

Classification of the Outlying
Species of New World *Panicum*
(Poaceae: Paniceae)

Fernando O. Zuloaga
and *Thomas R. Soderstrom*



SMITHSONIAN INSTITUTION PRESS

City of Washington

1985

ABSTRACT

Zuloaga, Fernando O., and Thomas R. Soderstrom. Classification of the Outlying Species of New World *Panicum* (Poaceae: Paniceae). *Smithsonian Contributions to Botany*, number 59, 63 pages, 25 figures, 2 tables, 1985.— In the present study a number of species originally assigned to *Panicum* but not fitting well within its boundaries have been examined. Some of the characters that have been used in the past to distinguish genera in the tribe have been re-examined, including type of hilum, spikelet compression, relative length of the glumes, consistency of the upper antherium and whether crested or not, and carriage of the spikelet relative to the axis. Further characters of taxonomic importance have been revealed by studies made with the scanning electron microscope (SEM) at higher magnifications than previously possible. The results of these studies indicate that several species should be removed from *Panicum* and transferred to other genera. Accordingly the following changes have been made: *P. megastachyum* Nees ex Trinius and *P. albicomum* Swallen & García Barriga have been transferred to *Brachiaria*, *P. glutinosum* Swartz and *P. villaricense* Mez to *Homolepis*, *P. grandifolium* Doell to *Ichnanthus*, *P. killipii* Hitchcock to *Paspalum*, and *P. macranthum* Trinius to *Streptostachys*. *Panicum arnacites* Trinius forms the basis of a new genus, *Tatianyx*. With these changes in content the descriptions of *Homolepis* and *Streptostachys* are emended, two new species—*Brachiaria tatanianae* and *Streptostachys ramosa*—are described, and the unusual species *P. aristellum* Doell is characterized and a possible relationship discussed. A chart is presented that compares the characters of the genera covered in the present investigation, *P. aristellum* and the two new species are illustrated, and SEM photomicrographs of all taxa are included.

OFFICIAL PUBLICATION DATE is handstamped in a limited number of initial copies and is recorded in the Institution's annual report, *Smithsonian Year*. SERIES COVER DESIGN: Leaf clearing from the katsura tree *Cercidiphyllum japonicum* Siebold & Zuccarini.

Library of Congress Cataloging in Publication Data

Zuloaga, Fernando.

Classification of the outlying species of New World *Panicum* (Poaceae: Paniceae).

(Smithsonian contributions to botany ; no. 59)

Bibliography: p.

Supt. of Docs. no.: SI 1.29:59

1. *Panicum*—Classification. 2. Grasses—America—Classification. 3. Grasses—Classification. 4. Botany—America—Classification. I. Soderstrom, Thomas R. II. Title. III. Series

QK1.S2747 no. 59 [QK495.G74] 581s [584'.92] 84-600221

Contents

	<i>Page</i>
Introduction	1
Methods and Materials	3
Acknowledgments	3
Key to the Genera of Paniceae	3
<i>Brachiaria</i>	4
<i>Brachiaria megastachya</i> , new combination	5
<i>Brachiaria tatiana</i> e, new species	7
<i>Brachiaria albicoma</i> , new combination	11
⟨Comparison of <i>Homolepis</i> and <i>Panicum</i> ⟩	11
<i>Homolepis</i> , emended	14
Key to the Species of <i>Homolepis</i>	14
<i>Homolepis aturensis</i>	15
<i>Homolepis glutinosa</i> , new combination	19
<i>Homolepis isocalyca</i>	24
<i>Homolepis longispicula</i>	27
<i>Homolepis villaricensis</i> , new combination	29
<i>Ichnanthus</i>	31
<i>Ichnanthus grandifolius</i> , new combination	31
⟨Taxonomic Position of <i>Panicum aristellum</i> ⟩	33
<i>Panicum</i>	36
<i>Panicum aristellum</i>	36
⟨Taxonomic Position of <i>Panicum killipii</i> ⟩	40
<i>Paspalum</i>	40
<i>Paspalum killipii</i> , new combination	40
⟨Taxonomic Position of <i>Streptostachys</i> ⟩	42
<i>Streptostachys</i> Desvaux, emended	46
Key to the Species of <i>Streptostachys</i>	46
<i>Streptostachys asperifolia</i>	47
<i>Streptostachys macrantha</i> , new combination	50
<i>Streptostachys ramosa</i> , new species	52
⟨Taxonomic Position of <i>Tatianyx</i> ⟩	55
<i>Tatianyx</i> Zuloaga & Soderstrom, new genus	56
<i>Tatianyx arnacites</i> , new combination	56
Literature Cited	61

Classification of the Outlying Species of New World *Panicum* (Poaceae: Paniceae)

Fernando O. Zuloaga
and *Thomas R. Soderstrom*

Introduction

The genus *Panicum*, described by Linnaeus in 1753, is one of the largest genera of grasses, with approximately 600 species of worldwide distribution; the majority of these are tropical or subtropical. Because of its size and widespread occurrence the genus has been subjected to the scrutiny of many investigators but none has studied it in its entirety. The African members received a rather thorough review in the early part of this century by Otto Stapf of Kew, who allocated them to a number of sections. On this side of the Atlantic the American agrostologists Alfred S. Hitchcock and Agnes Chase made detailed studies of the North American species and grouped most of them according to natural affinity. Their chief studies were published in "The North American species of *Panicum*" in 1910 and "Tropical North American species of *Panicum*" in 1915. Chase also wrote a series of papers (1906, 1908, 1911) giving detailed analyses of New World genera in the tribe Paniceae. Among the most recent works on *Panicum* and allied

genera is that of Pilger (1931), who divided the genus into eight subgenera and 11 sections, and of Hsu (1965), who made a complete analysis of the tribe—*Panicum* in particular—reorganizing it into five subgenera and 25 sections. Hsu utilized newly recognized characters pertaining to such structures as the ligule, midnerve of the blade, lodicules, and epidermis of the leaf and upper lemma.

Since the time of Chase, especially during the past decade, herbarium holdings of tropical American *Panicum* have expanded dramatically due to an increase in collecting activity. As new species have been described and known ones restudied, the most interesting problems have continued to be the delimitation of the genus itself and its position within the tribe.

In the present study we have examined a number of species that were originally described in *Panicum* but did not seem to be well accommodated in it. This review has prompted us to re-examine some of the characters that have been used in the past to distinguish genera in the tribe, such as type of hilum, spikelet compression, relative length of the glumes, consistency of the upper antherium and whether crested or not, and carriage of the spikelet relative to the axis. Some of the most important characters that we

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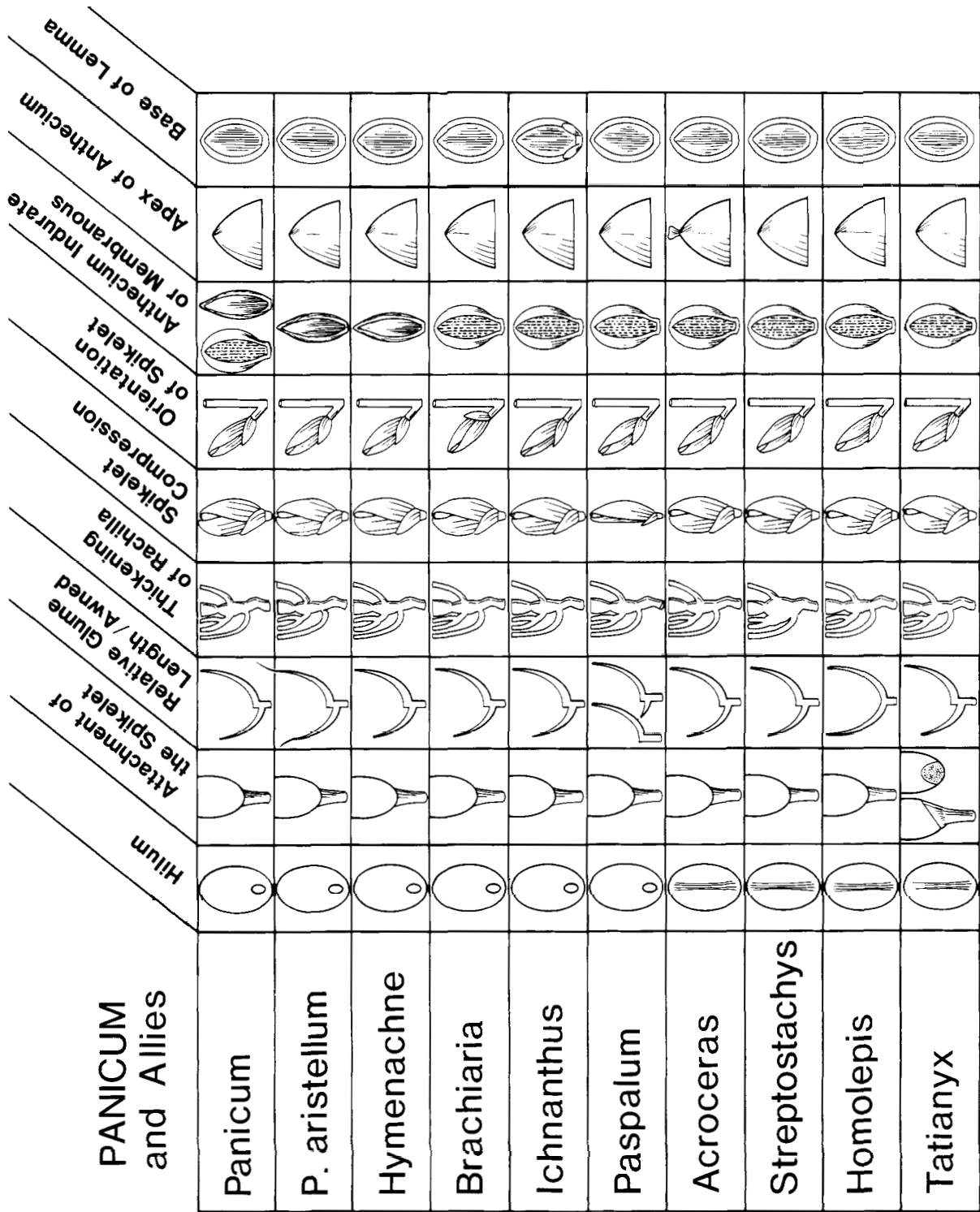


FIGURE 1.—Scheme of panicoid taxa and some distinguishing characters.

have found to be of generic value are illustrated in Figure 1.

Information derived from studies made with the scanning electron microscope (SEM) on the surface of the lemmas and paleas of the upper floret has been especially useful in the present study. Characters revealed at the higher magnifications often corroborate decisions based on gross morphology.

We have concluded that several species described in *Panicum* should be transferred to other genera, such as *Brachiaria*, *Ichnanthus*, and *Paspalum*. One of the species does not fit within the boundaries of any described genus and we are thus elevating it to that rank with the name of *Tatianyx*.

A study of gross morphological characters as well as those revealed by the SEM should be extended to all species of *Panicum*. When these data are collected for the entire genus we will be able to compare them more meaningfully and arrive at a fuller understanding of the genus and relationships of allied taxa.

Rather than refer to the two florets (anthechia) of the typical panicoid spikelet as fertile and sterile, we designate them by their position in the spikelet. The fertile anthechium is thus the "upper anthechium" and what is usually called the sterile floret is referred to as the "lower anthechium." This avoids the biased use of the word sterile, which is really incorrect, because this floret or anthechium usually contains stamens. Our use of the term anthechium is for the unit that includes the lemma and palea and when we refer to these structures we again use their position: upper lemma, upper palea, lower lemma, lower palea.

As the earlier spelling of "oecology" has given way to "ecology" and "gynoecium" to "gynecium" in modern American usage, we have adopted these more evolved forms. Following the same rules we are also using "anthechium" and "andro-

cium" instead of "anthoecium" and "androecium."

Data in "Additional Specimens Seen" and "Paratypes" sections have been quoted from specimen labels without editing, except for abbreviations of distance and direction.

A synopsis of New World Paniceae is reflected in the Contents, with background notes and comparisons set off with angle brackets.

METHODS AND MATERIALS.—Classical taxonomic methods have been used in the present study, utilizing a Wild M5 dissecting microscope and Leitz Ortholux compound microscope. Observations at higher magnification were made using the scanning electron microscope. For these studies, anthechia were removed from dried herbarium specimens, secured on stubs, carbon coated in a vacuum evaporator, and then coated with a gold-palladium alloy. The specimens so treated were then viewed in a Cambridge S4-10 or Cambridge Stereoscan 250 Mk 2 scanning electron microscope operating at 10–20 kV.

In addition to the extensive herbarium collections available at US, we relied on specimens lent by the following herbaria: B, BAA, BAF, CTES, F, GH, LIL, LP, M, MO, NY, S, and SI.

ACKNOWLEDGMENTS.—The senior author is grateful to the Consejo Nacional de Investigaciones Científicas y Técnicas de la República Argentina (CONICET) for a grant that allowed him to spend two years (1982–1983) at the Smithsonian Institution as a post-doctoral fellow. The junior author appreciates the opportunity afforded him by the New York Botanical Garden to participate in an expedition to the Brazilian cerrados in 1964, at which time he collected material of the new genus *Tatianyx*. To Ms. Alice Ruth Tangerini we are both indebted for her skillful rendering of the illustrations of panicoid grasses in this paper and the chart of genera and characters depicted in Figure 1.

Key to the Genera of Paniceae

(*Acroceras* and *Hymenachne* are not treated in this paper)

1. Hilum of caryopsis linear 2
2. Spikelets densely villous and positioned obliquely on the falcate pedicel, with a callus on the

- dorsal face *Tatianyx*, new genus
2. Spikelets glabrous and positioned evenly on the truncate pedicel, without a callus 3
 3. Lower and upper glumes equal in length, shape, and nervation; upper antherium chartaceous with the margins of the lemma flat, the lemma not crested at the apex and rachilla not thickened between the lower glume and upper antherium *Homolepis*, emended
 3. Lower glume shorter than the upper, differing in shape and nervation; upper antherium indurate with the margins of the lemma inrolled, the lemma crested at the apex or with the rachilla thickened between the lower glume and the upper antherium 4
 4. Upper antherium crested at the apex; rachilla not thickened between the lower glume and upper antherium *Acroceras*
 4. Upper antherium not crested at the apex; rachilla thickened between the lower glume and upper antherium *Streptostachys*, emended
 1. Hilum of caryopsis punctiform, rarely oblong 5
 5. Upper antherium membranous, hyaline, with the palea free at the apex, not covered by the lemma; lower palea absent; panicles spiciform to contracted, dense *Hymenachne*
 5. Upper antherium indurate, when membranous the palea completely covered by the lemma at its apex; lower palea sometimes present; panicles lax to contracted, rarely spiciform . . . 6
 6. Spikelets with the back of the upper lemma turned away from the rachis, the lower glume facing it *Brachiaria*
 6. Spikelets with the back of the upper lemma facing the rachis, the lower glume turned away from it 7
 7. Upper antherium with appendages or "excavations" at the base; spikelets keeled and somewhat compressed laterally *Ichnanthus*
 7. Upper antherium without appendages or "excavations" at the base; spikelets not keeled nor compressed laterally 8
 8. Spikelets plano-convex, shortly pedicellate on unilateral racemes; lower glume commonly absent, small when present *Paspalum*
 8. Spikelets biconvex, commonly arranged in panicles, less frequently in unilateral racemes, variously pedicellate; lower glume always present, variable in size *Panicum*

Brachiaria

In 1853 Grisebach elevated to the level of genus the section *Brachiaria* of *Panicum*, which Trinius had established in 1826. As the type-species of his new genus, Grisebach cited *B. eruciformis* (*Panicum eruciforme* Smith). Chase (1911) accepted the genus and underscored its distinctive type of panicle and spikelets, the former consisting of spike-like racemes and the latter inverted in position, with the lower glume adjacent to the rachis. She also pointed out that the

upper antherium is frequently papillose-rugose, a character that Stapf (1919) also used to delimit the genus.

