide; main axis and branches scabrous and with long hairs, axils of the branches pilose, spikelets crowded and paired, unilaterally disposed on first-order branches, second-order branches absent to occasionally present at the base of the inflorescence, the branches divergent to ascending, pedicels scaberulous, short, 0.4–1 mm long. Spikelets narrowly elliptic, 1.2–1.5 mm long, 0.5–0.6 mm wide, biconvex, glabrous to sparsely pilose. Lower glume 0.7–1 mm long, 3-nerved, the keel scabrous toward the apex. Upper glume 1.3–1.5 mm long, 5-nerved, the keel scabrous. Lower lemma 1.2–1.4 mm long, 3-nerved. Lower palea 0.4–1.1 mm long, 0.2–0.5 mm wide, equaling in length the lower lemma to small, membranous. Upper antheridium narrowly elliptic, 1.2–1.4 mm long, 0.4–0.6 mm wide, glabrous, smooth, finely scabrous at the apex and with simple papillae over the lemma and palea. Caryopsis broadly elliptic, brownish, 0.8 mm long, 0.5 mm wide; hilum punctiform, embryo $\frac{1}{2}$ the length of the caryopsis.

Distribution and ecology. Widely distributed from Mexico and the West Indies to South America, from Colombia to Argentina. It is usually found at margins of woods or in disturbed places.

Selected specimens examined. ARGENTINA. CORRIENTES: Puesto de Prefectura, 42 km E de Ituzaingó, *Zuloaga et al.* 623, 2303 (SI*). MISIONES: San Ignacio, Peñón del Teyucuaré, *Zuloaga et al.* 3194 (SI*). BELIZE. CAYO: Cave Branch Section, Humming Bird Highway, *Gentle* 8868, 8869 (F). TOLEDO: upper reach, Golden Stream, *Gentle* 4582 (MO). STANN CREEK: along road and

stream at Dry Creek, *Croat 24516* (MO, SI). BOLIVIA. BENI: Guayamerín, *Krapovickas & Schinini 35017* (SI). COCHABAMBA: San Rafael, *Steinbach 482* (GH, NY). LA PAZ: Mapi, *Buchtien 78* (BAF, SI, SP). SANTA CRUZ: Ichilo, de Montero a Puerto Grether, *Renvoize & Cope 3956* (K, LPB). BRAZIL. ACRE: Rio Branco, *Calderón & Soderstrom 2308* (US). ALAGOAS: Porto Calvo, Fazenda Macaitá, *Campelo 2181* (CEN). AMAPA: Estrada de Fazendinha, Macapá, *Rabelo et al. 3319* (MO). AMAZONAS: km 65, on road from Manaus to Bôa Vista, *Lasseign P21166* (US). BAHIA: Itacararé, near the mouth of the Rio de Contas, *Harley et al. 17567* (CEPEC, MO). CEARA: Guarimiranga, Serra do Baturité, *Fernández & Matos 9649* (IBGE). DISTRITO FEDERAL: 10 km S of Brasília, Fazenda Vargem Bonita, *Irwin et al. 12285* (F, NY, US). GOIAS: Serra do Morcego, ca. 35 km NE of Formosa, *Irwin et al. 15255* (MO, SP, US). MARANHÃO: Caxias to Barra do Corda, *Swallen 3532* (SP), 3603, 3589 (US). MATO GROSSO: Poconé, Porto Cercado, *Allem & Viera 1608* (CEN, MO). MINAS GERAIS: ca. 15 km N of São João da Chapada, *Irwin et al. 28155, 28158* (MO). PARA: Conceição do Araguaia, range of low hills ca. 20 km West of Redenção, *Plowman et al. 8595* (MO). PARAIBA: Areia, Escola de Agronomia do Nordeste, *Coelho de Moraes 750* (P). PARANA: Porto de Cima, *Dusén 14334* (MO, SI). PERNAMBUCO: vicinity of Recife, *Chase 7668* (MO). PIAUI: Serra de Araripe, *Luetzelburg 26304* (M). RIO DE JANEIRO: Parque Nacional Itatiaia, Picada Macieiras, *Zuloaga et al. 2355* (MO, RB, SI, US). RIO GRANDE DO SUL: São Leopoldo, *Rambo 41663* (LIL). RONDONIA: Forte Príncipe da Beira do Igarapé da Viúva, *Rodríguez & Wilson 4224* (NY). RORAIMA: along Boa Vista-BV 8 road (BR-174), km 197, *Coradin & Cordeiro 895* (CEN, IAN). SANTA CATARINA: Azambuja, *Smith & Reitz 6005* (SI). SÃO PAULO: São Paulo, grounds of the Instituto Botânico, 860 m, *Davidse 10440* (MO). COLOMBIA. AMAZONAS: Rio Igará-Paraná, Puerto Buenaventura, *Sastre 2423* (COL). ANTIOQUIA: road to Nechi, ca. 14 km from Caucasia-Planeta Rica road, Hacienda Candelaria, *Brant & Escobar 1253* (MO). BOLIVAR: ca. 16 km NW of San Jacinto, Cerro Maco, ca. 200 m SE of radar installation, *Zarucchi & Cuadros 4029* (MO). CALDAS: Santa Cecilia, *von Sneider 5064* (F, LIL). CAQUETA: 23 km N of Florencia along main road to Garzón, E slope of Eastern Cordillera, 560 m, *Davidse et al. 5760* (COL, MO). CASANARE: Tauramena, *Uribe 4054* (COL). CAUCA: Guapi, Parque Nacional Isla de Gorgona, camino a Playa Blanca, *Lozano & Rangel 5616* (COL). CHOCO: Bahía de Solano, *Gentry & Forero 7177* (COL, MO). GUAINIA: Raudal Pilón, en el Río Guainia, *Pabon et al. 308* (COL). MAGDALENA: Santa Marta, *Smith 203* (COL, G, MO, W). META: de Cumaral a San Nicolás, 10 km del desvío a San Nicolás, 480 m, *Zuloaga 3868, 3882* (COL, MO, SI). NARIÑO: Mocoa, *Bristol 235* (GH). PUTUMAYO: selva higrófila del Río San Miguel en la quebrada del Sipenae, *Cuatrecasas 10986* (COL). VALLE: Buenaventura, Vereda Puerto Patiño, *Muñoz 14-48* (COL). VAUPES: Alto Vaupés, alrededores de Miraflores, *Gutiérrez & Schultes 725* (COL). VICHADA: 27 km NE de San José de Ocuté, *Hermann 11013* (COL). COSTA RICA. ALAJUELA: 6 km W of Venicia, 450 m, *Pohl & Davidse 11254* (US). GUANACASTE: road to Upala, ca. 24 km NNE of CIA, *Pohl 12635* (MO). HEREDIA: La Selva, 3 km SE de Puerto Viejo, *Opler 551A* (MO, SI). LIMON: hills 2 airline km SSE of Islas Buena Vista in the Río Colorado, *Davidse & Herrera 31121* (MO, SI). PUNTARENAS: Osa Península, Rincón, *Pohl & Davidse 10744* (US). SAN JOSE: Basin

of El General, *Skutch & Barrantes 5111* (MO, US). CUBA. HABANA: Herradura, *van Hermann 763* (W). ISLA DE LA JUVENTUD: Sierra Las Casas, *Killip 44160* (US). ORIENTE: Sierra de Nipe, in pinares, *Alain et al. 8797* (US). PINAR DEL RIO: vicinity of Sumidero, limestone hills, *Shafer 13505* (P). SANTA CLARA: banks of Guayabo River, Banao hills, *León 3982* (US). DOMINICA. South Chiltern Estate between Pointe Michel and Soufrière Bay, *Ernst 1318* (US). DOMINICAN REPUBLIC. LA VEGA: vicinity of Piedra Blanca, *Allard 13145* (US). SEIBO: along road between Miches and El Seibo at crest of Cordillera Oriental, 30 km from El Seibo, 600 m, *Gastony et al. 710* (US). ECUADOR. CARCHI: trail from Pailón to Gualpi Chico area of Awa Reservation, 1.5 km past Río Blanco, *Hoover et al. 2388* (MO). ESMERALDAS: Parroquia de Concepción: Playa Rica, *Mexía 8482* (MO). NAPO: Reserva Biológica Jatún Sacha, Río Napo, 8 km al E de Misahualli, *Ceron 1038* (MO). PASTAZA: Curaray, *Neill & Palacios 6569* (MO, SI). PICHINCHA: Carretera Quito-Puerto Quito, km 113, 10 km al norte de la carretera principal, *Balslev & Balseca 4703* (MO). FRENCH GUIANA. Haut Marony, *Sastre & Moretti 3847* (MO, P). GRENADA. St. Georges, *Broadway s.n.* (US). GUATEMALA. ALTA VERAPAZ: Panzós, along road to Hidrochulac and Cahabón from Tactic-El Estor road, *Stevens et al. 25341* (MO*). IZABAL: slopes WNW (above) El Estor, along margin of open pit nickel mine, *Stevens & Martínez 25219* (MO*). SUCHITEPEQUEZ: near Patulul, *Standley 62150* (US). GUYANA. Wismar, *Hitchcock 17447* (F, IAN, NY, P, US). HONDURAS. ATLANTIDA: vicinity of La Ceiba, *Yunker et al. 8203* (MO). COLON: Trujillo, Río Negro, SE del cerro Copiro, *Clotter 12* (MO). COMAYAGUA: Centro Acuicola El Carao, *Casco 48* (MO). COPAN: San Francisco mountain, between San Isidro and San Cristóbal, about 10 miles south of Copán Ruinas, *Molina 30696* (MO). CORTES: just S of Puerto Cortés, *Pohl & Davidse 12054* (MO). GRACIAS A DIOS: Alrededores de Puerto Lempira, *Gorgun 19* (MO). OLANCHO: montaña Chifiringo, 20 km de Campamento, *Izaguirre 113* (MO, SI). SANTA BARBARA: above El Mochito, *Pohl & Davidse 12094* (MO). YORO: Cerro between Río Guan Guan and Río Texiguat, E of Cerro Guan Guan, *MacDougal et al. 3258* (MO). JAMAICA. Near Claverty Cottage, Portland, *Harris 11524* (P). MARTINIQUE. Près St. Pierie, *Hahn 787* (G, P). MEXICO. GUERRERO: 8 km al NE de Paraíso, carretera a Puerto del Gallo, *Tenorio et al. 1401* (MO). NAYARIT: steep hillsides 2 miles west of Mazatán, *McVaugh 19104* (US). OAXACA: 8 km del Río Lana rumbo a Palomares, *Beetle M-5063* (MO). QUINTANA ROO: a 25 km al Sur de F. Carrillo Puerto, *Tellez 3025* (MO). SAN LUIS POTOSI: 2 miles east of Tamzunchale, on north side of river, *Hitchcock & Stanford 7304* (US). TABASCO: near the 21 km post W of Huimanguillo on the Huimanguillo-Francisco Rueda road, *G. & J. Davidse 9383* (MO). VERACRUZ: El Mirador, *Beetle M-2254* (MO). NICARAGUA. MATAGALPA: carretera al Tuma, approx. 28 km NE de la ciudad de Matagalpa, finca El Diamante, en los márgenes del Río Yasica, *Guzmán et al. 914* (MO). RIO SAN JUAN: Quebrada Santa Crucita, *Moreno 23441* (MO). ZELAYA: Corn Island, N and W shore, Sand Fly Point to Southwest Bay, *Stevens 19943* (MO). PANAMA. BOCAS DEL TORO: Al NW del campamento Changuinola 1 de Corriente Grande, Cerro Bracha, *Correa et al. 3157A* (MO). CANAL ZONE: between Mindi and Colón, *Hitchcock 7942* (US). COCLE: along road to Coclesito near Saw Mill, *Hammel 4062* (SI). COLON: 5 miles northeast of Sabanita towards Portobello, *Wilbur & Luteyn 11629* (MO). DARIEN: vicinity of Paya,

Río Paya, *Stern et al.* 380 (MO). HERRERA: disturbed area surrounding Chepo de las Minas, *Folsom et al.* 7026 (MO). PANAMA: Cerro Ancón, *González* 12 (MO). SAN BLAS: mainland opposite Playón Chico, 0–3 miles from Caribbean, *Gentry* 6357 (MO). VERAGUAS: roadside adventures, road at base of Cerro Tuti, Santa Fé, *Folsom* 3002 (MO). PARAGUAY. ALTO PARANA: in regione fluminis Alto Paraná, *Fiebrig* 6008 (G, K, LIL, SI). AMAMBAY: in altiplanitie Sierra de Amambay, *Hassler* 11993 (G). CAGUAZU: Coronel Oviedo, *Rojas* 14402 (BAF). CANINDEYU: ruta 10, 80 km W de Guairá, cruce Ybyrobara, *Carnevali* 3763 (SI). CANTERA: Cantera, *Montes* 7222 (SI). GUAIRA: Azucarera de Tebicuary, Arroyo Yhacá, *Schinini* 5842 (G, SI). PARAGUARI: Mbocaiati, près de Paraguari, *Balansa* 2944 (BAF, G, K, P). PERU. HUANUCO: Tingo María, *Vera* 4080 (LIL). LORETO: Dto. Iquitos, Río Nanay, de Pampachica al caserío de Santa Rita, *Rimachi* 8014 (MO). MADRE DE DIOS: Río La Torre, Explorer's Inn, near confluence of Río Tambopata & Río La Torre, 39 km SW of Puerto Maldonado, *Smith* 359 (NY). SAN MARTIN: Tingo María, 625–1,100 m, *Allard* 20431 (US). SURINAME. Lucie Rivier, 2 km below affluence of Oost Rivier, *Irwin et al.* 55199 (MO, NY, US). ST. LUCIA. Savanne Edmund district, southeast of Piton Troumassée, *Proctor* 17958 (US). ST. VINCENT. Along Chateubelair River, *Morton* 5216 (US). TRINIDAD-TOBAGO. Castara, *Broadway* 4063 (G, P). VENEZUELA. AMAZONAS: tall rainforest ESE of Puerto Ayacucho, 10–30 km on road to Gavilán, *Steyermark et al.* 113908 (MO). APURE: Dto. Paéz. Selva de Cutufi, between Cutufi on the Río Cutufi and the Río Sanare, *Davidse & González* 21866 (MO*). ARAGUA: Parque Nacional Henry Pittier, Estación Rancho Grande, camino a La Toma, *Zuloaga & Ortíz* 4513 (MO, SI*, VEN). BARINAS: Boca de Uribante, 19 km más allá del Caño Anaru, *Trujillo et al.* 14951 (F). BOLIVAR: 35 km SW of Caicara del Orinoco, *Steyermark et al.* 131246 (SI). DELTA AMACURO: without locality, *Tamayo* 3635 (SI). LARA: 30 km SW of Barquisimeto, near road to Cerrata, *Meijer et al.* 51 (LIL). FALCON: F6, entre Sanare y el Río Tocuyo, *Wingfield* 6855 (MO). GUARICO: Dto. Infante, Parque Nacional Aguaro-Guariquito, Caño Carnestolendo, *Delascio et al.* 11482 (MO). MIRANDA: Guatopo, selvas pluviales, *Bernardi s.n.* (NY). PORTUGUESA: Camino hacia "La Estación," Municipio de Ospino, 1,200 m, *Stergios et al.* 4616 (MO, PORT). SUCRE: entre Barcelona y Cumaná, carretera secundaria a 8 km al sur de Santa Fé, 300 m, *Zuloaga et al.* 4366 (MO, SI, VEN). TACHIRA: Dto. Córdoba, Cerro La Camiri, just south of the town of Río Negro, *Davidse & González* 21545 (MO). ZULIA: Dto. Colón, forested slopes at the settlement of Río de Oro along the Río de Oro, *Davidse et al.* 18667 (MO).