Hitchcock (1935, 1951), Gardner and Hubbard (1938), Pilger (1940, 1954), and Jacques-Félix (1962), among others, considered spikelet position as an important character to differentiate the genus. Ascertaining the position of the lower glume in species with long pedicels, however, is difficult, but Gardner and Hubbard pointed out a way to overcome this. They suggested that the spikelet just below the terminal

one on the axis or on a branch of the panicle be examined to determine the position of the lower glume, because the spikelet is generally short-pedicellate and appressed to the rachis. They commented that the orientation is still occasionally unclear due to suppression or rudimentary development of the lower spikelet of the pair, in which case the terminal spikelet appears to be solitary and in an abaxial position.

In 1969 Parodi, detailing and confirming the findings of Gardner and Hubbard, utilized the character of spikelet position in transferring to *Brachiaria* five species that had previously been included in the Fasciculata group of *Panicum*. In some of these—*B. echinulata*, *B. lorentziana*, and *B. mollis*—the spikelets are borne on rather long pedicels and their position is difficult to ascertain, a situation reminiscent of some African species such as *Brachiaria ramosa* (L.) Stapf and *B. deflexa* (Schumacher) Hubbard. Although she noted difficulty in differentiating the Brazilian species of *Brachiaria* on the basis of spikelet position, Sendlisky (1978) accepted the character as valid and did not provide further ones.

Unlike previous authors, Blake (1958) did not consider spikelet position a definitive enough character to separate *Brachiaria* from *Panicum*, offering other characters instead: the texture of the upper antherium, presence or absence of a rupture line, and type of areole on the dorsal face of the upper lemma toward its base. According to him,

In one, characteristic of *Panicum* subgen. *Panicum* (the *Panicum* type), the fertile floret is more or less biconvex and muticous with the lemma smooth over the whole of the back and the rupture line and areole resemble the rest of the back in surface in curvature. In the trend represented by *Urochloa* (*Urochloa*-type), the fertile floret is plano-convex or nearly so, sometimes apiculate or aristulate, with the lemma more or less strongly transversely rugose, the rupture line is prominent and the areole more or less flattened or depressed, less rugulose than elsewhere.

Unfortunately, these characters are not invariable. Pohl (1980) discounted the presence or absence of a rupture line as a generic character in

the Paniceae; and while the texture of the upper antherium may be rugose or papillose in most *Brachiarias*, it is smooth in the type species! *Panicum maximum*, *P. millegrana*, *P. sellowii*, and *P. trichoides* are examples of species in which the upper antherium is rugose.

In the present study spikelet position is considered to be of generic value, in concordance with most agrostologists, and is the basis on which we are transferring the following species of *Panicum* to *Brachiaria*: *P. megastachyum* Nees ex Trinius, 1826; *P. megastachyum* Nees, 1829, not Nees ex Trinius, 1826; and *P. albicomum* Swallen & García-Barriga.

***Brachiaria megastachya* (Nees ex Trinius)
Zuloaga & Soderstrom, new combination**

FIGURE 2

Panicum megastachyum Nees ex Trinius, 1826:205. [Type: "V. spp. Brasil. Langsdorff." Holotype, LE, not seen; fragment of the type, US sheet no. 974713. "In saxosis umbrosis Serra da Lapa," cited under *Panicum megastachyum* Nees, 1829:155, refers to this specimen.]

Plants perennial (?), the base not seen. *Culms* cylindrical, hollow, glabrous. *Nodes* obscure, glabrous. *Sheaths* pale, glabrous. *Ligule* ~1.5 mm long, membranous, long-ciliate above; collar glabrous, inconspicuous. *Blades* lanceolate, acuminate, flat, approximately 12 cm long, 0.8–1 cm wide, subcordate with the adaxial surface pubescent, the abaxial glabrous and margins scabrous. *Panicles* lax, diffuse, many-flowered, ~25 cm long, 10 cm wide, the branches alternate to subopposite and diverging from the rachis, the spikelets diffused; axis angular, scabrous, with thick evenly distributed papillose-pilose hairs; branches hirsute with hairs similar to those present on the axis, the axils densely pubescent, the spikelets 2 or 3 on each branch, one subsessile, the other long-pedicellate, the pedicels 1–12 mm long, triquetrous, hirsute. *Spikelets* long-ellipsoid, 3.8–3.9 mm long, 1.4–1.5 mm wide, stramineous to brown, with the lower glume adjacent to the rachis. *Lower glume* ovate, acute, 1.8–2.2 mm

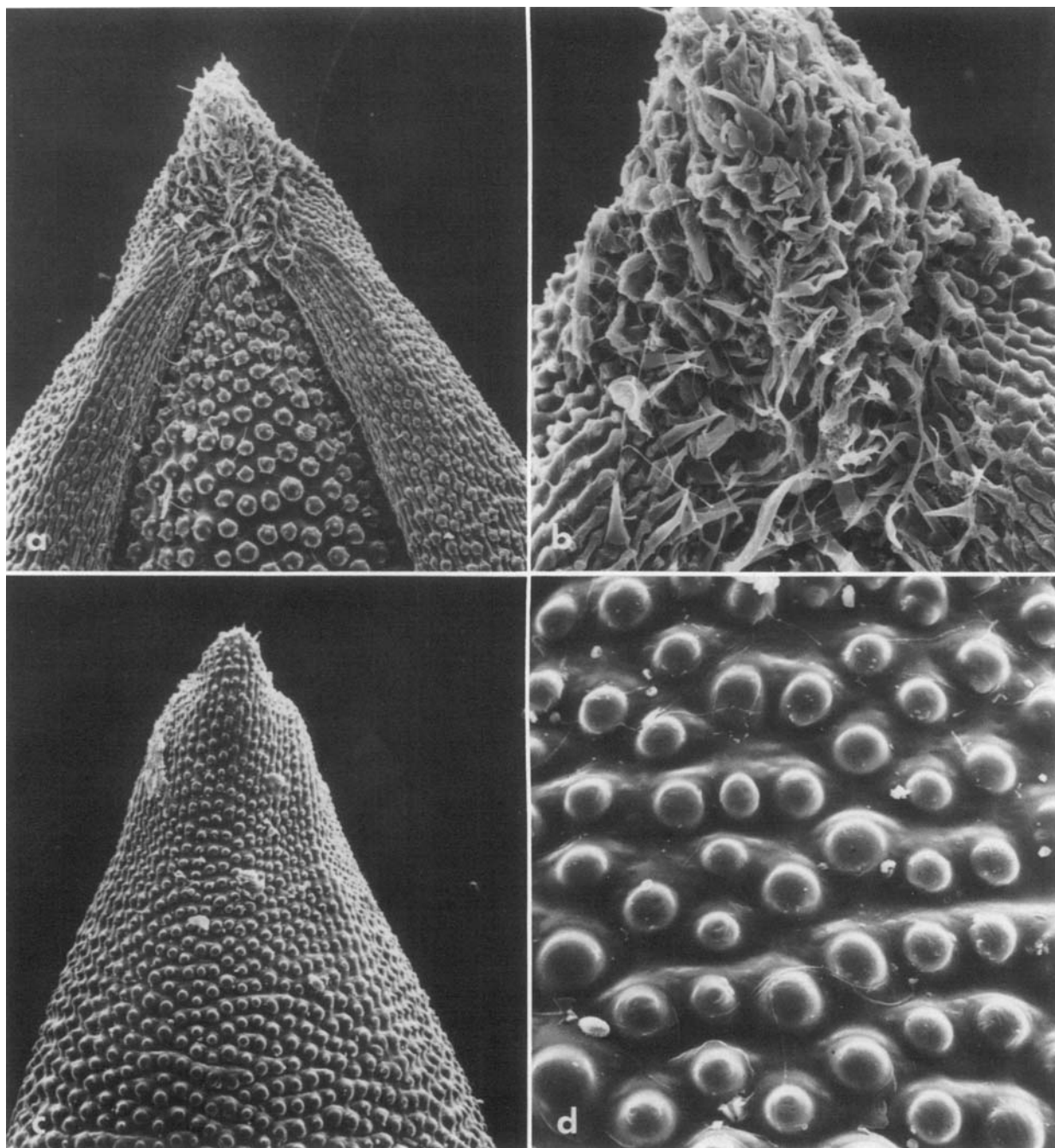


FIGURE 2.—*Brachiaria megastachya*, new combination: *a*, upper antherium, palea side ($\times 100$); *b*, apex of lemma, detail of *a* showing flat macrohairs ($\times 400$); *c*, upper antherium, lemma side ($\times 100$); *d*, detail of *c* showing simple papillae evenly distributed over the surface, making it rugose ($\times 500$). All photomicrographs based on *Riedel 96* (US).

long, glabrous, 3–5-nerved, the nerves anastomosed toward the glabrous to pubescent summit. *Upper glume* obtuse to subacute, 3.3–3.5 mm long, usually not covering the upper antherium, 5–7-nerved, the nerves anastomosed toward the short-lanate summit. *Lower lemma* subacute, glume-like, lanate on the margins, 3.6–3.7 mm long, 5-nerved, the nerves anastomosed. *Lower palea* narrowly elliptic, conspicuous, 3.2–3.4 mm long, 1–1.2 mm wide, membranous, glabrous except for flat hairs toward the apex; male flower present with 2 lodicules and 3 anthers, 2.2 mm long. *Upper antherium* narrowly ellipsoid, acute, 3.2–3.4 mm long, 1.1–1.3 mm wide, plano-convex, stramineous to brown, glabrous, covered with evenly distributed simple or compound papillae, the apex of the upper lemma with numerous hooks. *Caryopsis* not seen.

ADDITIONAL SPECIMENS SEEN.—BRAZIL. Without locality, *Riedel 96 (US), 1143 (NY)*.

DISCUSSION.—In 1829 Trinius added the following data in his description of the species (as translated):

Culms 1.8–2.4 m tall, cylindrical, glabrous, branching, shortly geniculate. Sheaths glabrous. Blades linear-lanceolate, flat. Panicle much-branched, with the branches spreading from the rachis, more than 30 cm long.

His illustration depicts a much-branched panicle with spikelets occurring mostly in pairs on the racemes, one subsessile and the other long-pedicellate.

On a sheet with a fragment of the type specimen at US, Chase made the following annotation:

Culms 4–6 ft., blades 1 ft. or more, ½ inch wide, glabrous, sheath wholly glabrous or silky on the collar, panicle about 1 ft., erect, contracted, rachis & branches and pedicels pilose, spikelets about 4 mm, fruit slightly roughened, not shiny. Type of Nees ex Trin. 1826, not Nees ipse.

Even though the terminal spikelet in this species is borne on a long pedicel, the inherent position of the spikelet is obvious in a subsessile member, which always occurs with the lower glume adjacent to the rachis.

Brachiaria tatariana Zuloaga & Soderstrom, new species

FIGURES 3, 4

TYPE SPECIMEN.—BRAZIL, MINAS GERAIS: "Habitat in marginibus sylvarum Districtus Adamantum ad Tejuco etc. provinciae Minarum generalium." (Holotype, M; fragment of the holotype, US sheet no. 974752.) Basis of *Panicum megastachyum* Nees, 1829:154, not Nees ex Trinius, 1826. The specimen was collected by Martius.

Culmi erecti, simplices. Ligula membranaceo-ciliata. Laminae lanceolatae, subcordatae. Paniculae laxae, diffusae, pyramidales, 30–35 cm longae, 15–30 cm latae, racemis spiciformibus spiculas binatas ferentibus. Spiculae ellipsoideae, 6–6.8 mm longae. Gluma inferna ovata longitudine ½ spiculae aequans, 5–7-nervata. Gluma supera obtusa, 9-nervata. Lemma infernum 5–7-nervatum. Palea inferna longi-ellipsoidea, florem masculinum gerens. Anthoecium superum longi-ellipsoideum, glabrum, omnino confertim et aequaliter papillosum; rhachilla super anthoecium superum extensa.

Perennial (?), the base not seen. *Culms* erect, cylindrical, sparsely pubescent near the nodes to glabrous, many-noded, simple. *Nodes* brown, pubescent. *Sheaths* longer than the internodes, ~13–15 cm long, pubescent, especially toward the upper part, pale. *Ligule* membranous, ciliate, ~1.5 mm long; collar villous. *Blades* lanceolate, acuminate, flat or with involute margins, ~23 cm long, 1 cm wide, rigid, subcordate at the base, pubescent on both surfaces, especially toward the base, the margins smooth. *Panicles* lax, diffuse, pyramidal, many-flowered, 30–35 cm long, 15–30 cm wide, spikelets in pairs on spike-like racemes, one subsessile, the other short-pedicellate; axis angled, hispid, the branches alternate or subopposite, the lower verticillate, diverging from the axis, naked at the base, hispid above, flexuous; pedicels 0.8–4 mm long, shorter than the spikelets, triquetrous, with long thick hairs



FIGURE 3.—*Brachiaria tatiánae*, new species: *a*, habit of culm ($\times 1$); *b*, panicle ($\times 1$); *c*, spikelet, upper glume side ($\times 12$); *d*, spikelet, lower glume side ($\times 12$); *e*, upper anthercium, palea side ($\times 12$); *f*, upper anthercium, palea side showing prolongation of rachilla ($\times 12$); *g*, lower glume ($\times 12$); *h*, upper glume ($\times 12$); *i*, lower lemma ($\times 12$); *j*, lower palea ($\times 12$); *k*, spikelet, lateral view ($\times 12$); *l*, branch of panicle ($\times 9$); *m*, developed lemma of third anthercium ($\times 12$); *n*, upper palea with gynecium and lodicules ($\times 12$); *o*, upper palea with stamens and lodicules ($\times 12$). All drawings based on the holotype (M).