Panicum pilosum is a very variable species, ranging from small specimens with a reduced panicle to others nearly 1 m tall with large inflorescences. For this reason, *P. coenosum* and *P. mil-leflorum* are synonymized, the first representing the smaller plants and the latter the larger ones.

In *P. pilosum* the spikelets are paired on secondary branches, as is the case in *P. leptachne* and *P. longum*. Occasionally, small branchlets may be present toward the base of the inflorescence on large specimens. Another peculiar feature of *P. pilosum* is the absence of ligules in most specimens.

11. *Panicum polygonatum* Schrader in

Schultes, *Mantissa* 2: 256. 1824. *Setaria polygonata* (Schrader) Kunth, *Rev. Gram.* 1: 47. 1829. *Panicum pilosum* Sw. var. *polygonatum* (Schrader) Doell, in C. Martius, *Fl. Bras.* 2(2): 211. 1877. TYPE: Brazil. Bahia: Ilheus, 1816, *Prince Maximilian s.n.* (holotype, LE, fragment, US 80925). Figures 3, 15, 23.

Panicum potamium Trin., *Gram. Panic.*: 239. 1826. TYPE: Brazil. Without locality, *Langsdorff s.n.* (holotype, LE, fragment, US 81301).

Panicum bourgaei Fourn., *Mexic. Pl.* 2: 25. 1886. TYPE: Mexico. Veracruz: "In valle Cordovense, Januario," *Bourgeau* 1662, pro parte (isotype, P).

Panicum boliviense Hackel, *Repert. Spec. Nov. Regni Veg.* 11: 19. 1912. TYPE: Bolivia. La Paz: Antahuacana, Espíritu Santo, 1909, *Buchtien* 2501 (holotype, W, fragment, US 80488; isotype, US*, photo of type, K).

Panicum ecuadorensis Mez, *Bot. Jahrb. Syst.* 56, Beibl. 125: 3. 1921. TYPE: Ecuador. Without locality, *Eggers* 15064 (holotype, B, fragment, US 80635).

Plants perennial, shortly rhizomatous, with culms decumbent, rooting and branching at the lower nodes, then becoming erect, 0.15–0.50(–1) m tall, upper nodes branching or not, internodes cylindric, glabrous to sparsely papillose-pilose, 5–12 cm long, nodes dark, compressed, densely pilose with appressed, retrorse hairs, occasionally glabrous. *Sheaths* shorter than the internodes, 2.7–3.5 cm long, glabrous or rarely papillose-pilose toward the distal portion, the margins membranous, with one margin long-ciliate with papillose-pilose hairs toward the distal portion, collar pilose. *Ligules* membranous, laciniate, 0.3–0.5 mm long. *Blades* lanceolate, 4–15(–20) cm long, 0.6–1.5(–2.5) cm wide, shortly pseudopetiolate, pseudopetiole pilose or glabrous, cordate to subcordate, sparsely pilose with appressed hairs on both surfaces or glabrous, the margins scaberrulous, the lower ones ciliate with caducous hairs. *Inflorescence* a lax, pyramidal panicle 8–20(–25) cm long, 3–15 cm wide; *main axis* sparingly hirsute to scabrous, first-order branches alternate, ascending, triquetrous and with or without long hairs, with one side flattened, the spikelets paired on short pedicels on short second-order branches. *Spikelets* narrowly elliptic, 1.3–1.6 mm long, 0.5–0.6 mm wide, pointed at the apex, greenish, pubescent or more commonly glabrous. *Lower glume* ovate, 0.7–0.9 mm long, ½ the length of the spikelet, 1–3-nerved, the keel scaberrulous toward the apex. *Upper glume* 1.2–1.4 mm long, glabrous, 5-nerved, acute. *Lower lemma* 1.2–1.4 mm long, 3–5-nerved, acute. *Lower palea* 1.1–1.3 mm long, 0.2–0.4 mm wide, hyaline, glabrous to more commonly absent; lower flower absent, occasionally present with 3 stamens. *Upper an-*

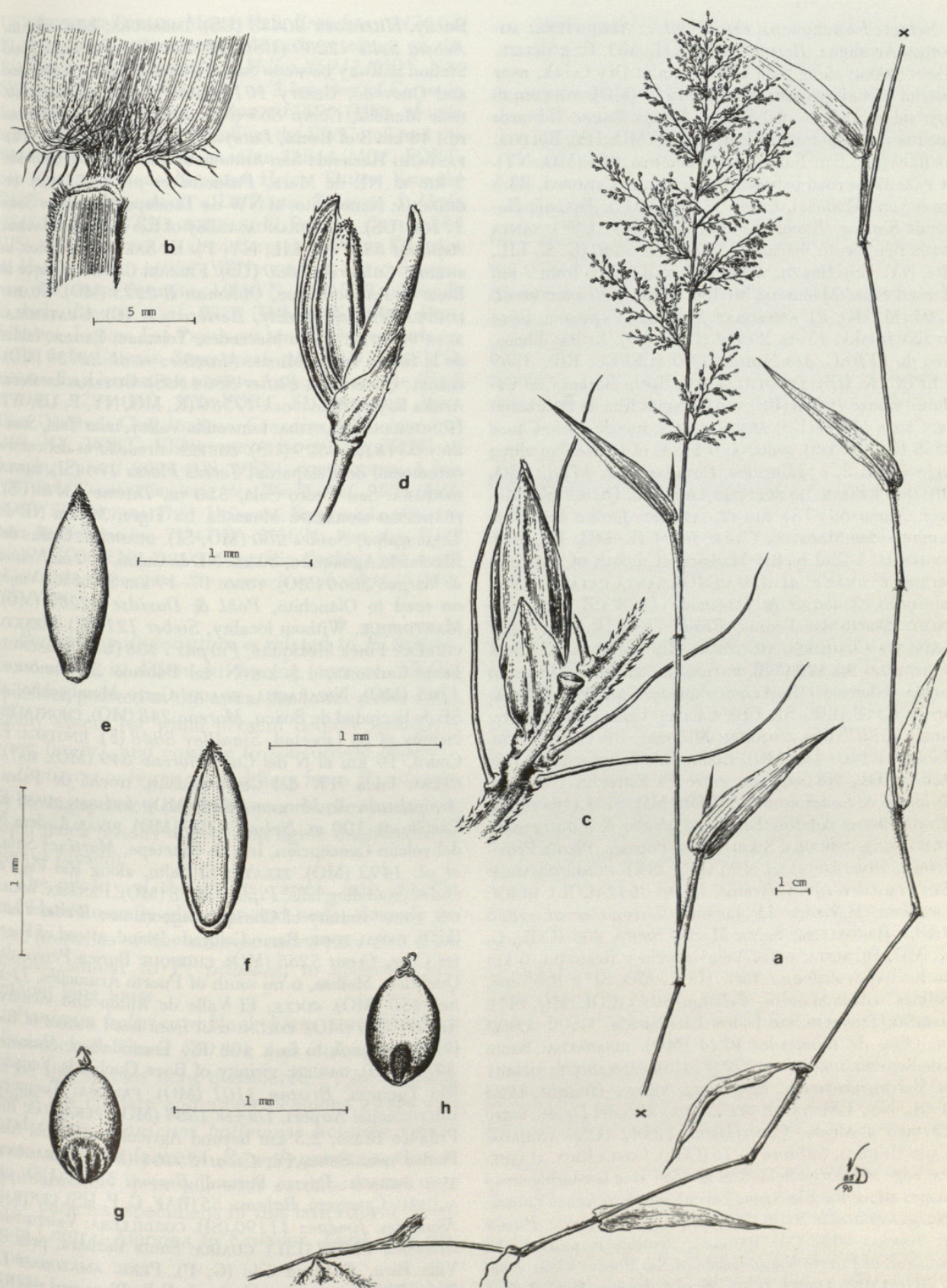


FIGURE 23. *Panicum polygonatum* (a, based on Chase 8555; b-h, on type specimen).—a. Habit.—b. Ligule and base of blade.—c. Branch of a panicle with spikelet.—d. Spikelet, lateral view.—e. Upper anthecium, lemma view.—f. Upper anthecium, palea view.—g. Caryopsis, embryo view.—h. Caryopsis, hilum view.

theceum elliptic, 1.1–1.3 mm long, 0.5 mm wide, stramineous, smooth, indurate, scabrous at the apex; anthers 3, 0.3–0.5 mm long. *Caryopsis* elliptic, brownish, 0.8 mm long, 0.5 mm wide; hilum oblong, embryo $\frac{1}{3}$ the length of the caryopsis.

Distribution and ecology. Widely distributed from Mexico to Paraguay, Bolivia and Brazil, occasionally present in Northwestern Argentina. It is found at borders of woods, swamps or in wet places, to 1,600 m elevation.

Selected specimens examined. ARGENTINA. MISIONES: Acaragua, *Bertoni* 2822 (LIL, MO, US). BELIZE. STANN CREEK: along road and stream at Dry Creek, near District of Cayo border, *Croat* 24517 (MO). TOLEDO: in high ridge, at base of hill near Manga Camp, Edwards Road beyond Columbia, *Gentle* 6537 (MO, US). BOLIVIA. COCHABAMBA: San Rafael, *R. Steinbach* 484 (MO, NY). LA PAZ: along road between Unduavi and Caranavi, 83.5 km beyond Unduavi, *Croat* 51586 (MO*); Tipuani, Hacienda Simaco, *Buchtien* 5334 (MO, NY, US*). SANTA CRUZ: Río Surutu, bañados, *Steinbach* 6840 (G, K, LIL, MO, NY, US). BRAZIL. ACRE: trail to Río Iaco from 7 km of road Sena Madureira to Río Branco, *Prance et al.* 7703 (M, MO, P). AMAZONAS: Solimoes, Copatana, beira do Rio Jutahy, *Froes* 20594 (IAN, US). BAHIA: Ilheus, area do CEPEC, *dos Santos* 3397 (CEPEC, RB), 3789 (CEPEC, K, RB). ESPIRITO SANTO: Santa Barbara do Caparaó, *Chase* 10073 (US). GOIAS: Santa Rita do Paranahyba, *Chase* 11630 (US). MINAS GERAIS: Juiz de Fora, *Chase* 8555 (F, NY, US). PARANA: 9 km E of Guaraniau along highway BR-277 to Curitiba, *Davidse et al.* 11283 (MO, UB). RIO GRANDE DO SUL: São Leopoldo, Quinta São Manuel, *Dutra* 601 (R). RIO DE JANEIRO: Jardim Botânico, caminho dos Macacos, *Chase* 8434 (F, MO, RB, US). RONDONIA: Island in Río Madeira at mouth of Río Jaciparana, *Prance et al.* 5343 (MO). SANTA CATARINA: Florianópolis, *Zuloaga & Deginani* 1878 (SI, US). SAO PAULO: Morro das Pedras, *Brade* 7815 (R, SP), 9162 (IAN, R). COLOMBIA. AMAZONAS: Río Loretoyacu, *Black & Schultes* 46-122 (US). ANTIOQUIA: carretera al mar en los alrededores del Río Ampurrumiado, *Gutiérrez & Barkley* 17C172 (LIL, SI, US). CALDAS: Chinchina, *Cuatrecasas* 23387 (US). CAQUETA: Miramar, Río Caquetá, *Soderstrom* 1401 (K, MO). CASANARE: Tauranema, *Uribe* 4268 (COL, NY). CAUCA: entre El Estrecho y Balboa, *Zuloaga & Londoño* 4238 (COL, MO, SI*). CHOCO: Río Atrato, bocas del Río Tanando, *Idrobo & Cuatrecasas* 2665 (US). CORDOBA: 3 km SW of Popales, Planta Providencia, *Alverson et al.* 196 (MO, NY). CUNDINAMARCA: San Francisco-Alto Guarama, *Wood* 3642 (COL). HUILA: La Plata, Hacienda La Limona, *Lozano et al.* 4826 (COL). MAGDALENA: Santa Marta, *Smith* 206 (COL, G, K, MO, P). META: entre Villavicencio y Restrepo, 6 km de Restrepo, *Zuloaga* 4087 (COL, MO, SI*); Restrepo, Salinas, subida al cerro, *Zuloaga* 3913 (COL, MO, SI*). NARIÑO: Trayecto San Isidro-La Planada, 1,500–1,800 m, *Olga de Benavides* 9214 (MO). RISARALDA: Santa Cecilia, *von Sneidern* 5192 (F, US). SANTANDER: vicinity of Barrancabermejo, Magdalena valley, *Haught* 1923 (COL, NY, US). VALLE DEL CAUCA: Alto del Dinde, entre Cartago y Alcalá, *Cuatrecasas* 22941 (US). VICHADA: Caño Urimica, *Cabrera* 2276 (COL). COSTA RICA. ALAJUELA: edge of cleared fields and wooded area bordering steep slopes above the Río Aguas Zarcas, south of Aguas Zarcas, *Burger & Stolze* 5136 (MO). CARTAGO: Turrialba, *Pittier & Tonduz* 4092 (M). HEREDIA: roadside in pasture, 10 km SSE of Puerto Viejo, E side of Río Puerto Viejo, *Pohl* 12818 (MO). LIMON: 6 km W of Guapiles, *Pohl & Calderón* 10017 (MO). PUNTARENAS: forest along trail between Las Alturas and Lotonsito, *Davidse* 24387 (MO, SI). SAN JOSE: 10 km by road SW of Santiago de Puriscal, *Pohl & Pinette* 13287 (MO). ECUADOR. CHIMBORAZO: entre Bucay y Heda, Rosa Mercedes, *Acosta Solís* 5254a (F). COTOPAXI: Tene fuerte, Río Pilato, *Dodson & Gentry* 12248 (MO). EL ORO: Porto Velho, *Hitchcock* 21256 (US). ESMERALDAS: Parroquia de Concepción, Playa Rica, *Mexía* 8417 (MO, US). GUAYAS: Teresita, 3 km west of