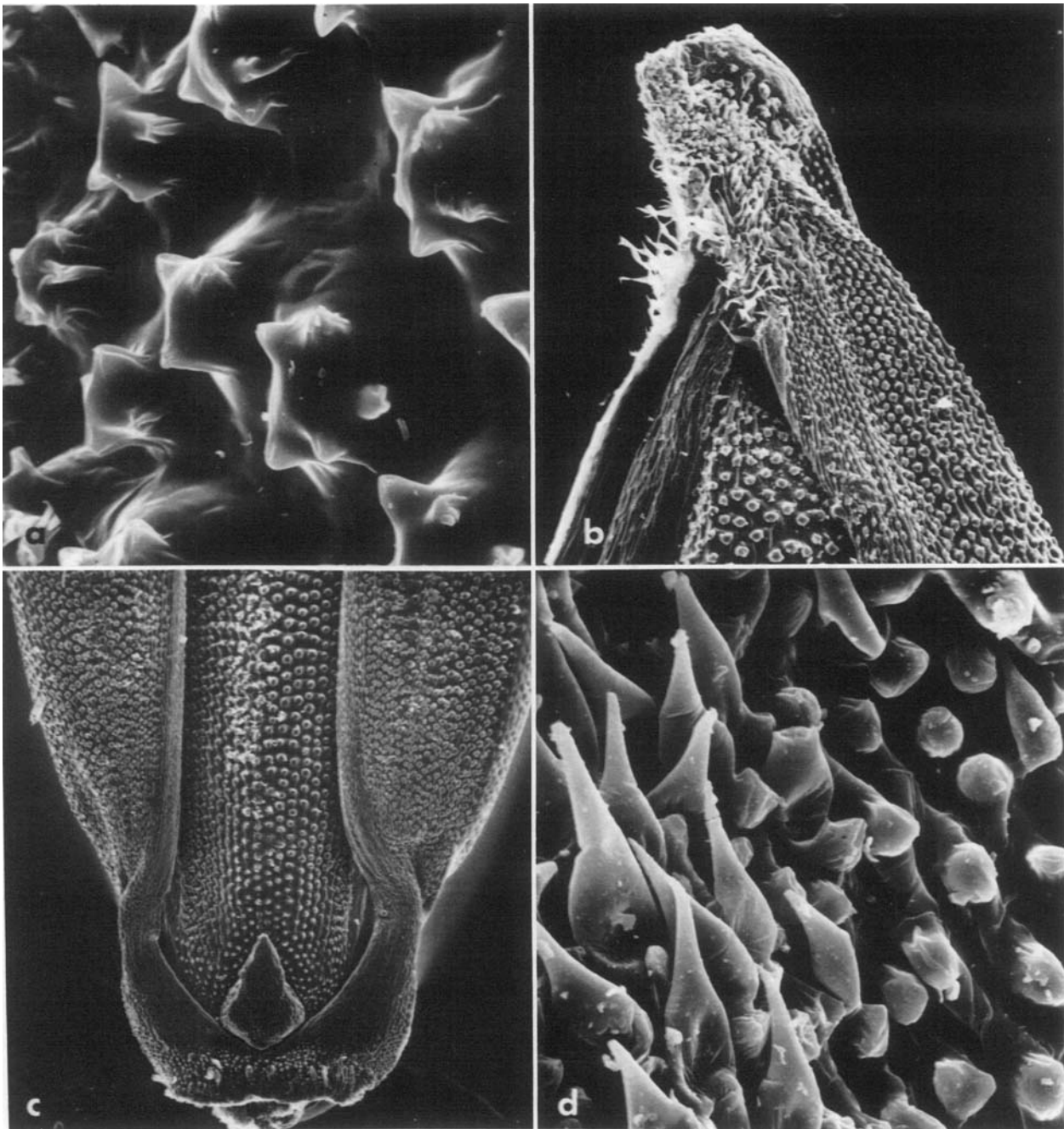


FIGURE 4.—*Brachiaria tatiana*, new species: *a*, upper anthercium, palea side, showing compound papillae ($\times 1000$); *b*, upper anthercium, palea side, showing apiculate summit of lemma and flat macrohairs ($\times 100$); *c*, upper anthercium, palea side at base showing prolongation of rachilla ($\times 50$); *d*, detail of summit of lemma as shown in *b* ($\times 1000$). All photomicrographs based on the holotype (M).

toward the apex and base. *Spikelets* ellipsoid, 6–6.8 mm long, 2.2–2.4 mm wide, lanate on the apex of the glumes and lower lemma, otherwise glabrous, the glumes and lower lemma with prominent nerves, the upper glume, lower lemma, and upper antherium subequal. *Lower glume* ovate with a rounded to acute apex, 4–4.3 mm long, half as long as the spikelet or a little longer, 5–7-nerved, the nerves anastomosed toward the apex, the summit and upper margins short-lanate. *Upper glume* obtuse, 5.3–6.3 mm long, 9-nerved, lanate, not covering the apex of the upper antherium. *Lower lemma* glume-like, acute, 5.3–6.3 mm long, 5–7-nerved, the nerves anastomosed. *Lower palea* long-elliptical, 4.9–5.9 mm long, 1.6–2.1 mm wide, membranous, short-pilose or glabrous in the middle part and on the margins; male flower present with 2 lodicules and 3 anthers. *Upper antherium* long-ellipsoid, 4.7–5.9 mm long, 1.6–2.1 mm wide, brown, densely papillose throughout, the papillae simple or compound, the margins of the lemma covering the palea, with numerous hooks on the apex of the lemma and flattened hairs on its upper margins; rachilla prolonged into a short acute mucro above the upper antherium, conspicuous in varying degrees on different spikelets; lodicules 2, truncate; anthers 3, violet. *Caryopsis* not seen.

PARATYPE.—BRAZIL. "*Panicum megastachyum*. Fl. Bras. var *pedunculis* basi et apice barbatis,

Sellow 1276" (fragments, BAA, US sheet no. 974752).

DISCUSSION.—In his *De Graminibus Paniceis* of 1826, Trinius described many species recognized by C.G. Nees von Esenbeck, indicating after each name: "N. ab Es! in Mart. Fl. Bras. ined." Three years later Nees in his *Agrostologia Brasiliensis* published these taxa as new, presumably unaware that they had already appeared in print. In most of the species described—*P. chloroticum*, *P. elephantipes*, *P. decipiens*, *P. milioides*, *P. cyanescens*, and *P. ligulare*, for example—the descriptions of both authors refer to the same species and usually cite the same type specimen. However, in at least two cases the type indicated by both authors is different. One of these, *P. campestre* Nees ex Trinius, 1826, is a valid species of the *Rudgeana* group and distinct from *P. campestre* Nees, 1829, which is a valid species of the section *Panicum*. Henrard described the latter as new in 1940, giving it the name of *Panicum peladoense*.

The other case in which two species have masqueraded under the same name is *Panicum megastachyum*. The two are characterized in Table 1.

Nees in fact referred to both specimens in his original description, the one a collection of Martius and the other of Langsdorff. However, the description of Nees agrees closely with the Martius specimen but not with that of Langsdorff. Trinius cited only the Langsdorff gathering.

TABLE 1.—Comparison of *P. megastachyum* Nees ex Trinius and *P. megastachyum* Nees.

<i>P. megastachyum</i> Nees ex Trinius, 1826	<i>P. megastachyum</i> Nees, 1829
spikelets 3.8.–3.9 mm long	spikelets 6–6.8 mm long
spikelets long-pedicellate	spikelets short-pedicellate
rachilla not prolonged beyond the upper antherium	rachilla prolonged as a conspicuous mucro beyond the upper antherium
axis and branches hirsute with thick papillose-pilose hairs; pedicels hirsute with thin, evenly distributed hairs	axis and branches hispid with papillose-pilose hairs only at the base; pedicels papillose-pilose at the apex and base
lower glume 3–5-nerved	lower glume 5–7-nerved
upper glume 5–7-nerved	upper glume 9-nerved

Doell (in Martius, 1877) reiterated what Nees had written but noted that spikelet size and pubescence of the pedicels differed in the two specimens. Steudel (1855) had also observed the difference in pedicel pubescence.

***Brachiaria albicoma* (Swallen & García Barriga) Zuloaga & Soderstrom,
new combination**

FIGURE 5

Panicum albicomum Swallen & García Barriga, 1943:303, fig. c. [Type: Colombia: "Dept. del Cauca. El Ramal to Río Sucio, west of Popayán, Cauca valley, Pennell & Killip 8129." Holotype, US; isotypes, GH, NY.]

Annuals 1.6–2 m tall. *Culms* cylindrical, erect, geniculate at the base, simple or branched, hollow, hispid. *Nodes* short- to long-pubescent with whitish hairs. *Sheaths* usually longer than the internodes, 12–19 cm long, densely to sparsely hispid, short-ciliate on the margins. *Ligule* membranous, ciliate, 1–1.6 mm long; collar lanate. *Blades* linear-lanceolate, acuminate, 18–24 cm long, 1.4–1.8 cm wide, flat, subcordate, densely hispid, especially toward the base on the adaxial surface, the margins scabrous with short, appressed hairs, the midnerve prominent. *Panicles* oblong, lax, 22–30 cm long, 8–14 cm wide, the branches ascending, the spikelets short-pedicellate in pairs or in threes, with the lower glume facing the axis; branches and pedicels angular, densely hirsute to villous, with long whitish hairs up to 5 mm long, thick toward the apex and with shorter hairs intermixed; the branches alternate, widely spaced and bearing spikelets to the base. *Spikelets* long-ellipsoid, 4.5–5.1 mm long, 1.6–1.8 mm wide, glabrous, pale to dark purple, the glumes and lower lemma with thin nerves. *Lower glume* ovate, acute to obtuse, 1.9–2.5 mm long, a third to half as long as the spikelet, 3-nerved, the apex scabrous. *Upper glume* acute, 7-nerved, the nerves anastomosed toward the scabrous apex. *Lower lemma* glume-like, 7-nerved, the nerves anastomosed toward the scabrous apex. *Lower palea* lanceolate, 3.7–3.8 mm long, 1.3

mm wide, hyaline, glabrous; male flower present, with 3 stamens. *Upper anthercium* ovoid, 3.3–3.7 mm long, 1.6–1.8 mm wide, glabrous, stramineous to brown, transversely rugose, with round papillae distributed evenly; lemma apiculate, 5-nerved with a scabrous apex; lodicules 2, truncate, plicate, enclosing the basal margins of the palea; with 3 stamens. *Caryopsis* not seen.

So far known only from the Department of Cauca, Colombia, at elevations of 1600 to 1900 m.

ADDITIONAL SPECIMENS SEEN.—COLOMBIA. Without state and locality, *Mutis 5522* (US). CAUCA: El Tambo, *García Barriga 4426* (US); Chisquíá, Finca Los Derrumbos, *Asplund 10778* (US).

DISCUSSION.—This species is apparently most closely related to *Brachiaria mollis* (Swartz) Parodi, which differs in its smaller spikelets, 3.5–4 mm long, and wider pubescent glumes.

Comparison of *Homolepis* and *Panicum*

Homolepis was established in 1911 by Agnes Chase, who based the genus on *Panicum aturense* H.B.K., deriving its name from the Greek *homo* (similar) plus *lepis* (scale), in reference to the subequal glumes. In addition to the type species, *H. aturense* (H.B.K.) Chase, two further species were included: *H. isocalycia* (Meyer) Chase and *H. longispicula* (Doell) Chase, both transferred from *Panicum*.

Diagnostic characters given by Chase were the subequal glumes that are 7–9-nerved and enclose both anthercia; enclosure of the upper anthercium by the lemma of the lower anthercium, which is subequal to the glumes; and presence of a palea in the lower anthercium. Furthermore, the upper anthercium is not indurate but rather delicate and fragile and the margins of its lemma are flat rather than inrolled, enclosing most of the palea. Several vegetative characters were also given for the genus: plants perennial, stoloniferous or creeping, decumbent and rooting on the lower nodes. These latter characters, however, do not apply to plants of *H. longispicula*, which are ces-

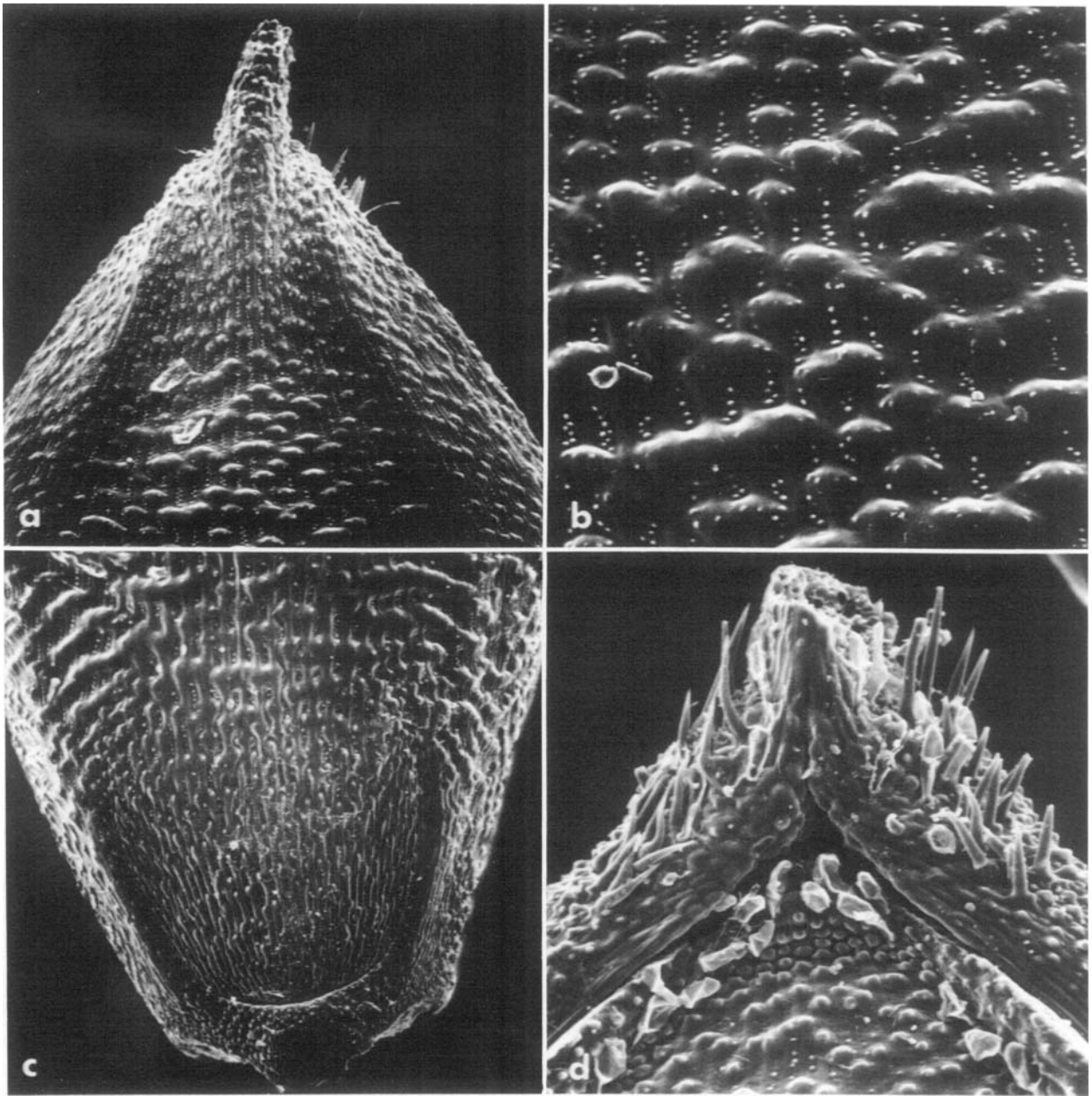


FIGURE 5.—*Brachiaria albicoma*, new combination: *a*, upper antherium, lemma side, showing apiculate summit of lemma ($\times 1000$); *b*, detail of lemma surface, showing rugose surface and simple papillae ($\times 200$); *c*, upper antherium, lemma side at base, showing rupture line ($\times 70$); *d*, upper antherium, palea side, showing bicellular microhairs and prickly hairs ($\times 200$). All photomicrographs based on *García Barriga 4426* (US).

pitose, erect, and in vegetative and habitat characters totally distinct from the remainder of the species. Its spikelets, nevertheless, are those of *Homolepis*.

Regional floras with references to *Homolepis* include Hitchcock (1913, 1922, 1927, 1930a,b), Swallen (1943, 1955), Amshoff and Henrard (1948), and Pohl (1980). In all of these *Homolepis* is distinguished from *Panicum* by the long lower glume, non-indurate upper antherium, and thin, flat margins of the upper lemma. These criteria were also used by Pilger in 1954, but Hsu in his 1965 study of the Paniceae made no mention of the genus.

Our studies have shown that two additional species of *Panicum*, *P. glutinosum* and *P. villaricense*, share the generic characters of *Homolepis* and should be transferred to it, bringing to five the number of species in this American genus. The former becomes the most widely distributed member, occurring from Mexico and the West Indies to Argentina. *Homolepis isocalyca* is found in Mexico (where only the type of one of its synonyms, *Panicum langei*, has been collected), Panama, and South America, while *H. aturensis* ranges from Mexico to Bolivia and Brazil. Two species are known only from South America: *H. longispicula* is endemic to the cerrados of Brazil and *H. villaricensis* is restricted to Paraguay, Argentina, and southern Brazil.

New features, as revealed by SEM studies, corroborate the previous separation of *Panicum* and *Homolepis* that was based on characters of the spikelet, flower, and fruit. The major differences between these genera are summarized in the following paragraphs.