Bucay, *Hitchcock* 20433 (US). IMBABURA: Lita, 500 m, *Acosta Solís* 12239 (US). LOS RIOS: Río Palenque Field Station halfway between Santo Domingo de los Colorados and Quevedo, *Gentry* 10191 (MO). MORONA-SANTIAGO: near Mendez, *Camp* 865 (NY, US). NAPO: Baeza-Tena rd., 46 km S of Baeza, *Luteyn & Boom* 8360 (MO, NY). PASTAZA: Hacienda San Antonio de Baron von Humboldt, 2 km al NE de Mera, *Palacios et al.* 137 (MO). PICHINCHA: Nanegalito, al NW de Tandapaya, *Acosta Solís* 17166 (US). TUNGURAHUA: valley of Río Pastaza, Machai, *Asplund* 8527 (G, LIL, NY, P). EL SALVADOR. Ateos, in swamp, *Calderón* 1880 (US). FRENCH GUIANA. Crique la Boue de l'Approuague, *Oldeman B-2225* (MO). GUADALOUPE. Without locality, *Bertero s.n.* (G). GUATEMALA. ALTA VERAPAZ: Finca Mercedes, Teleman, Panzos, faldas de la Sierra de las Minas, *Martínez et al.* 22729 (MO). IZABAL: Quebradas, *Pittier* 8564 (US). GUYANA: Issorora, Aruka River, *Hitchcock* 17589 (K, MO, NY, P, US, W). HONDURAS. ATLANTIDA: Lancetilla Valley, near Tela, *Standley* 53181, 53529 (US). CORTES: alrededores del centro ceremonial de Pulapanza, *Torres Flores* 176 (SI). SANTA BARBARA: San Pedro Sula, 350 m, *Thieme* 5578 (US). FRANCISCO MORAZAN: Montaña La Tigra, 30 km NE de Tegucigalpa, *Soihet* 200 (MO, SI). OLANCHO: Orillas del Riachuelo Aguaquire, 30 km NE de Culmi, 700 m, *Nelson & Vargas* 2660 (MO). YORO: 17–19 km SE of Río Viejo, on road to Olanchito, *Pohl & Davidse* 12089 (MO). MARTINIQUE. Without locality, *Sieber* 121 (W). MEXICO. CHIAPAS: Finca Mexiquito, *Purpus* 7408 (US). VERACRUZ: Jesús Carranza, 1.5 km N del Poblado 2, *Zambrano* 1165 (MO). NICARAGUA. BOACO: Cerro Mombachito, al SE de la ciudad de Boaco, *Moreno* 248 (MO). CHONTALES: vicinity of La Libertad, *Standley* 8848 (F). JINOTEGA: El Cedro, 19 km al N del Cuá, *Moreno* 849 (MO). MATAGALPA: falda NW del Cerro Musún, trocha de Palan, *Araquistain & Moreno* 2438 (MO). RIO SAN JUAN: El Castillo, 0–100 m, *Nelson* 5190 (MO). RIVAS: Ladera N del volcán Concepción, Isla de Ometepe, *Martínez Salas et al.* 1493 (MO). ZELAYA: El Salto, along Río Pis Pis and surrounding hills, *Pipoly* 3578 (MO). PANAMA. BOCAS DEL TORO: vicinity of Chiriquí Lagoon, *von Wedel* 1121 (MO). CANAL ZONE: Barro Colorado Island, at end of Fierres Cove, *Croat* 5255 (MO). CHIRIQUI: Burica Península, Quebrada Mellize, 6 mi south of Puerto Armuelles, *Liesner* 450 (MO). COCLE: El Valle de Antón and vicinity, *Seibert* 485 (MO). COLON: trail from head waters of Río Boqueron back to fork with Río Escandaloso, *Hammel* 3973 (MO). DARIEN: vicinity of Boca Quebrada Venado, Río Tuqueza, *Bristan* 1101 (MO). PANAMA: Tocumen International Airport, *Dwyer* 1864 (MO). VERAGUAS: Río Primero Braso, 2.5 km beyond Agriculture School Alto Piedra near Santa Fè, *Croat* 25464 (MO). PARAGUAY. ALTO PARANA: Puerto Bertoni, *Bertoni* 5356 (US). CAAGUAZU: Caaguazú, *Balansa* 55 (BAF, G, P, US). CENTRAL: Asunción, *Jiménez* 11190 (SI). CORDILLERA: Valenzuela, *Schwarz* 11078 (LIL). GUAIRA: Santa Bárbara, près de Villa Rica, *Balansa* 54a (G, P). PERU. AMAZONAS: La Poza, Río Santiago, strip between Calle Piura and the Río Santiago, *Berlin* 3678 (MO). HUANUCO: Prov. Pachitea, Comunidad Nativa Santa Marta, on bank of Sungaruyacu, *Smith* 1251 (MO, NY). JUNIN: Colonia Perené, *Hitchcock* 22059 (US), 22124 (US). LORETO: lower Río Huallaga, *Williams* 4469 (US). MADRE DE DIOS: Tambopata Nature Reserve, *Barbour* 5245 (MO, NY). PASCO: Oxapampa, Río Iscozacín, tributary of Río Palcazu, *Knapp et al.* 7821 (MO). SAN MARTIN: on trail from Lamas to San Antonio east of Río Chupiseña, *Belshaw* 3497 (MO, SI).

US). TRINIDAD-TOBAGO. Mason Hall, *Broadway* 4476 (G, P). VENEZUELA. AMAZONAS: Neblina base camp, on the Río Mawarinuma, *Davidse & Miller* 26917 (MO*, NY, SI); along Río Mawarinuma, 1 to 3 km west of Cerro de La Neblina Base Camp, *Liesner* 15696 (MO). APURE: selva de Cutufi between Cutufi on the Río Cutufi and the Río Sanare, *Davidse & González* 21844 (MO*, PORT, SI). ARAGUA: Parque Nacional Henry Pittier, Estación Rancho Grande, camino a La Toma, *Zuloaga & Ortíz* 4515 (MO, SI, VEN). BOLIVAR: El Dorado, *Couret* 258 (US). DISTRITO FEDERAL: alrededores de la Planta Eléctrica de Mamo, *Pittier* 11082 (VEN). FALCON: Cerro Socopo, east side above Socopito, 10°30'N, 70°45'W, riverside in shade, *Liesner et al.* 8278 (MO, VEN). LARA: Dto. Iribarren, Laguna Los Papelones, en la selva nublada en la Fila de las Goteras, *Steyermark et al.* 103711 (VEN). MERIDA: La Llorona, on road to Amparo, *van der Werff & Ortíz* 5754 (MO, NY, PORT, SI). MIRANDA: Dto. Páez, Quebrada Chaguaramas, *González & Davidse* 946 (MO, NY, PORT, VEN). MONAGAS: 10 km WSW of Jusepín, *Pursell* 9094 (US, VEN). PORTUGUESA: 5 km NW de la Concepción, *van der Werff et al.* 7521 (MO, PORT, SI). TACHIRA: Dto. Uribante, Empresa Las Cuevas near La Fundación, 71°47'W, 8°50'N, *van der Werff* 4900 (MO, VEN). ZULIA: along Río Cachiri, just north of hacienda Salamanca, *Steyermark et al.* 123448 (MO, NY, VEN).

Panicum polygonatum is related to *P. laxum*, from which it differs in having narrow, elliptic spikelets, pointed at the apex, the lower palea commonly absent (or when present usually without a lower flower), and cordate to subcordate blades.

Panicum polygonatum differs from *P. pilosum* by having spikelets on short second-order branches, lower palea usually absent and ligule membranous, always present.

The pilosity of the plants varies, with sheaths and blades usually glabrous and nodes densely pilose; branches of the inflorescences vary also from hirsute, similar to *P. pilosum*, to scabrous and without long hairs.

Panicum boliviense Hackel was considered by Hitchcock & Chase (1910), and Zuloaga (1981) to be the species here considered *P. hylaeicum*, which has cordate and amplexicaulous leaves and rigid culms. *Panicum boliviense* actually represents a robust form of *P. polygonatum* that is approximately 1 m tall with cordate leaves and large panicles; specimens of this latter form range from Central America to Ecuador, Peru, and Bolivia.

The specimen *Idrobo & Cuatrecasas* 2665 has the lower lemma indurate, similar to the one on the upper antherium.

12. *Panicum stagnatile* A. Hitchc. & Chase, Contr. U.S. Natl. Herb. 17: 528, fig. 141. 1915. TYPE: Panama. Canal Zone: Frijoles, 12 Oct. 1911, *Hitchcock* 8388 (holotype,

US* 693328; isotypes, F, G, K, MO, NY, P, US, W, fragment of type, BAA). Figure 5.

Panicum bernoullianum Mez, Bot. Jahrb. Syst. 56, Beibl. 125: 3. 1921. TYPE: Guatemala. Mazatenango: *Bernouille* 543 (holotype, B; isotypes, G, K, NY, fragment of type, US 80485).

Plants perennial, the culms prostrate, decumbent and rooting at the lower nodes, then ascending, 1 to 2 m tall, simple or occasionally with sterile branches, internodes 12–20 cm long, cylindric, hollow, glabrous, compressed, brownish, puberulent; nodes compressed, glabrous. *Sheaths* striate, glabrous, the margins ciliate. *Ligules* membranous, short-ciliate at apex, ca. 0.8 mm long. *Blades* lanceolate, 22–35 cm long, 1.5–3 cm wide, flat, with long hairs at the base of the adaxial surface behind the ligule, short-pilose on the adaxial surface and glabrous on the abaxial surface, subcordate to cordate, acuminate at the apex. *Inflorescence* a terminal, pyramidal panicle, 20–40 cm long; *main axis* wavy, scabrous, pulvini pilose, numerous slender first-order branches ascending or spreading, spikelets unilateral on slender second-order branches, axis of the branches and pedicels triquetrous, scabrous. *Spikelets* loosely clustered, lanceolate, 1.6–1.8 mm long, 0.4–0.5 mm wide, pointed, brownish to purplish, scabrous, especially on the keels of glumes and lower lemma. *Lower glume* 0.6–0.9 mm long, $\frac{1}{3}$ to $\frac{1}{2}$ as long as the spikelet, 1–3-nerved, acute. *Upper glume* 3(–5)-nerved, not covering the apex of the upper antherium, obtuse to acute. *Lower lemma* 3-nerved, acute. *Lower palea* absent; lower flower absent. *Upper antherium* lanceolate, 1.5 mm long, 0.4 mm wide, membranous, scabrous at the apex, whitish, the margins of the lemma inrolled only at the base; anthers 0.4–0.8 mm long. *Caryopsis* unknown.

Distribution and ecology. Southern Mexico to Panama, growing commonly in swamps or margins of rivers or ponds, from sea level to 100 m.

Additional specimens examined. BELIZE. CAYO: Humming Bird Highway, Pry Creek, *Gentle* 8909 (G). STANN CREEK: Humming Bird Highway, *Gentle* 8408 (US*); Middlesex, *Gentle* 3029 (NY). EL SALVADOR. LA LIBERTAD: Near Ateos, 31 km W of San Salvador, *Fassett* 28272 (US). GUATEMALA. IZABAL: Puerto Barrios, *Hitchcock* 9153 (US). RETALHULEU: Río Coyote, along road 4 km W of Retalhuleu, 300 m, *Standley* 87507 (US). HONDURAS. ATLANTIDA: vicinity of Tela, *Standley* 54473 (US). MEXICO. CHIAPAS: Escuintla, *Matuda* 1861 (GH, US); Acacoyagua, *Matuda* 18416 (US). TABASCO: between San Juan Bautista and San Sebastián, *Rovirosa* 625 (K, US). VERACRUZ: Campo Experimental de Hule, El Palmar, Zongolica, *Vera Santos* 2655 (US). PANAMA. Without locality, *Hayes* 214 (K).

Panicum stagnatile is related to *P. pernambucense*; it differs by its lax panicles, with the spikelets more diffuse on the branchlets, plants smaller with culms decumbent, rooting or not at the lower nodes. Spikelets are similar to those of *P. polygonatum*.

13. *Panicum stevensianum* A. Hitchc. & Chase, Contr. U.S. Natl. Herb. 17: 498, fig. 77. 1915. TYPE: Puerto Rico. Campo Alegre, near Laguna del Tortuguero, 25 Nov. 1913, Chase 6616 (holotype, US* 693323; isotypes, NY, US). Figure 5.