Spikelet: The lower and upper glumes in *Homolepis* are similar, equal in length and not differing in their morphology, and the margins of all bracts are overlapping. The length of the lower glume in *Panicum* varies from $\frac{1}{5}$ to $\frac{3}{4}$ that of the spikelet, not equalling it nor the upper glume. In a few species, where the lower glume is more developed, it differs from the upper in such features as type of apex, nervation, and pubescence. This occurs in *Panicum obtusum*, *P.*

longipedicellatum, and in species of the Parvifolia group, for example. With few exceptions, the upper antherium is indurate in *Panicum* and the margins of the upper lemma are inrolled over the palea (Figure 12). In *Homolepis* the upper antherium is chartaceous and the margins of the lemma are flat and not inrolled over the palea (Figure 9). The lower lemma of *Homolepis* normally exhibits differing degrees and types of pubescence, while the glumes are glabrous (pilose up to the margins in *H. aturensis* and *H. longispicula*). Conversely, when the spikelet is pubescent in *Panicum*, the hairs occur on both glumes and more sparsely over the lower lemma.

Caryopsis: The hilum of *Homolepis* is linear, a character that clearly distinguishes it from *Panicum*, in which this structure is punctiform or rarely oblong. While linear in *H. glutinosa* and *H. villaricensis* it is somewhat broader and occupies half or a little more the length of the caryopsis. Chase made no mention of the caryopsis in her description of the genus.

Silica Cells: The presence of a particular type of silica cell in the epidermis of the upper antherium is a previously unrecorded character that further differentiates the two genera. Such silica cells in *Homolepis* are dumbbell-shaped and alike in all species. Silica cells also occur toward the tip of the upper antherium in certain species of the Lorea and Laxa groups of *Panicum* but are rare, randomly disposed, and markedly different from those in *Homolepis*.

The literature contains relatively few studies concerned with the surface of glumes and antherium, among these Baum (1971), Baum and Hadland (1973), Clark and Gould (1975), Thomason (1978a,b), Shaw and Seims (1979), Shaw and Webster (1981), and Terrell and Wergin (1979, 1981). Clark and Gould (1975) utilized differential characters of the antherium surface to separate *Dichantherium* from *Panicum*, pointing out that the upper palea in the former is covered evenly with simple papillae, while in the latter they do not occur or are crowded together and distributed at random. Terrell and Wergin (1981) studied silica cells present on the surface

of the pistillate lemmas in *Zizania*, showing that the four species of the genus could be separated by the different types of silica cells present in each.

Chromosome Numbers: Gould and Soderstrom (1970) reported the first counts for the genus with $2n = 40$ for *H. isocalycia* and $2n = 22$ for *H. aturensis*, although Pohl and Davidse (1971) and Davidse and Pohl (1978) found the latter to be $2n = 20$, concluding that the genus has a basic number of $x = 10$. These authors have also reported counts for *H. glutinosa* (as *Panicum glutinosum*) in their papers of 1971, 1972, 1974, and 1978. The most common basic number in *Panicum* is $x = 9$, although $x = 10$ occurs in species of the Laxa and Mertensia groups.

Leaf-blade Anatomy: *H. glutinosa* is a non-Kranz or C_3 species according to the data given by Brown (1977) under *Panicum glutinosum*. Brown also listed *Homolepis aturensis* and *H. isocalycia* as C_3 species.

***Homolepis* Chase, 1911, emended Zuloaga & Soderstrom**

Homolepis Chase, 1911:146.

Plants perennial, stoloniferous or creeping, decumbent and rooting at the lower nodes, then becoming erect, rarely cespitose. Spikelets short- to long-pedicellate, arranged in lax panicles.

Spikelets lanceolate to long-ellipsoid or obo-

void, blunt or with an acute or acuminate apex, greenish or brown, compressed dorsiventrally, articulated below the glumes; glumes subequal or the lower somewhat larger than the upper, completely covering the lower lemma and upper antherium or occasionally leaving exposed the summit of both antheria. *Lower glume* 5–9-nerved, glabrous, its margins enclosing the upper. *Upper glume* 7–9-nerved, commonly glabrous, its margins enclosing the lower lemma. *Lower lemma* glume-like, 5–7-nerved, pilose, its margins broadly enclosing the upper antherium. *Lower palea* membranous, often equal in size to its lemma and conspicuous; male flower sometimes present. *Upper antherium* ellipsoid, chartaceous, compressed dorsiventrally, acute or acuminate, glabrous (sometimes with bicellular microhairs or hooks toward the apex), pale, covered with suborbicular silica cells evenly distributed over the lemma and palea; lemma with flat margins, not inrolled over the palea and enclosing the greater part of it; palea of similar texture; lodicules 2, conduplicate; anthers 3; stigmas 2, plumose. *Caryopsis* obovoid to oblong, brown, with a linear hilum and embryo more or less half its length.

An exclusively American genus with species occupying humid habitats and shady places in forests or woods from Mexico to Bolivia, Brazil, Paraguay, and Argentina, with one species endemic to the cerrados of Brazil.

TYPE-SPECIES.—*Panicum aturense* H.B.K.

Key to the Species of *Homolepis*

1. Spikelets 9–11 mm long, 2–2.9 mm wide; glumes and lower lemma pubescent, lower lemma with long submarginal hairs; lower palea conspicuous, as long as its lemma; male flower present; plants cespitose with the culms few-noded, erect, not branching; ligule ciliate; sheaths keeled, rigid; blades linear-lanceolate, rigid, involute, 0.2–0.6 cm wide. Cerrados in the north of Brazil ***H. longispicula***
1. Spikelets 2.7–8 mm long, 1–1.8 mm wide; upper glume usually glabrous, lower lemma sparsely pubescent; lower palea small, never equal in size to the lemma; male flower rarely present; plants stoloniferous to decumbent, rooting and branching at the lower nodes; ligule membranous to membranous-ciliate; sheaths rounded, herbaceous; blades oblong-lanceolate to ovate-lanceolate, flat, 0.6–2.3 cm wide. Inhabiting forests or woods, never in cerrados 2

2. Spikelets 2.7–3.7 mm long; lower lemma without thick hairs in the central part; caryopsis with a broadened linear hilum half or a little more than half as long as the caryopsis; upper antherium scabrous at the apex 3
3. Panicle 12–25 cm long, 7–22 cm wide, with the lower branching verticillate; plants robust, 0.6–1.8 m tall; blades 10–43 cm long, 0.6–2.3 cm wide *H. glutinosa*, new combination
3. Panicle 5–11 cm long, 1.5–5 cm wide, with opposite or alternate branches, not verticillate; plants small, 0.2–0.4 m tall; blades 4–12 cm long, 0.6–0.9 cm wide *H. villaricensis*, new combination
2. Spikelets 4.6–8 mm long; lower lemma with thick hairs in the central part; caryopsis with a narrow, linear hilum as long as the caryopsis; upper antherium glabrous 4
4. Spikelets ellipsoid, acute, 4.6–7.5 mm long; lower lemma sparsely pubescent between the lateral nerves and with thick hairs on the middle part or glabrescent; upper antherium acute, chartaceous *H. isocalycia*
4. Spikelets lanceolate, acuminate, 6.2–8 mm long; lower lemma densely pubescent between the lateral nerves and with thick papillose-pilose hairs up to the apex of the middle and toward the sides; upper antherium acuminate, thin, of weak consistency *H. aturensis*

Homolepis aturensis (H.B.K.) Chase

FIGURE 6

Homolepis aturensis (H.B.K.) Chase, 1911:146.

Panicum aturense Humboldt, Bonpland, and Kunth, 1816:103, pl. 33. [Type: "Crescit ad cataractas Aturensis." Holotype, P, not seen; fragment of the type, US sheet no. 80535.]

Panicum viridiflorum Nees, 1829:135. [Type: "Habitat in herbario nostro occurrit, nescio nunde illatum." Type not located.]

Panicum blepharoporum J.S. Presl in K.B. Presl, 1830:312. [Type: "Habitat in Mexico." Holotype, PR, not seen; fragment of the type, US sheet no. 80486.]

Panicum tumescens Trinius, 1834:316. [Type: "V. spp. Bras." Holotype, LE, not seen; isotype, NY; fragment of the type, US sheet no. 81158.]

Stoloniferous perennials, 20–60 cm tall. *Culms* compressed, glabrous, erect or geniculate-ascending and rooting at the lower nodes, the internodes hollow, 2–11 cm long. *Nodes* brown, compressed, glabrous or with long whitish hairs. *Sheaths* 3–7 cm long, the margins pilose with thin whitish hairs, glabrous over the rest of the surface or papillose-pilose; collar brown, pubescent to glabrous. *Ligule* membranous, short-ciliate on

the upper part, 0.3–0.6 mm long. *Blades* oblong-lanceolate, acuminate, 6–12 cm long, 0.7–1.5 cm wide, flat, with a short pseudopetiole, the base cordate, the margins ciliate or scabrous, with strigose pubescence on both surfaces or glabrous, tessellate. *Panicles* lax, ellipsoid, 3.5–9 cm long, 1–4 cm wide, the branches shortly divergent from the axis with the spikelets congested along the branches; axis glabrous, smooth, undulate, the branches alternating, infrequently opposite, glabrous, the axils glabrous. *Spikelets* fusoid, acuminate, 6.2–8 mm long, 1.3–1.8 mm wide, greenish to pale, herbaceous, strongly compressed dorsiventrally, glumes and lower lemma faintly nerved. *Lower glume* acuminate, as long as the spikelet, enclosing part of the the upper glume, 5–9-nerved, glabrous. *Upper glume* 7–9-nerved, frequently tessellate, short- to long-pubescent between the lateral nerves in the zone covered by the lower glume, the hairs delicate, the rest of the surface glabrous. *Lower lemma* glume-like, 7-nerved, densely pubescent between the lateral nerves, the hairs purplish and whitish, the central nerves inconspicuous, with thick tuberculate hairs in the middle and oblong bicellular

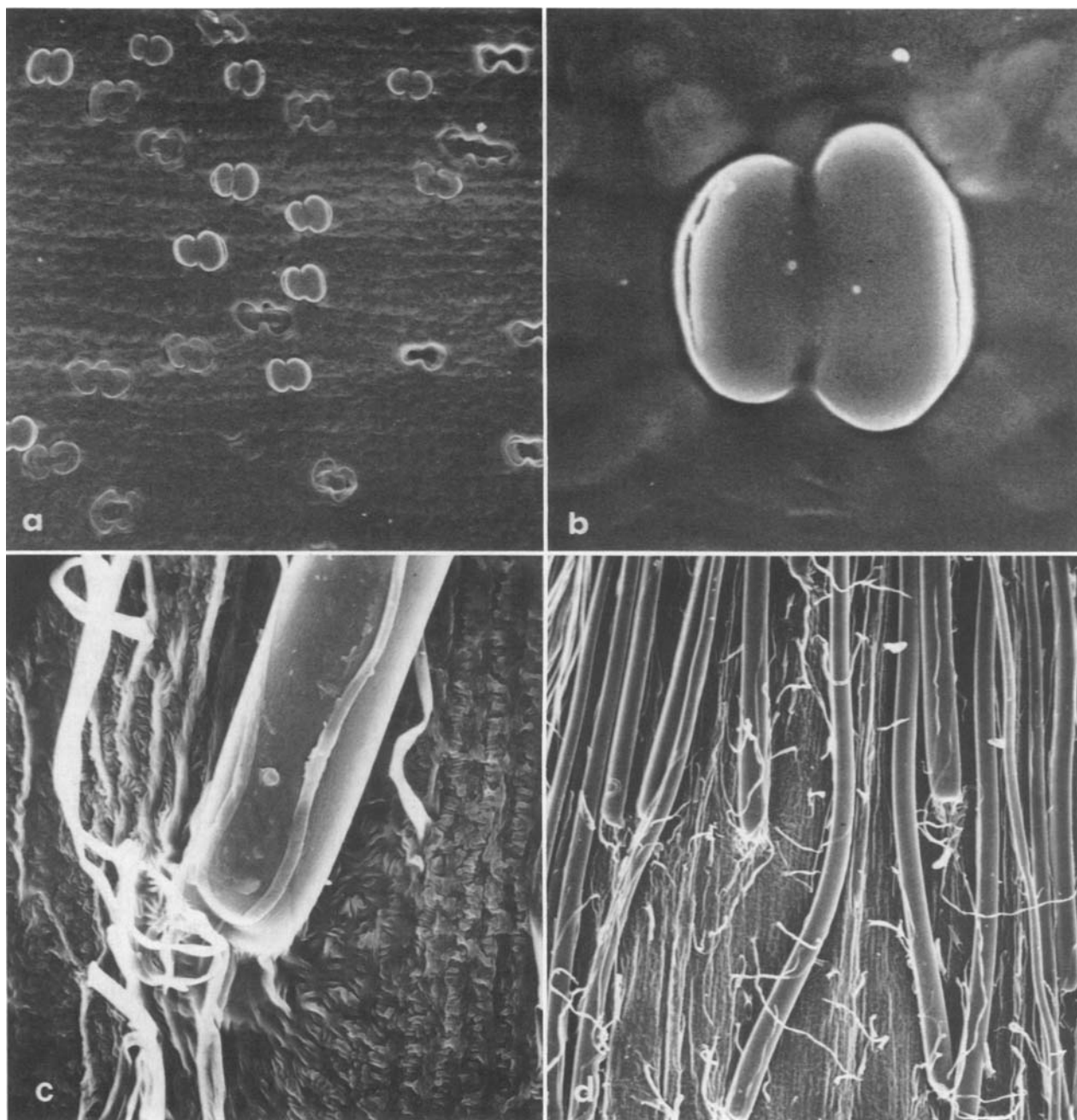


FIGURE 6.—*Homolepis aturensis*: *a*, upper antheridium, lemma side ($\times 500$); *b*, detail of upper palea showing a suborbicular silica cell ($\times 5000$); *c*, lower lemma showing base of a macrohair ($\times 500$); *d*, lower lemma showing macrohairs ($\times 100$). Photomicrographs *a* and *b* based on *Archer 1426* (US), *c* and *d* on *Prance 2860* (US).

microhairs. *Lower palea* lanceolate, 2–3.2 mm long, 0.5–0.9 mm wide, whitish, hyaline, glabrous; male flower rarely present. *Upper antheridium* ellipsoid, acuminate, 4.6–5.3 mm long, 1.1–1.4 mm wide, glabrous, pale to whitish, herbaceous, with silica cells distributed evenly, the lemma 5-nerved, its wide margins enclosing the palea. *Caryopsis* broadly obovoid, 2.5 mm long, 1.3 mm wide, brown, with a linear hilum, as long as the caryopsis; embryo less than half the length of the caryopsis.

DISTRIBUTION.—Widely distributed from Mexico to Bolivia and northern Brazil. Found commonly in margins of forests or woods or in open inundated or swampy places and along the margins of rivers in wet and sandy soils. This species, which occurs from sea level to 1700 meters elevation, has been reported as a weed of plantations in Brazil.

ADDITIONAL SPECIMENS SEEN.—BELIZE. EL CAYO: Central Farm, *Reyes* 4 (US); Cohune Ridge, *Lundell* 6425 (US); Augustine, Mountain Pine Ridge, *Hunt* 101 (US); Cayo Road, *Gentle* 9704 (US). STANN CREEK: near Stann Creek town, *Gentle* 9097 (US); Stann Creek, *Schipp* 896 (NY, US). TOLEDO: Punta Gorda-Cero Road, *Gentle* 6835 (US); edge of pineland, condemned Branch Pine Ridge, *Gentle* 7752 (US); in sacatal, near Machaca, *Gentle* 6891 (US); between cattle landing and Rio Grande, *Gentle* 6879 (US); Gracie Rock, Sibun River, *Gentle* 1629 (NY, US); Temash river, *Schipp* 1373 (NY, -US); Masons Lease, *Smart* 54 (US); Little Cocquericot, Belize river, *Lundell* 3878 (US).