Plants of indefinite duration, probably perennials, culms prostrate, spreading, decumbent and rooting at the lower nodes, then becoming erect, 20–100 cm tall, internodes glabrous, nodes brownish, glabrous. Sheaths striate, glabrous or sparsely papillose-pilose with caducous hairs, one margin ciliate toward the apex, collar brownish, glabrous. Ligules membranous, shortly ciliate at the apex, 0.4–1 mm long. Blades lanceolate, 10–25 cm long, 0.5–1.7 cm wide, flat, subcordate to cordate at the base, the lower margins ciliate to sparsely pilose on the adaxial surface or completely glabrous. Inflorescence a terminal, lax to contracted panicle, 8–28 cm long, 1–6 cm wide; main axis wavy, scabrous, first-order branches alternate, axis of the branches and pedicels scabrous, spikelets secund or in short second-order branchlets, paired on short pedicels. Spikelets narrowly elliptic, 1.9–2.6 mm long, 0.6–0.7 mm wide, greenish or tinged with purple, glabrous, biconvex, upper glume and lower lemma subequal or the upper glume slightly shorter, pointed. Lower glume 0.8–1.1 mm long, nearly ½ the length of the spikelet, acuminate, 3-nerved, the keel scabrous. Upper glume 5-nerved, the keel scaberulous. Lower lemma 5-nerved. Lower palea lanceolate, 2 mm long, 0.6 mm wide, hyaline, the margins scaberulous; lower flower bisexual to male or occasionally absent, lodicules 2, truncate, anthers 3, 1.2 mm long, stigma purple, plumose. Upper antheridium narrowly ovate, 1.7–1.9 mm long, 0.5 mm wide, whitish, firmly membranous, scabrous at the apex, the rest of its surface papillose and with silica bodies. Caryopsis unknown.

Distribution and ecology. West Indies, in Cuba, Puerto Rico, and Guadeloupe, and South America, collected in Colombia, Venezuela, and occasionally in northeastern Brazil.

Additional specimens examined. BRAZIL. PERNAMBUCO: Dois Irmaos, vicinity of Recife, Chase 7717

(US*). COLOMBIA. CASANARE: cerca del Hato Gandul, al sur del Río Pauto, Blydenstein s.n. (SI, US). CUBA. HABANA: Laguna de Ariguanabo, Ekman 11516, 13093 (both G, NY, P, R, UB, US*), 16929 (US), León 9030 (NY, US); Laguna de Castellano, Ekman 16796 (NY, P, R, UB, US*), Wilson 9558 (NY, US); Batabanó, Ekman 12630 (US*); clearing in a swampy wood, W of Batabanó, León 14200 (US). GUADALOUPE. Without locality, L'Hermier s.n. (G, P, US). VENEZUELA. GUARICO: Hato Flores Moradas, carretera Calabozo–Camaguán, Ramia 1213, 1288 (both VEN).

EXCLUDED SPECIES

Panicum scabridum Doell in Martius, Fl. Bras. 2(2): 201. 1877. TYPE: Brazil. Amazonas: Manaus, Campo de Jauari, Spruce 1281-3 (holotype, K, fragment, US; isotype, P).

Panicum prieurii Mez, Bot. Jahrb. Syst. 125: 3. 1921. TYPE: French Guiana. Without locality, Leprieur s.n. (holotype, B? not seen, fragment, US 2830932).

Panicum manacalensis Swallen, Phytologia 14: 77. 1966. TYPE: Venezuela. Amazonas: Río Atabapo, Wurdack & Adderley 42986 (holotype US; isotypes, F, GH, K, MO, NY, VEN).

This species was included by Zuloaga (1987) in section *Laxa*. *Panicum scabridum* resembles *P. laxum* in that it has a similar habit, ligule, inflorescence and spikelet type, with the lower glume 3-nerved, ½ the length of the spikelet, and the upper glume and lower lemma subequal, 5-nerved. It differs by having an indurate and smooth upper antheridium, with scattered simple papillae toward the apex, but without prickly hairs or silica bodies; also, the caryopsis is completely black in *P. scabridum*.

The leaf anatomy of *P. scabridum* has shown major differences in relation to species of section *Laxa*. In this species there are no fusoid cells, and there are usually two to four cells between contiguous vascular bundles. Aerenchyma is associated with the keel, and the inner mestome sheath has abundant starch grains.

Vouchers for anatomical study: Eiten & Eiten 10293, Leprieur 14, 452, Davidse 5444, 14617, Wurdack & Adderley 42986, Zuloaga 3984.

Panicum grande A. Hitchc. & Chase, Contr. U.S. Natl. Herb. 17: 529, fig. 143. 1915. TYPE: Panama. Gatun Lake, Hitchcock 9178 (holotype, US 693329; isotypes, G, K, NY, P, US, W).

Panicum myrianthum Mez, Bot. Jahrb. Syst. 56, Beibl. 125: 3. 1921. Not *P. miryanthum* Buse, in Miquel, 1854. SYNTYPES: Suriname. Without locality, Hostmann 434 (syntypes, K, US 974637), Hostmann et Kappler 253 (syntype, G).

This species differs from the others placed in section *Laxa* by having the upper antherium indurate with bicellular microhairs toward the apex, a character not present in the species of this section as here defined. Also, the spikelets are not disposed in unilateral branches as is characteristic of species in *Laxa*. In addition, *P. grande* lacks fusoid cells and has conspicuous lacunae in the mesophyll and superposed bundles.

Vouchers for anatomical study: *Black* 15352, *Pires* & *Silva* 4855, *Gentry* et al. 51575.

Panicum aristellum Doell, in C. Martius, Fl. Bras. 2(2): 22. 1877. TYPE: Brazil. Minas Gerais: without locality, *Widgren* s.n. (holotype, S not seen; isotype, US, fragment, US).

Related to section *Laxa* by its spikelet and upper antherium type, it differs mainly by having aristate glumes and by lacking fusoid cells in the leaves.

LITERATURE CITED

- BOUTON, J. H., R. H. BROWN, J. K. BOLTON & R. CAMPAGNOLI. 1981. Photosynthesis of grass species differing in carbon dioxide fixation pathways. *Pl. Physiol. (Lancaster)* 67: 433-437.
- BROWN, R. H. & W. V. BROWN. 1975. Photosynthetic characteristics of *Panicum milioides*, a species with reduced photorespiration. *Crop Sci. (Madison)* 15: 681-685.
- , J. H. BOUTON, P. T. EVANS, H. E. MALTER & L. L. RIGSBY. 1985. Photosynthesis, morphology, leaf anatomy, and cytogenetics of hybrids between C_3 and C_3/C_4 *Panicum* species. *Pl. Physiol. (Lancaster)* 77: 653-658.
- BROWN, W. V. 1977. The Kranz syndrome and its subtypes in grass systematics. *Mem. Torrey Bot. Club* 23: 1-97.
- CHRISTOPHER, J. & A. ABRAHAM. 1976. Studies on the cytology and phylogeny of South Indian grasses. III. Subfamily VI: Panicoideae, tribe Paniceae. *Cytologia* 41: 621-637.
- CLAYTON, W. D. & S. A. RENVOIZE. 1986. *Genera Graminum*. Kew Bull. Additional Series XIII. London.
- DAVIDSE, G. & R. W. POHL. 1972a. Chromosome numbers and notes on some Central American grasses. *Canad. J. Bot.* 50: 273-283.
- & ———. 1972b. Chromosome number, meiotic behavior, and notes on some grasses from Central America and the West Indies. *Canad. J. Bot.* 50: 1441-1452.
- & ———. 1974. Chromosome number, meiotic behavior, and notes on tropical American grasses (Gramineae). *Canad. J. Bot.* 52: 317-328.
- & ———. 1978. Chromosome numbers of tropical American grasses (Gramineae): 5. *Ann. Missouri Bot. Gard.* 65: 637-649.
- ELLIS, R. P. 1976. A procedure for standardizing comparative leaf blade anatomy in the Poaceae. I. The leaf blade as viewed in transverse section. *Bothalia* 12: 65-109.
- . 1979. A procedure for standardizing comparative leaf blade anatomy in the Poaceae. II. The epidermis as seen in surface view. *Bothalia* 12: 641-672.
- . 1987. A review of comparative leaf blade anatomy in the systematics of the Poaceae: the past twenty-five years. Pp. 3-10 in T. R. Soderstrom, K. W. Hilu, C. S. Campbell & M. E. Barkworth (editors), *Grass Systematics and Evolution*. Smithsonian Institution Press, Washington, D.C.
- . 1988. Leaf anatomy and systematics of *Panicum* (Poaceae: Panicoideae) in southern Africa. *Monogr. Syst. Bot. Missouri Bot. Gard.* 25: 129-156.
- GOULD, F. W. & T. R. SODERSTROM. 1967. Chromosome numbers of tropical American grasses. *Amer. J. Bot.* 54: 676-683.
- HITCHCOCK, A. S. & A. CHASE. 1910. The North American species of *Panicum*. *Contr. U.S. Natl. Herb.* 15: 1-396.
- & ———. 1915. Tropical North American species of *Panicum*. *Contr. U.S. Natl. Herb.* 17: 459-539.
- Hsu, C. C. 1965. The classification of *Panicum* (Gramineae) and its allies, with special reference to the characters of lodicule, style-base and lemma. *J. Fac. Sci. Univ. Tokyo, Sect. 3 (Bot.)* 9: 43-150.
- KILLEEN, T. & L. G. CLARK. 1986. Fusoid-like cells in *Panicum* section *Laxa* (Poaceae: Panicoideae). *Amer. J. Bot.* 73: 771.
- KU, M. S. B. & G. E. EDWARDS. 1978. Photosynthetic efficiency of *Panicum hians* & *Panicum milioides* in relation to C_3 and C_4 plants. *Pl. Cell Physiol.* 19: 665-675.
- , ——— & R. KANAI. 1976. Distribution of enzymes related to C_3 and C_4 pathways of photosynthesis between mesophyll and bundle sheath cells of *Panicum hians* and *Panicum milioides*. *Pl. Cell Physiol.* 64: 257-262.
- LAZARIDES, M. 1980. The tropical grasses of Southeast Asia. *Phanerogamum Monographiae Tomus XII*. Cramer. Vaduz.
- MEHRA, P. N. 1982. Cytology of East Indian grasses. P. N. Mehra, Chandigarh.
- & J. D. CHAUDHARY. 1976. In IOPB chromosome number reports. LIV. *Taxon* 25: 631-649.
- & ———. 1981. Male meiosis in some grasses of the tribe Paniceae. II. Genus *Panicum* from Northeastern India. *Cytologia* 46: 685-698.
- MORGAN, J. A. & R. H. BROWN. 1979. Photosynthesis in grass species differing in carbon dioxide fixation pathways. *Pl. Physiol. (Lancaster)* 64: 257-262.
- MORGAN, J. A., R. H. BROWN & B. J. REGER. 1980. Photosynthesis in grass species differing in carbon dioxide fixation pathways. III. Oxygen response and enzyme activities of species in the *Laxa* group of *Panicum*. *Pl. Physiol. (Lancaster)* 65: 156-159.
- NÚÑEZ, O. 1952. Investigaciones cariosistémáticas en las Gramíneas argentinas de la tribu Paniceae. *Revista Fac. Agron. Univ. Nac. La Plata* 28: 229-255.

- PALACIOS, R. A. 1968. Variaciones en la estructura de las espiguillas en algunas especies argentinas de *Panicum*. Bol. Soc. Argent. Bot. 12: 38-43.
- PILGER, R. 1931. Bemerkungen zu *Panicum* und verwandten gattungen. Notizbl. Bot. Gart. Berlin-Dahlem 104: 237-247.
- . 1940. Gramineae. III: Unterfamilie Panicoideae. Pp. 8-15 in A. Engler & K. Prantl (editors), Die Natürlichen Pflanzenfamilien, 2nd edition, 14e. Engelmann, Leipzig.
- POHL, R. W. 1980. Gramineae. In: W. Burger (editor), Flora Costaricensis. Fieldiana, Botany 4: 350-392.
- & G. DAVIDSE. 1971. Chromosome numbers of Costa Rican grasses. Brittonia 23: 293-324.
- & N. R. LERSTEN. 1975. Stem aerenchyma as a character separating *Hymenachne* and *Sacciolepis* (Gramineae: Panicoideae). Brittonia 27: 223-227.
- RENOUVE, S. A. 1988. Hatschbach's Paraná Grasses. Royal Botanic Gardens, Kew.
- TATEOKA, T. 1962. A cytological study of some Mexican grasses. Bull. Torrey Bot. Club 89: 77-81.
- WATSON, L., H. T. CLIFFORD & M. J. DALLWITZ. 1985. The classification of Poaceae: subfamilies and supertribes. Austral. J. Bot. 33: 433-484.
- WILSON, J. R., R. H. BROWN & W. R. WINDHAM. 1983. Influence of leaf anatomy on the dry matter digestibility of C₃, C₄, and C₃/C₄ intermediate types of *Panicum* species. Crop. Sci. (Madison) 23: 141-146.
- ZULOAGA, F. O. 1981. Notas sinonímicas en el género *Panicum* (Gramineae). Darwiniana 23: 639-649.
- . 1987. Systematics of New World species of *Panicum* (Poaceae: Paniceae). Pp. 287-306 in T. R. Soderstrom, K. W. Hilu, C. S. Campbell & M. E. Barkworth (editors), Grass Systematics and Evolution. Smithsonian Institution Press, Washington, D.C.
- & T. SENDULSKY. 1988. A revision of *Panicum* subg. *Phanopyrum* sect. *Stolonifera* (Poaceae: Paniceae). Ann. Missouri Bot. Gard. 75: 420-455.
- & T. R. SODERSTROM. 1985. Classification of the outlying species of New World *Panicum* (Poaceae: Paniceae). Smithsonian Contr. Bot. 59: 1-63.
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