BOLIVIA. BENI: Guayamerin, *Krapovickas & Schinini* 35109 (US). SANTA CRUZ: Buena Vista, *Steinbach* 1844 (NY), 5120 (US).

BRAZIL. ACRE: Cruzeiro do Sul, road Cruzeiro do Sul-Japim, *Prance et al.* 2860 (US). AMAZONAS: Barcelos, Negro river, *Baldwin* 3330 (US); Icana river, Santa Ana, *Fróes* 28472 (US); Japura river, *Rodrigues* 620 (US); 30–50 km from Manaus, along the Manaus-Itacoatiara road, *Eiten & Eiten* 5267 (US); Manaus, km 8 da BR 17, *Rodrigues & Chagas* 3083 (US); Manaus, rua Duque de Caxias, *Rodrigues & Coelho* 3076 (US);

Moura, Negro river, *Baldwin* 3365 (US); Reserva Florestal Ducke, km 26, *Prance et al.* 2627 (US); Santa Isabel, Negro river, *Baldwin* 3457 (US). GOIÁS: Rio Doce, 65 km W of Rio Verde, *Chase* 11727 (US); W of Rio Verde, *Chase* 12072 (NY, US). MARANHÃO: Barra do Corda to Grajau, *Swallen* 3670 (US); km 427, margens da Rod. BR-316, *Rosa & Vilar* 3136 (NY). PARÁ: Belém, *Kuhlmann s.n.*, 13 Aug 1923 (US); Bragança railroad, *Goeldi* 43 (NY, US); Castanha, Fazenda Setenta-dois, *Mexia* 5909 (US); Lagoa Agua Preta, *Drouet* 2028 (NY, US); Mosqueira, *Swallen* 4891 & 1/2 (US); Santarém, *Spruce* 30 (NY, US), 765 (US); 36 km SE of Vigia, *Davidse et al.* 17591 (NY). PERNAMBUCO: Dois Irmãos, vicinity of Recife, *Chase* 7725 (US); Recife, *Pickel* 3608 (US).

COLOMBIA. Angelópolis, vicinity of Medellín, *Toro* 270 (NY, US); Buenaventura, *Hitchcock* 19905 (US); vicinity of Medellín, *Toro* 474 (NY, US); Santa Marta, *Smith* 170 (NY, US). AMAZONAS: about 6 km N of Leticia at Santa Isabel, *Gillett & Dickenson* 16520 (US); Loretoyacu river, *Schultes* 6015 (US). ANTIOQUIA: Puerto Berrio, *Juzepczuk* 4862 (US); Santa Catalina, *Bosse* 3670 (US); Venecia, granja de las Mercedes, *Gutierrez & Barkley s.n.* (US 2184160). CAUCA: Chisquío, Finca Los Derrumbos, *Asplund* 10558 (US); Córdoba, Dagua valley, *Pittier* 560 (US); El Tambo, *García Barriga* 4416 (US); La Esmeralda, near Jamundi, Cauca valley, *Pittier* 936 (US); Río Sucio, W of Popayán, *Pennell & Killip* 8163 (US). CHOCO: Atrato river, above Quibdó, Sabuidero, *Cuatrecasas & Llano* 24062 (US); Andagoya, *Killip* 35497 (US); Atrato river, near Quibdó, *Molina & Barkley s.n.* (US 2206657); between La Oveja and Quibdó, *Archer* 1690 (US); Quibdó, quebrada la Platina, *Idrobo & Cuatrecasas* 2705 (US); San Juan river, *Cuatrecasas* 21372 (US); Serrano river, *Forero et al.* 1371 (NY). EL VALLE: Río Calima, Aguaclara, *Cuatrecasas* 21167 (US); Alto del Dinde, between Cartago and Alcalá, *Cuatrecasas* 22939 (US); Buenaventura, *Asplund* 4984 (US); Buenaventura, Córdoba, *Idrobo* 6250 (US); Cajambre river, Pacific coast, *Cuatrecasas* 16955 (US); Calima river, Pacific coast, *Cuatrecasas & Willard* 26071 (US); Pacific coast, Yu-

rumanguí river, Veneral, *Cuatrecasas* 15895 (US); Isla del Guayabal, in the mouth of Cajibambre river, *Cuatrecasas* 16222A (US); Naya river, Puerto Merizalde, Pacific coast, *Cuatrecasas* 14001 (US); Calima river, between La Esperanza y Bellavista, *Cuatrecasas* 16796 (US). META: along Río Ocoa, SE of Villavicencio, *Killip* 34371 (US); Villavicencio, *Cuatrecasas* 1973 (US), *Pennell* 1514 (US), *Pérez* 5336 (US). SANTANDER: Granja Experimental Agua Caliente, N of Playon, *Robinson Jr.* 3010 (US); La Gómez, 40 km E of Puerto Wilches, *Fosberg & Fassett* 21767 (US); Puerto Wilches and vicinity, *Killip & Smith* 14813 (NY, US). VAUPÉS: Río Guainía, Puerto Colombia and vicinity, *Schultes et al.* 18149 (US).

COSTA RICA. CARTAGO: Instituto Interamericano de Ciencias Agrícolas, Turrialba, *Davidse* 935 (US); between Pavones y Charia, Turrialba, *Jiménez* 751 (NY). LIMÓN: Hamburg Finca, on the Río Reventazón below Cairo, *Standley & Valerio* 48682 (US); 3 mi S of Puerto Limón, *Lathrop* 5542 (US); between Río Limón y Río Banano, *Jiménez* 2830 (NY); Río Cimarrón, crossing of highway, E of Siquirres, *Pohl* 13185 (NY); valleys of Sixalooa river, 2 km W of Bambu, *Pohl & Pinette* 13198 (NY). PUNTARENAS: 0.5 km W of Buenos Aires, *Pohl & Pinette* 13262 (NY); Buenos Aires, *Tonduz* 4876 (US).

ECUADOR. ESMERALDES: Playa Rica, Parroquia de Concepción, *Mexia* 8946 (US); in clearings near Borbon, *Jativa & Epling* 2141 (NY). LOS RÍOS: Hacienda Sta. Lucía, canton Vinces, *Mexia* 6584 (US); Río Palenque Biological Station, *Dodson* 5813 (US). NAPO-PASTAZA: Tena, *Asplund* 8954 (US). PICHINCHA: between Santo Domingo and Quininde, *Acosta Solís* 13694 (US).

GUATEMALA. ALTA VERAPAZ: Chama, *Johnson* 456 (US); Cobán, *von Tuerckheim* 1255 (NY, US), 3772 (US); Cubilquitz, *von Tuerckheim* 7698 (NY, US); Finca Socuyo, NE of Carcha, *Standley* 70285 (US); S of Cubilquitz, *Steyermark* 44560 (US); vicinity of Secanquim, *Pittier* 248 (US). IZABAL: between Bananera and La Presa, in Montaña del Mico, *Steyermark* 38074 (US); Cristina, *Blake* 7598 (US); vicinity of Quirigua, *Standley* 24017 (NY, US). PETEN: Dolores, km

85, W of road, *Contreras* 2955 (US); Puerto Barrios, *Brenckle* 47-184 (NY), *Hitchcock* 9156-1/2 (US); vicinity of Puerto Barrios, *Standley* 24725, 24978 (US).

FRENCH GUIANA. CAYENNE: vicinity of Cayenne, *Broadway* 703 (NY, US).

HONDURAS. CORTES: Yojoa Lake, *García* 93 (NY); Agua Azul, on shores of Lake Yojoa, *Morton* 7699 (US); Puerto Cortés, *Carleton* 623 (US); between Agua Azul y Pito Solo, *Molina* 5584 (US). MORAZAN: near El Hombre river, NW of La Venta, *Molina* 13420 (US). GRACIAS Á DIOS: along Plátano river, *Pohl & Gabel* 13342 (NY).

MEXICO. CHIAPAS: near the junction of the Río Perlas and Río Jatate at San Quintín and near Laguna Miramar, *Sohns* 1633 (US). OAXACA: Chiltepec, *Martínez Calderón* 721 (US), 981 (NY); Comaltepeque, *Galeotti* 5859 (US); Santa María de Lovani, *Vera Santos* 3440 (NY, US); 1 km S of Valle Nacional, on the road to San Mateo, *Rzedowski* 33792 (NY). TABASCO: Mayito, *Rovirosa* 425 (NY, US); Ocuapán, near Huimanguillo, *Archer* 3973 (US). VERACRUZ: along the Trans-Isthmian Highway, 4 Km NE of Minatitlán, *King* 1070 (US); El Palmar, Zongolica, *Vera Santos* 2304 (NY, US); Sabana Palenque, *Matuda* 3736 (US); Jicaltepec, *Liebmann* 391 (US).

NICARAGUA. State unknown: La Tronquera, *Molina* 14956 (NY); region of Braggman's Bluff, *Englesing* 295 (US); El Recreo, *Semple* 110 (US). ZELAYA: field S of airport, *Neill* 6485 (NY).

PANAMA. BOCAS DEL TORO: SW of Bocas, Macaw Hills, *von Wedel* 529 (US); Isla Colón, *von Wedel* 2801 (US). CHIRIQUÍ: Chiriquí Viejo river, *McCorkle* 690 (NY); vicinity of El Boquete, *Hitchcock* 8352 (US). COLÓN: around Empire, Canal Zone, *Pittier* 3727 (US); Barro Colorado Island, Fairchild Point, *Ebinger* 278 (US); Fort Sherman Military Reservation, between Chagres Batteries and Fort San Lorenzo, Canal Zone, *Maxon & Valentine* 7031 (US); between France Field and Catival, *Standley* 3039 (US); between Corozal and Ancón, Canal Zone, *Pittier* 2635 (US); between Gorgona and Tabernilla, Canal Zone, *Hitchcock* 7963 (US); between Mindi and Colón, Canal Zone, *Hitchcock* 7940 (US); Culebra,

Canal Zone, *Hitchcock* 7893 (US); Darien Station, Canal Zone, *Standley* 31558 (US); Ft. Kobbe, near beach, *Duke* 4181 (US); Juan Mina, Canal Zone, *Piper* 5268 (US); Gatun Lake, Goodyear, *Seibert* 1527 (US); Toro Point, Canal Zone, *Hitchcock* 8051 (US); vicinity of Fort Shermann, Canal Zone, *Standley* 30997 (US); vicinity of Summit, Canal Zone, *Standley* 30071 (US); Canal Zone, *Popenoe* 14 (NY). DARIEN: Tuyra river, near the mouth of Río Yape, *Allen* 332 (US). PANAMA: near Arraiján, *Woodson Jr.* 1379 (NY, US); Chorrera, *Hitchcock* 8129 (US); E of Orange river, *Cormann* 2572 (US); Tecumen, *Dwyer* 2558 (US); Tecumen river, *Standley* 26513 (US). VERAGUAS: road between Santiago & David, *Stern et al.* 1004 (US); Anchon Hill, *Killip* 4196 (US).

PERU. CORONEL PORTILLO: environs of Pucallpa, on Ucayali river, *Fosberg* 28887 (NY). LORETO: Caballo-Cocha, on the Amazon river, *Williams* 2205 (US); Iquitos, *Anderson* 1086 (US), *Asplund* 13922 (US), *Williams* 2964 (US); Maynas, Nanay river, Picuruyacu road below Bellavista, *Rimachi* 4816 (NY); lower Huallaga river, *Williams* 4210 (US); lower Nanay river, *Williams* 262, 311 (US); Santa María, about 25 km below Yurimaguas on Río Huallaga, *Allard* 22452 (US); Yaguasyacu river, *Plowman et al.* 6798 (US); Yurimagua, outside of town, *Anderson* 254 (US), *Ferreyra* 10177 (US).

VENEZUELA. AMAZONAS: Alto Orinoco, Esmeralda savanna, *Williams* 15338 (US); El Temblador, Orinoco river between San Antonio and Kirare, *Foldats* 256A (US); Guainía river, just E of Maroa, *Maguire et al.* 41703 (US). TÁCHIRA: Granja del Estado, San Cristóbal, *Tamayo* 2294 (US). TRUJILLO: ¼ mile from La Ceiba, *Reed* 932 (US).

CHROMOSOME NUMBERS.— $2n = 20$ (Pohl and Davidse, 1971); $2n = 22$ (Gould and Soderstrom, 1970); $n = 10$ (Davidse and Pohl, 1978).

***Homolepis glutinosa* (Swartz) Zuloaga & Soderstrom, new combination**

FIGURE 7

Panicum glutinosum Swartz, 1788:24. [Type: "Jamaica." Holotype, S, not seen; fragments of the type, BAA, US sheet no. 80678.]

Panicum obtusiflorum Richard, 1853:305. [Type: "Crescit ad marginem rivuli Cauta in provincia Santiago de Cuba (Linden n. 2143)." Holotype, P, not seen; fragment of the type, US sheet no. 80887.]

Panicum lindenii Grisebach, 1866:233. [Based on *Panicum obtusiflorum* Richard.]

Robust perennials 0.6–1.2 m tall. *Culms* decumbent, rooting and branching at the lower nodes, rarely stoloniferous, geniculate, cylindrical to compressed, pubescent (more so toward the upper part) to glabrous; internodes hollow, 5–20 cm long. *Nodes* purplish, compressed, glabrous. *Sheaths* 5.5–18.4 cm long, generally shorter than the internodes, papillose-pilose to glabrescent. *Ligule* membranous, truncate, 0.1–0.3 mm long, with short hairs on the adaxial surface toward the base of the blade; collar dark brown, densely pubescent with whitish hairs. *Blades* oblong-linear or lanceolate, 10–43 cm long, 0.6–2.3 cm wide, flat, glaucous, distally attenuate, papillose-pilose on both surfaces to glabrescent, the margins scaberulous to papillose-pilose below, the base narrowed, the midnerve prominent. *Panicles* lax, diffuse, many-flowered, exserted (included or not when young in the upper leaves), 12–25 cm long, 7–22 cm wide, the branches spreading, the spikelets separated on the branches; axis wavy and scaberulous, the lower branches in verticils, the upper alternate and opposite, the axils of the branches densely pubescent; pedicels scaberulous, 2–11 mm long. *Spikelets* obovoid to ellipsoid, 2.7–3.5 mm long, 1–1.6 mm wide, greenish to olivaceous, viscous at maturity, the glumes whitish along the margins. *Lower glume* acute to obtuse, 2.4–3.1 mm long, 5–9-nerved, as long as or longer than the upper glume, glabrous. *Upper glume* obtuse, 2.4–2.8 mm long, 7–9-nerved, usually not enclosing the upper antherium, glabrous. *Lower lemma* glume-like, acute, 2.6–3.3 mm long, 5–7-nerved, slightly to markedly scabrous at the apex, covered with oblong bicellular microhairs, with the basal cell short and the upper cell elongated, 43–80 μm long, 11–22 μm wide. *Lower palea* ovate-lanceolate, smaller than the lemma, 1.9–2.4 mm long, 0.4–0.5 mm wide, membranous, glabrous;

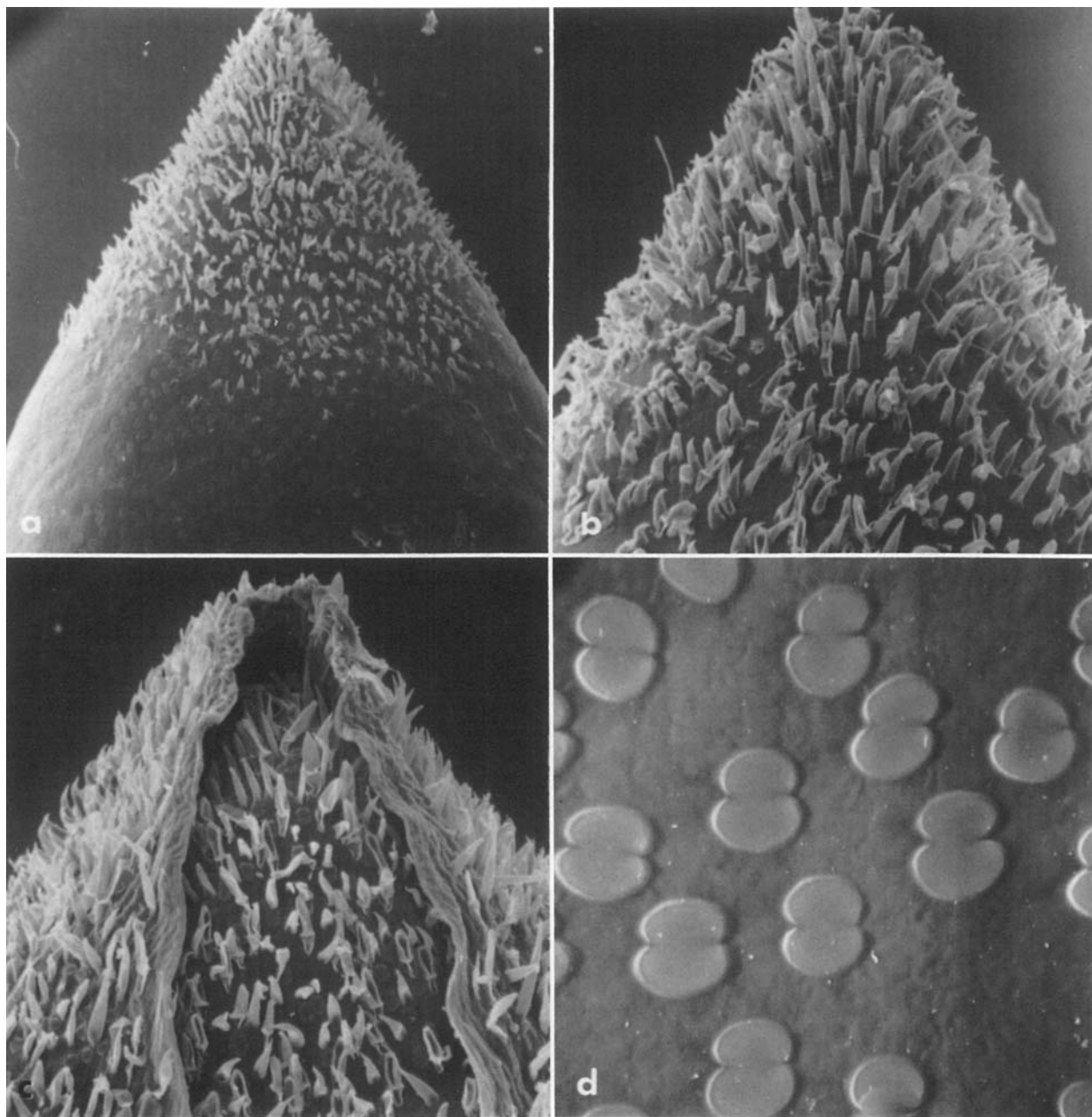


FIGURE 7.—*Homolepis glutinosa*, new combination: *a*, upper anthecium, lemma side ($\times 100$); *b*, detail of *a* showing dense aggregation of prickly hairs and bicellular microhairs ($\times 200$); *c*, upper anthecium, palea side, showing the same as in *b* ($\times 200$); *d*, detail of upper palea showing suborbicular silica cells ($\times 1000$). All photomicrographs based on *Eiten 3183*.

male flower absent. *Upper antheridium* ellipsoid, 2.5–3.3 mm long, 1–1.5 mm wide, smooth, with numerous hooks and bicellular microhairs at the apex, shining, pale and whitish, covered throughout by silica cells; anthers light brown. *Caryopsis* rounded, 1.7–2 mm long, 1.3–1.8 mm wide, pale; hilum linear, somewhat broad, half as long as the caryopsis or a little longer; embryo half the length of the caryopsis.

DISTRIBUTION.—In forests of Mexico, Central America, the West Indies, and South America to Paraguay and Argentina; from sea level to 2500 m elevation.

ADDITIONAL SPECIMENS SEEN.—ARGENTINA. **CORRIENTES:** arroyo Chimiray, *Krapovickas et al.* 25199 (CTES); arroyo Santa Isabel y ruta 12, *Schinini & Quarin* 8495 (CTES); desembocadura del arroyo Garapé en el Río Paraná, 45 km E de Ituzaingo, *Schinini et al.* 11089 (CTES); Estancia Santa Teresa, *Pedersen* 2645 (US); Rincón Ombú Chico, *Schinini et al.* 11260 (CTES); Santa Ana, *Carnevali* 2365 (CTES); ruta 40, 18 km NE de Santo Tomé, *Krapovickas et al.* 25306 (CTES). **MISIONES:** Bernardo de Irigoyen, *Burkart* 28255 (SI); Campo Viera, *Montes* 15364 (SI); Fracrán, *Parodi* 5674 (BAA); Loreto, *Montes* 11189 (LP); Montecarlo, *Montes* 15397 (BAA), *Porta* 203 (BAA), *Schwindt* 1329 (US); Parque Nacional Iguazú, *Cabrera, Gebhard y Corte* 201 (LP); Picada San Martín, *Schwarz* 4486 (LIL); Puerto Maní, *Schwarz* 10274 (LIL); San Pedro a Tobuna, *Schwindt* 4080 (US); San Pedro, *Parodi* 5614 (BAA); Santa Ana, *Rodriguez* 77 (MO, US).

BOLIVIA. State unknown: Hacienda Simaco, road to Tipuani, *Buchtien* 5316 (F, MO, SI, US); Mapiri, *Rusby* 244 (US); San Carlos, *Buchtien* 23 (BAA, US). **LA PAZ:** Coroico, *De la Sota* 454 (BAA); Zongo valley, *Renvoize & Cope* 4251 (MO). **SANTA CRUZ:** Buena Vista, *Steinbach* 2015 (SI), 14952 (US).

BRAZIL. Without state and locality, *Weddell* 1932 (NY). **GOIÁS:** vicinity of Goiabeira, *Chase* 11496 (US). **MINAS GERAIS:** without locality, *Chase* 9536 (US), *Regnell III.* 1370 (US), *Widgren* 912, 1299, 1845 (US), Campinas, *Novaes* 1247 (US), *Chase* 9442 (US); Juiz de Fora, *Chase* 8570

(F, MO, NY, US); Viçosa, *Bailey* 1011 (US), *Kuhlmann s.n.*, 9 Apr 1935 (US). **PARANÁ:** without locality, *Dusén* 3828 (US); Acungui, *Mattos & Labouriau s.n.*, 1 Mar 1948 (US); Carijo, *Hatschbach* 3040 (US); Curitiba, *Swallen* 8512 (US); Doce Fino, *Hatschbach* 4011 (US); Fazenda Reserva, 85 km SW of Guarapuava, *Lindeman et al.* 4692 (NY, US); Guarapuava, *Swallen* 8822 (US); Ponta Grossa, *Swallen* 8357 (US); Rio Espingarda, *Hatschbach* 4401 (US); Jaguariahyva, *Dusén* 16717 (MO, US); Tres Barras, *Dusén* 17551 (NY); Vossoreoca, *Kummrov* 318 (NY); Rio Lageado, *Hatschbach* 13745 (US); Rio Passa Dois, *Hatschbach* 15990 (US); Fazenda Lagoa, *Hatschbach* 14259 (US). **RIO GRANDE DO SUL:** Porto Alegre, Faculdade de Agronomia, *Valls* 2005 (US); Quinta near Rio Grande do Sul, *Malme* 1574 (US); Azevedo, near Cai, *Rambo* 41438 (US); Estação Guianuba, *Rambo* 40548 (US); Jacaré, *Rambo* 40950 (US); Morro Agudo, near Porto Alegre, *Rambo* 41040 (US); Parecí, near Montenegro, *Rambo* 52770 (US); São Leopoldo, *Rambo* 36987 (US). **RIO DE JANEIRO:** Alto Macahé, *Glaziou* 18647 (F, US); Alta Boa Vista, *Chase* 12136 (US); Alto da Serra, S of Petrópolis, *Chase* 9791 (US); Petrópolis, *Chase* 12178 (US); Tijuca, *Brade s.n.*, 31 Mar 1929 (US), *Smith & Brade* 2206 (US). **SANTA CATARINA:** 33 km SE of Caçador, *Smith & Klein* 12189 (NY, US); 17 km W of Campo Alegre, *Smith & Klein* 12035 (NY, US); Campo Alegre, Morro do Iquererim, *Reitz & Klein* 6389 (US); Canela Gaucha, São Miguel do Oeste, *Klein* 5068 (US); Chapeco, *Klein* 5287 (US); Ilha de Santa Catarina, Morro Itacorubí, *Reitz* 4582 (US), *Smith & Reitz* 6166 (US); Itajaí, Praia Braba, *Klein* 374 (US); Serra dos Ilhéus, *Smith & Klein* 16032 (US); 14 km N of Abelardo Luz, *Smith & Klein* 11437 (US); Papanduva, Picadas, km 181 da ERF, *Reitz & Klein* 12510 (US); Pinheiral, 11 km W of Caçador, *Smith & Klein* 10911 (NY, US); Rio Caçador, *Swallen* 8246 (US). **SÃO PAULO:** without locality, *Usteri* 9916, 9918 (US); Cambucy, *Chase* 11158 (US); Fazenda Canchim, 8 km NE of São Carlos, *Eiten et al.* 3183 (MO, US); Estação Florestal do Paraguaçu Paulista, *Clayton* 4558 (NY, US); Parque do Es-

tado, 1 km E of São Paulo, *Fonseca 52* (MO, US); near Piedade, 124 km from S. Paulo, *Smith 6324* (US); São Paulo, 10 km S of center of city, *Sendulsky 339* (US).

COLOMBIA. Without locality, *Moritz 759* (US). ANTIOQUIA: Hatillo, *Daniel 417* (US); Venecia, Granja de las Mercedes, *Barkley & Gutierrez 1657* (NY, US). CALDAS: Salento, *Killip et al. 8761* (US). CAUCA: Chisquío, Finca los Derrumbos, *Asplund 10561* (US); El Ramal to Río Sucio, W of Popayán, *Pennel et al. 8090* (US); El Tambo, *Kjell von Sneidern 2116* (F, US); Popayán, near Tunia, *Arbelaes et al. 6326* (US). CHOCÓ: between La Oveja and Quibdó, *Archer 1680* (US). CUNDINAMARCA: Fusagasugá, *Pennel 2697* (NY, US). EL VALLE: Cordillera Occidental, Pichinde, *Cuatrecasas 18237* (US); Cordillera Occidental, al S de Las Brisas, *Cuatrecasas 22644* (US); La Cumbre, *Pennel 5165* (NY, US); La Manuelita, Palmira, *Pennel et al. 6172a* (US); Las Nieves, W of Cali, *Killip et al. 39209* (US); Monte Frío, Yanaconas, *Killip et al. 33852* (US). HUILA: San Agustín, *Daniel 4096* (US). MAGDALENA: Sierra Nevada de Sta. Marta, *Barkley & Gutierrez 1874* (US). TOLIMA: La Trinidad, Líbano, *Pennel 3329* (NY, US); vicinity of Medellín, *Toro 1020* (NY).

COSTA RICA. Without province: Cucasacha, *Lankester 211* (US); Helechales del General, *Pittier 12002* (US); ALAJUELA: Piedades, near San Ramón, *Brenes 4477* (US); Río Jesús de San Ramón, *Brenes 22890* (NY); La Palma de San Ramón, *Brenes 4477* (NY). CARTAGO: 2 km NE of San Cristóbal, Intersección Norte, *Pohl 13253* (NY); 5 km E of Bajo Pacuare, along road, *Pohl 13148* (NY); Alto de la Estrella, *Standley 39042* (US). PUNTARENAS: Cañas Gordas, *Pittier 11017* (US). SAN JOSÉ: Santa María de Dota, *Standley 41582* (US).

CUBA. Without locality, *Wright 757* (NY, US); Las Villas, Buenos Aires, *Morton 4153* (US). ORIENTE: Gran Piedra, *Shafer 9014* (NY, US); S of Guaro, *Hitchcock 23416* (US); La Bayamesa, crest of the Sierra Maestra, *Morton 9282* (US); La Perla, *Leon 3790* (NY, US); Río Yao, W of Sierra Maestra, *Morton et al. 3489* (US); Sierra Maestra, Alto de Iberia, *Ekman 8298* (US); crest of Sierra

Nipe, *Morton & Acuna 3208* (US), *Shafer 2993* (NY). PINAR DEL RIO: Taco-Taco, Sierra de Los Organos, *Morton 4389, 4484* (US). SANTA CLARA: banks of Yayabo river, *Leon 3998* (US).

ECUADOR. ARCHIPIELAGO DE COLÓN: Isla Santa Cruz, above Bella Vista, *Wiggins & Porter 644* (US); Mt. Crocker, Indefatigable Island, *Howell 9224* (US). ORO: between Portobelo and El Tambo, *Hitchcock 21300* (US). SANTIAGO-ZAMORA: Macas, *Asplund 1920* (NY).

GUATEMALA. ALTA VERAPAZ: Cobán, *Johnson 29* (US). BAJA VERAPAZ: Sierra de las Minas, 3 km SE of Purulhá, *Williams et al. 43168* (F, US). HUEHUETENANGO: between Barillas and Cerro Victoria, *Steyermark 49697* (US); Ixcán and Finca San Rafael, Sierra de los Cuchumatanes, *Steyermark 49466* (F, US). QUEZALTENANGO: Retalhuleu, *Koninck 236* (US).

GUYANA. Kamana Falls, *Maguire et al. 45963a* (NY); Waru-Waru creek, Pomeroon, *Bartlett 8124* (US).

HAITI. Without locality, *Ekman 623* (US); vicinity of Furcy, *Leonard 4337* (NY, US); vicinity of Marmelade, *Leonard 8212* (US); northward from Morne Jeffrard, *Bartlett 17557* (US); Source-Rouille, Massif de la Selle, *Ekman 6827* (US); Terre Froid, *Holdridge 1760* (US).

HONDURAS. EL PARAÍSO: Yuscaran mountain, *Molina 613* (US).

JAMAICA. Without locality, *Hart 792* (US); Arntully, *Orcutt 2643, 3110* (US); Cinchona, *Harris 11264* (US), *11440, 11508* (MO, US), *Hitchcock 9708* (US); Diablo Mt., *Ridley 25, 38* (US), *Maxon & Killip 443* (US); Ewarton to Moneague, *Hitchcock 9451* (US); Gordontown, *Hitchcock 9321b* (US); near Ipswich, *Hitchcock 9627* (US); Mason River Savanna, W of Kellits, *Fosberg 42773* (US); Newport, *Britton 3193* (US); Red Hills, St. Andrew, *Harris 11836* (MO, US); road to Salt Hill, *Harris 11395* (US); vicinity of St. Helen's Gap, St. Andrew, *Maxon & Killip 595* (US); St. Thomas, Cuna Cuna trail, *Maxon & Killip 185* (US); Troy, *Harris 12607* (MO, US), *Hitchcock 9785* (US), *Maxon 2816* (US).

MEXICO. Without state: Mirador, *Mohr s.n., in 1857* (US). HIDALGO: Zacual[ti]pán, *Purpus*

2903 (US). CHIAPAS: Turubula, *Nelson 3357* (US). OAXACA: Huantla de Jiménez, *Schultes et al. 185* (US); San Ildefonso de Villa Alta, *Yetzelala, Vera Santos 3503* (MO, US). ORIZABA: San Cristóbal, *Bourgeau 3192* (US). PUEBLA: 30 km N of Zacapoaxtla, *Koch 7724* (US). VERACRUZ: near Jalapa, *Hitchcock s.n.* (US); Zacualpán and vicinity, *Purpus 2156* (US).

PARAGUAY. Without state: Alto Paraná, Ñandunday, *Montes 10949* (US); Asunción, Jardín Botánico, *Rojas 14546* (BAA); Caacupé, *Insfran 1087* (SI); Carapeguá, *Rojas 3400* (US); Carobeni Nuevo, road to Itape, *Rosengurt 5896* (LP); Isla Teresa, *Bertoni 4294* (LIL); Lago Ipacaray, *Hassler 12544* (F, MO, US); Pedro Juan Caballero, *Rojas 6690* (BAA); Piraretá, *Schinini 12183* (CTES); Apa River, *Hassler 11449* (US); Sapucay, *Hassler 13027* (US); Tacuru Pucu, *Fiebrig 6502* (BAA); Puerto Bertoni, *Rojas 8070* (BAA).

PERU. AMAZONAS: 1–5 km SE of Yambrasbamba, *Wurdack 1033* (US). HUÁNUCO: Pampa Hermosa, between Puente Durand & Exito, *Mexia 8243* (F, MO, US); Pampayacu, mouth of Río Chinchao, *Macbride 5101* (US). JUNÍN: Pichis trail, Yapas, *Killip & Smith 25589* (F, US). SAN MARTÍN: Juan Guerra-Mayo River, *Anderson 1096* (US); road between Tampoto and Juan Guerra, *Anderson 1108* (US).

PUERTO RICO. Alta de Bandera, E of Adjuntas, *Chase 6469* (US); Guavate, *Liogier 9771* (US); Maricao Insular forest, *Schubert 337* (US); Maricao, road to Indiera Fría, *Chase s.n., 1913-Oct-23* (US); vicinity of Maricao, *Chase 6199, 6250* (US); Mayagüez, *Sintenis 357* (US); Sierra de Yabucos, *Sintenis 2609* (US).

DOMINICAN REPUBLIC. AZUA: Cordillera Central, San Juan, *Ekman 13431* (US). LA VEGA: vicinity of Constanza, *Allard 16451, 16488* (US); Constanza, near Río Grande, *Jiménez 2129* (US); vicinity of Jarabacoa, *Allard 14886, 14909* (US); La Ciénaga, south bank of Río Los Guanos, *Gastony et al. 210* (US); Loma Campana, *Allard 18216* (US). MONTE CRISTI: Lagunas de Cenobí, *Valeur 54* (US); Las Cidras, *Valeur 520* (US).

VENEZUELA. State unknown: trail from Sanchorquiz to Galpán, *Pittier 9578* (US). ARAGUA:

Alto de Choroní, *Chardon 181* (US); road between Choroní and Maracay, *Pittier 13923* (US), *Soderstrom 976* (US), *Tamayo 1636* (US); Parque Nacional, *Chase 12456* (US). BOLIVAR: Santa Teresita de Kavanayen, *Steyermark 60529* (F, US). DISTRITO FEDERAL: on the old road to Caracas from La Guayra, *Pittier 5910* (US); Cerros del Ávila, Altos de Galipán, *Pittier 8301, 9915* (US); Cordillera Costanera, Junquito, *Chase 12432* (US); Hacienda Puerto La Cruz, *Pittier 8060* (US). LARA: between La Escalera y Cubiro, *Burandt Jr et al. 0032V* (US); near Sanare, Parque Yacambu, *Smith 1329V* (US). MIRANDA: La Providencia, *Pittier 13761* (US); road from Los Canales to El Encanto, *Lasser 660* (US); hills above Los Teques, *Pittier 11247* (US). TÁCHIRA: La Mulera, *Tamayo 2302* (US).

CHROMOSOME NUMBERS.— $2n = 20$ (Davidse and Pohl, 1972a,b, 1974, 1978), $2n = 40$ (Pohl and Davidse, 1971).

DISCUSSION.—This species was not placed in any group by Hitchcock and Chase in their publication of 1910. In an unpublished manuscript Chase later included it in the group *Glutinosa*, along with *P. millegrana* and *P. sellowii*, taxa to which we do not believe it to be related.

Homolepis glutinosa and *H. villaricensis* were included in section *Glutinosa* of *Panicum* (Zuloaga, 1978) on the basis of glume length and by the type of pubescence in the spikelet. In both species the lower and upper glumes reach about the same size and development and are indistinguishable morphologically; frequently the lower glume exceeds the upper in length. In relation to the spikelet the length of the glumes is variable, in certain cases enclosing the upper antherium entirely, in others leaving the apex exposed (especially on the dorsal face of the spikelet, as the upper glume is smaller). In young spikelets both glumes frequently enclose the antheria entirely. In this state the spikelet is compressed dorsiventrally and its form is ellipsoid. When the spikelets mature the upper antherium becomes more globose, exceeding both glumes and the lower lemma in length.

The lemma in both species produces varying

amounts of obovate to oblong bi- or tricellular secretory hairs. In *H. glutinosa* they are bicellular and oblong with the lower cell short and the upper elongated, whereas in *H. villaricensis* they are bi- or tricellular, globose, obovate, narrow at the base and globose toward the apex. The hairs contain a resin that is secreted when the spikelets mature and become dark brown. Although the resin is produced by the lower lemma, it exudes over the surface of the glumes and makes them viscous, for which reason they usually become covered with foreign particles. Stant (1973) referred to similar structures in *Gibasis* (Commelinaceae) as "glandular micro-hairs" and thought the distal cell, which is distended and rounded, to be secretory. In the other three species, *H. aturensis*, *H. isocalycia*, and *H. longispicula*, the lower lemma is pubescent with oblong bicellular hairs, similar to those present in *H. glutinosa*. These hairs also contain a substance that is dispersed on the glumes and lower lemma.

Scholz (1978) mentions the presence of bicellular hairs with a distal globose cell on anthercia of various species of *Panicum*. Such hairs are indeed found on the anthercia of many species, particularly in the Parvifolia group where their occurrence is universal.

Pohl (1980) indicated that the majority of the spikelets of *Panicum glutinosum* appeared to be cleistogamous in the specimens he observed from Costa Rica. He noted the characteristic viscosity of the "glumes" and felt the species was unrelated to any other species of the genus that he was treating.

Homolepis isocalycia (Meyer) Chase

FIGURE 8

Homolepis isocalycia (Meyer) Chase, 1911:146.

Panicum isocalycium Meyer, 1818:59. [Type: "In arenosis umbrosis continentis." Holotype, LE, not seen; fragment of the type, US sheet no. 80709.]

Panicum olyrachne Beurling, 1854:112. [Type: "Portobello No. 241. In palmetis." Type not located.]

Panicum renggeri Steudel, 1855:89. [Type: "Paraguay. Bahia." Holotype, P, not seen; fragment of the the type, US sheet no. 2903503.]

Panicum langei Fournier, 1886:23. [Type: "Teotalcingo (Liebmann n. 435. junio)." Holotype, C, not seen; fragment of the type, US sheet no. 80730.]

Perennials 50–100 cm tall. *Culms* firm, many-noded, stoloniferous or decumbent and branching and rooting at the lower nodes to cespitose, sparsely pilose to glabrous; internodes hollow, 5–9 cm long. *Nodes* brown, compressed, sparsely pilose to glabrous. *Sheaths* 5–8 cm long, prominently distichous, overlapping, papillose-pilose to glabrous, pubescent on the margins. *Ligule* membranous, ciliate, 0.3–0.4 mm long; collar brown, densely short-pubescent. *Blades* lanceolate to ovate-lanceolate, acuminate, 7–23 cm long, 1–1.8 cm wide, flat, greenish, pseudopetiolate, the base subcordate to cordate, the margins ciliate, the lower with long whitish hairs, tessellate, with long whitish hairs toward the base of the adaxial surface to densely pilose on both surfaces. *Panicles* lax, diffuse, sparse, 6–15 cm long, 1.5–5 cm wide, the branches spreading; axis cylindrical, glabrous, the branches alternate, the axils pilose. *Spikelets* broadly ellipsoid, 4.6–7.4 mm long, 1.6–2.1 mm wide, greenish, the glumes and lower lemma herbaceous with manifest nerves. *Lower glume* acute to acuminate, about as long as the spikelet, 5–9-nerved with transverse veinlets or not, glabrous on both surfaces or with the inner surface scabrous. *Upper glume* acute to acuminate, as long as the spikelet, 5–9-nerved, acute to acuminate, glabrous. *Lower lemma* glume-like, acute to acuminate, 5–7-nerved, sparsely pubescent on the outer surface toward the apex and upper margins, with oblong bicellular microhairs and sometimes with long, thin, whitish hairs between the two lateral nerves toward the apex, scabrous toward the apex of the inner surface. *Lower palea* lanceolate, 3.5–4 mm long, 0.5–0.8 mm wide, hyaline, transparent, glabrous; male flower rarely present. *Upper anthercium* ellipsoid, acute, 3.9–4.8 mm long, 1.1–1.6 mm wide, pale, glabrous, with hooks and bicellular microhairs at the apex of the palea, the lemma and palea covered with evenly distributed silica cells; lemma 5-nerved. *Caryopsis* obovoid, 2.5 mm

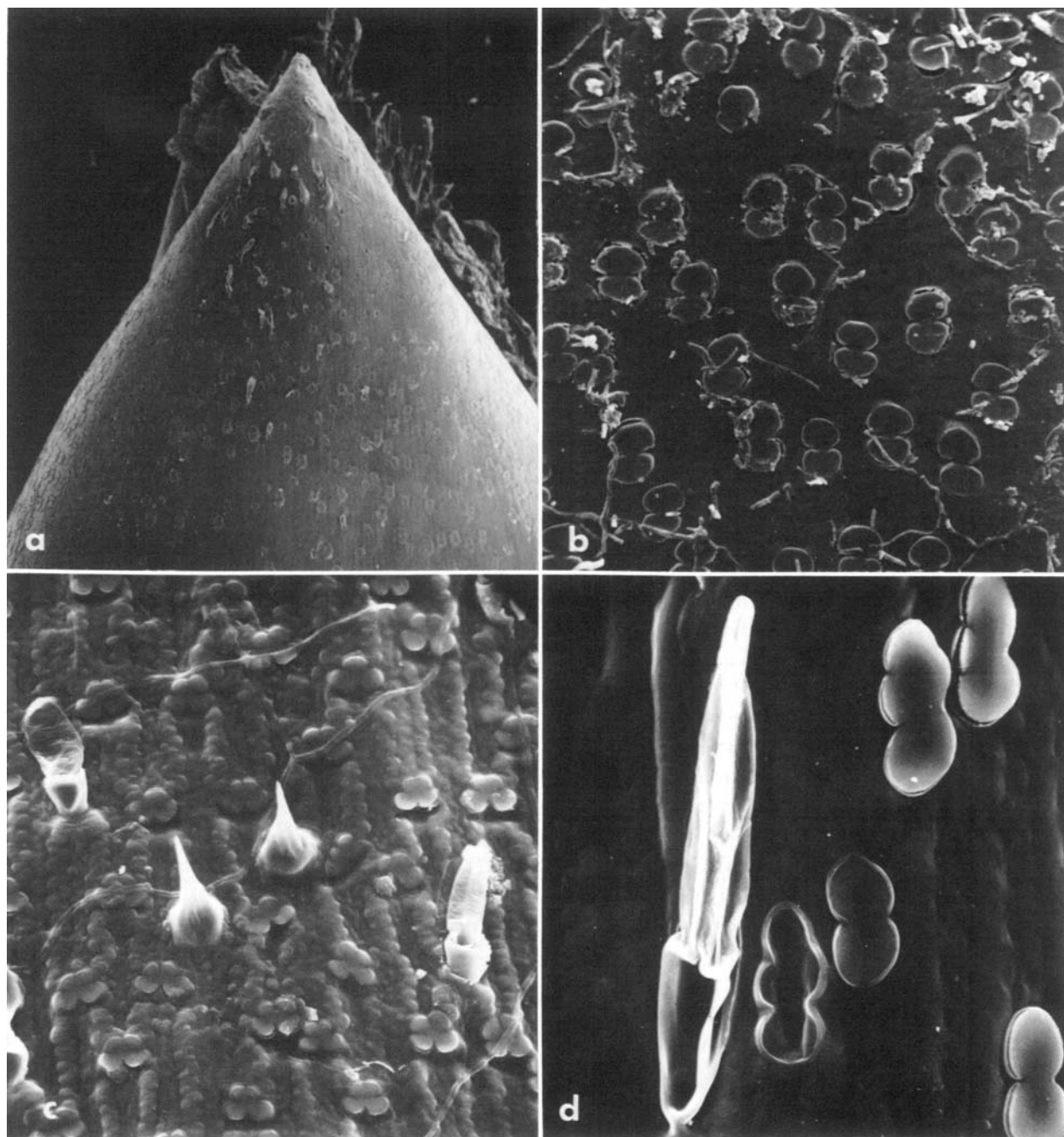


FIGURE 8.—*Homolepis isocalyca*: *a*, upper antherium, lemma side ($\times 100$); *b*, detail of upper palea showing suborbicular silica cells ($\times 500$); *c*, detail of lower lemma showing bicellular microhairs and prickly hairs ($\times 450$); *d*, detail of upper antherium, palea side, showing bicellular microhair and silica cells ($\times 1000$). All photomicrographs based on Duarte 6092 (US).

long, 1.3 mm wide, brown; hilum linear, as long as the caryopsis, embryo $\frac{1}{3}$ as long as the caryopsis.

DISTRIBUTION.—In moist and shaded woodlands or forests from Mexico and Panama to northern Brazil.

ADDITIONAL SPECIMENS SEEN.—**BRAZIL.** BAHÍA: near Bahía, *Salzmann s.n.* (US); Bahía, *Dorsett & Popenoe 444b* (US); de Brejão a Mucugé, *Lemos Frôes 19982* (US); Parafuso, 39 km NE of Bahía, *Chase 7976* (MO, US); Campo Santo to Bahía, *Chase 8048* (MO, US); 40 km S of Eunápolis, Porto Seguro, *Arruda 1* (MO); 5 km SE of Feira de Santana, *Davidse et al. 11702* (MO); Serra do Rio de Contas, 11 km S of Rio de Contas on side road to W of the road to Livramento do Brumado, *Harley et al. 15077* (US), 12–14 km N of town of Rio de Contas on the road to Mato Grosso, *Harley et al. 15179* (US); Serra do Sincorá, 9 km SW of Mucugé on road from Cascavel by the Rio Paraguaçu, *Harley et al. 15977* (US); 175 km N of Ubaitaba, near São Antonio de Jesús, on the BA 101 highway to Feira de Santana, *Harley et al. 17033* (US), 5.6 km N of Mucugé on road to Andaraí, *Harley et al. 18880* (US), ~10 km N of Barra de Estiva, on Ibicoara road, by the Rio Preto, *Harley et al. 15862* (US), ~6 km N of Barra da Estiva on Ibicoara road, *Harley et al. 15543* (US); south part of peninsula, vicinity of Bahía, *Chase 7858* (MO, US); Maraú, a 3 km do Porto, *Mori et al. 11390* (MO); Maraú-Ubaitaba, 45–50 km E of Ubaitaba, *Mori et al. 11950* (MO); 34 km E of Morro do Chapéu, *Davidse et al. 11870* (MO); Porto Seguro, BR 5, km 18, *Duarte 6092* (US); T. de Freitas, 12 km N of Cachoeira, *Chase 8076* (US); Cruz das Almas, *Pinto 124* (US); Serra da Agua de Rega, 27 km N of Seabra, *Irwin et al. 31010* (NY). CEARÁ: Campo Grande, *Swallen 4518* (US). MINAS GERAIS: 10–15 km da cidade, *Magalhães 14143* (US); 17 km SW of the Minas Gerais-Bahía border, along highway, *Davidse et al. 11615* (NY). PARÁ: Alto Quimina, *Sampaio 5784* (US); Igarapé das Borboledas, *Sampaio 5580* (US); Rio Pará, *Sampaio 5516* (US). PERNAMBUCO: Olinda, *Pickel 108* (US). RORAIMA:

plateau of Serra Tepequem, *Prance et al. 4482* (MO).

COLOMBIA. ANTIOQUIA: Cisneros, *Toro 1027* (NY, US). SANTANDER: Mesa los Santos, S of Bucaramanga, *Robinson Jr. 3181, 3195* (US).

FRENCH GUIANA. Road Iracoubo-Organabo, km 38, *Black & Muller 54-172393* (US); route de L'Acarouany, *Hook s.n.*, 11 Nov 1955 (NY).

GUYANA. Without locality, *Jenman 6000* (US); Kamakusa, upper Mazaruni river, *De la Cruz 2251, 4217* (MO, NY, US); Wanawa river, *De la Cruz 4057* (NY, US); Bartica, *Leng s.n.* (NY, US); Mazaruni river, *Bartlett 8059* (US); Kaieteur Fall, forest along left bank of Potaro river, *Cowan & Soderstrom 2002* (NY, US); vicinity of Penal settlement, on west side of Essequibo river, near mouth of Mazaruni river, *Hitchcock 17112* (NY, US); Waranawa Ranch, ~3 mi from Jacawa, *Harrison 1097* (US); Kaiken, Paruima, *Leakley 227* (NY); Kaieteur Plateau, *Maguire & Fanshawe 23287* (NY); Mazaruni river, Kalacoon, *Archer 2479* (US); Kartabo Point, at confluence of Cuyuni and Mazaruni rivers, *Sandwith 644* (US).

PANAMA. 1.5 miles S of Goofy Lake, *Dwyer 8027* (MO); Campo Tres, 3 mi NE Altos de Pacora, *Liesner 528* (MO); Cerro Azul, *Dwyer s.n.* (MO), *Ebinger 405* (MO), *Godfrey 2047* (NY), *Tyson 2132* (MO); Cerro Jefe, *Antonio 4701* (MO), *Davidse 10116* (MO), *Hammel 4814* (MO); road to Cerro Jefe, 21 km N of Panamerican Highway, *Folsom & Hartman 4620* (MO); road to Cerro Jefe, shore of Goofy Lake, *Witherspoon 8439* (MO); road to Cerro Jefe, beyond Goofy Lake along road, *Correa & Dressler 464* (MO); top of Cerro Jefe, *Tyson et al. 4411* (MO).

SURINAM. Kayser airstrip, 45 km above confluence with Lucie River, *Irwin et al. 55980* (MO, NY, US); Kayser airstrip, 25 km above confluence with Lucie River, *Maguire et al. 53956* (MO, NY, US); Sipalwini savanna, area on Brazilian frontier, *Oldenburger et al. 355* (NY).

VENEZUELA. BOLIVAR: Hato Divina Pastora, Gran Sabana, al pie del cerro Ceita, *Tamayo 2918* (US); Icabaru-Santa Elena, 70 km NE of Icabaru, *Croat 54228* (MO); Santa Elena, *Tamayo 2780*

(US). TÁCHIRA: road from Palmira to Mulera, Muller 889 (US). TRUJILLO: near Escuque, along road to Valera, Pittier 13141 (MO, NY, US).

DISCUSSION.—Although the species appears to be most common in northern South America, the type specimen of one of its synonyms, *Panicum langei*, comes from Mexico. Curiously, we have no specimens from Central America, except recent collections from Panama. Steudel cited only “Paraguay. Bahia” for another synonym of this species, *Panicum renggeri*. Given the geographical distribution of *H. isocalycia*, we may assume there is an error in the labeling of the type material and that it was collected in the state of Bahía, Brazil.

In spikelet shape, pubescence, and consistency of the upper antherium, this species appears to be most closely related to *H. glutinosa* and *H. villaricensis*. The upper antherium in these three species is somewhat more rigid than in *H. longispicula* and *H. aturensis*.

The label data of Irwin 55980 indicate that the culms of this species attain heights of 2.5 m; data from Chase 8076 indicate the plant has stolons reaching 3 m or more in length. In this species there is great variation in the size of the plants, panicles, and spikelets. The spikelets, for example, range from 4.6 to 7.4 mm in length, a variation that does not correlate with other characters. There are examples of small plants with spikelets 7 mm or more long and robust plants with smaller spikelets. For this reason we consider it prudent to maintain the material examined under a single species, *H. isocalycia*.

Homolepis longispicula (Doell) Chase

FIGURE 9

Homolepis longispicula (Doell) Chase, 1911:147.

Panicum longiflorum Trinius, 1834:317, not Gmelin, 1796.

[Type: “Habitat in Brasilia, loco accuratis non adnotato (herb. Acad. Petropolit.). Holotype, LE, not seen; fragment of the holotype, US sheet no. 80743.]

Panicum longispiculum Doell in Martius, 1877:261. [Type: the same as that of *Panicum longiflorum* Trinius.]

Ichnanthus longiflorus (Trinius) Bentham, 1881:145.

Homolepis longiflora (Trinius) Pilger, 1940:35.

Cespitose perennials, shortly rhizomatous, 40–90 cm tall. Culms few-noded, cylindrical, glabrous, erect, not branching, covered amply at the base by the sheaths; internodes hollow, 6–26 cm long. Nodes obscure, compressed, glabrous. Sheaths 6–21 cm long, the basal ones abbreviated, shorter than the lower internodes, the upper ones longer, pale, keeled, glabrous or papillose-pilose toward the upper margins. Ligule a short arc, ciliate, formed by a line of whitish hairs 0.3–0.6 mm long; collar glabrous or densely pubescent. Blades linear-lanceolate, subulate to acute, 6–20 cm long, 0.2–0.6 cm wide, rigid, narrow at the base, not clearly differentiated from the sheath, pubescent on both sides (more densely so on the abaxial side) to glabrous, the margins convolute, ciliate with thin, fragile hairs, mid-nerve prominent. Panicles contracted, exserted, 6–20 cm long, 1–7 cm wide, the branches appressed to the axis, the spikelets borne on long pedicels; axis cylindrical, undulate above, glabrous, smooth, purplish, the branches alternate or subopposite, smooth, glabrous, purplish, the pedicels claviform, 5–25 mm long, glabrous, smooth. Spikelets fusiform, 9–11 mm long, 2–2.9 mm wide, acuminate, greenish-violet, herbaceous, glumes and antheria separated by distinct internodes. Lower glume acute, 9–10 mm long, greenish, 5–7-nerved, glabrous or sparsely hirsute with caducous hairs. Upper glume acuminate, 8.2–10 mm long, 5-nerved, pubescent toward the margins, the hairs whitish and violet, the margins hyaline, the middle part hirsute, with caducous tuberculate hairs. Lower lemma ~8 mm long, 5–7-nerved, densely pubescent (especially toward the margins), the long hairs whitish and purplish with thick tuberculate hairs on the middle part (more so toward the apex and margins) and oblong, bicellular microhairs. Lower palea conspicuous, lanceolate, 6–7 mm long, 1–1.5 mm wide, as long as the lemma, hyaline, transparent, glabrous or pilose toward the upper margins; male flower present with 3 stamens. Upper antherium fusiform, 6.7–7.8 mm long, 1.4–2 mm wide, herbaceous, whitish, glabrous or pubescent toward the upper part, densely covered with

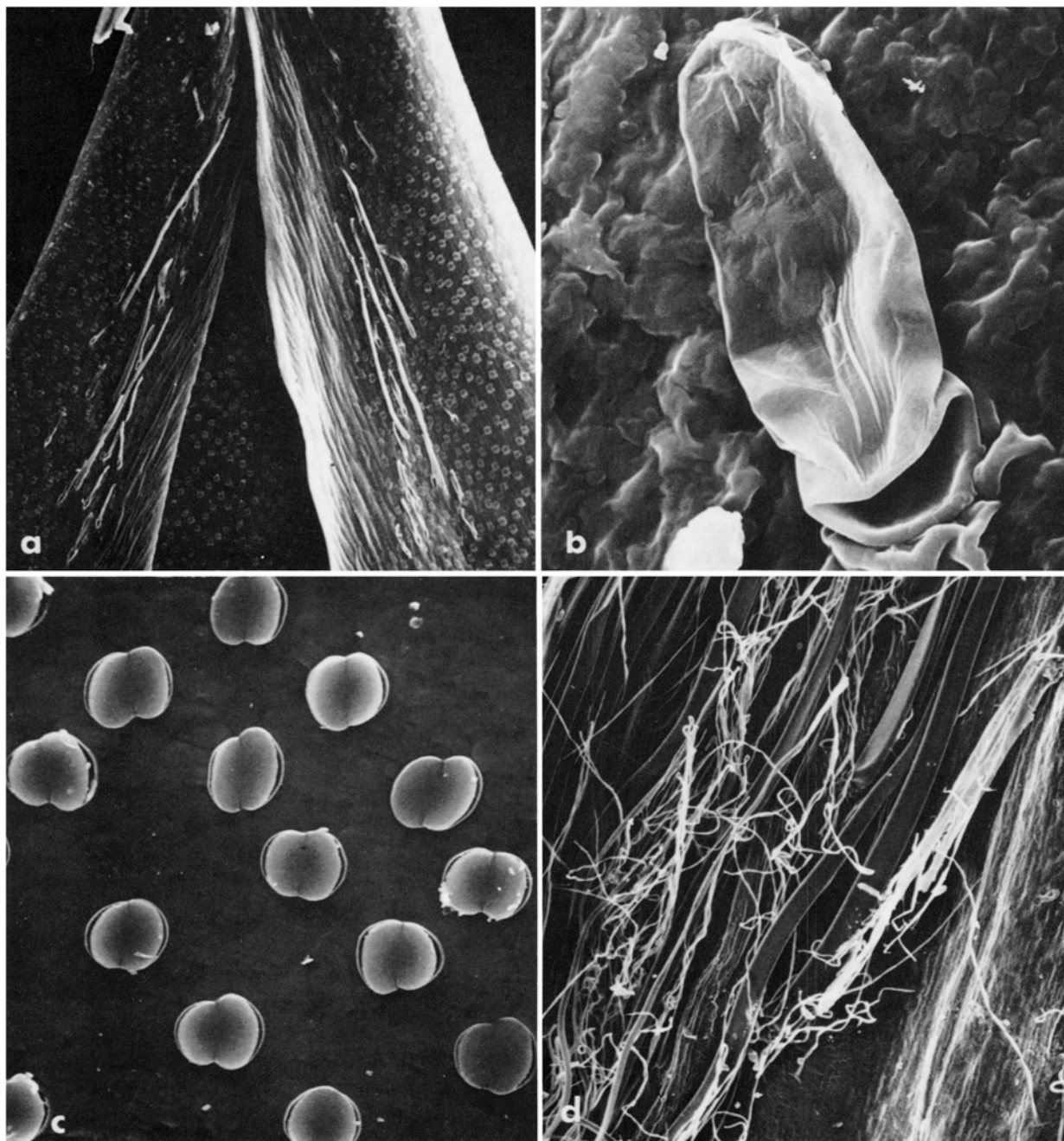


FIGURE 9.—*Homolepis longispicula*: *a*, upper anthercium, palea side, showing flat margins of lemma over palea and macrohairs on the lemma ($\times 100$); *b*, lower lemma showing oblong bicellular microhair with collapsed upper cell ($\times 1400$); *c*, upper palea showing suborbicular silica cells ($\times 1000$); *d*, lower lemma with thick and thin macrohairs ($\times 80$). Photomicrograph *a* based on Chase 10349 (US), *b* and *d* on Hatschbach 27965 (US), and *c* on a fragment of the holotype (US).

silica cells throughout, the hyaline margins of the lemma enclosing almost entirely the palea. *Caryopsis* oblong, 2.9 mm long, 1.5 mm wide, brown; hilum linear, as long as the caryopsis; embryo less than half as long as the caryopsis.

DISTRIBUTION.—In sandy soils of dry and open areas of the Brazilian cerrado in the states of Goiás, Distrito Federal, and Minas Gerais, between 1000 and 1500 m elevation. Plants of this species are exposed to frequent fires as evidenced by the large number of herbarium specimens with burnt bases.

ADDITIONAL SPECIMENS SEEN.—**BRAZIL.** **DISTRITO FEDERAL:** 10 km S of Brasília on road to Belo Horizonte, *Irwin et al.* 8591 (MO, NY, US). **GOIÁS:** 2 km NW of Veadeiros, road to Cavalcante, *Irwin et al.* 9489, 9491 (NY, US); valley of Rio Corumba, *Glaziou* 22470 (US). **MINAS GERAIS:** Diamantina, summit of Serra de São Antonio, *Chase* 10349 (MO, NY, US); 5–10 km W of Diamantina, serra de São Antonio, *Chase* 10426 (US); Serra do Espinhaço, *Hatschbach* 27809 (NY, US); Serra do Cipó, along the road at km 134–135, *Eiten & Eiten* 6750 (MO, US), 6754 (NY, US); road BR 259, *Hatschbach* 27965 (US); Serra do Cipó, 110 km NE of Belo Horizonte, *Chase* 9211 (MO, US).

DISCUSSION.—This species is clearly separable from others in the genus by its habit and habitat. The plants are caespitose with erect culms and densely covered at the base by hard, keeled sheaths that are resistant to fires. The blades are lanceolate, involute, rigid, and without a sharp differentiation between the sheath and the blade, and the ligule is ciliate, unlike that of the remaining species. The spikelet differs most notably in its conspicuous lower palea, which frequently encloses a well-developed male flower. In the remaining characters the spikelet conforms to the type common in the genus.

***Homolepis villaricensis* (Mez) Zuloaga & Soderstrom, new combination**

FIGURE 10

Panicum villaricense Mez, 1921:1. [Type: "Paraguay, Balansa n. 2." Isotype, BAF; fragments of the type, BAA, US sheet no. 2808940.]

Stoloniferous perennials 15–40 cm tall. *Culms* cylindrical or compressed, geniculate, branching at the lower nodes, glabrous; internodes hollow, 1.5–11 cm long. *Nodes* glabrous, obscure. *Sheaths* shorter than the internodes, 2–8 cm long, the margins papillose-pilose to glabrescent. *Ligule* membranous, lacinate, 0.4–0.8 mm long; collar dark brown, glabrous to pilose. *Blades* oblong-lanceolate, acuminate, 4–12 cm long, 0.6–0.9 cm wide, flat, narrowed at the base, the margins scaberulous, the lower with caducous tuberculate hairs, strigose on both surfaces, the midnerve prominent. *Panicles* lax, diffuse, 5–11 cm long, 1.5–5.5 cm wide, the axis scabrous, the lower branches alternate or opposite, the remaining ones alternate, the axils finely pubescent, pedicels scabrous, 3–18 mm long. *Spikelets* ellipsoid to obovoid, 3.2–3.7 mm long, 1.2–1.5 mm wide, glabrous, dark green to olivaceous, viscous at maturity, the glumes usually enclosing the lower lemma and upper antherium. *Lower glume* acute, 3.1–3.4 mm long, as long as or longer than the upper glume, 5–9-nerved, glabrous. *Upper glume* acute, 2.9–3.4 mm long, 7–9-nerved, glabrous. *Lower lemma* glume-like, acute, 2.8–3.3 mm long, 5–7-nerved, scabrous at the apex, the remainder of the surface densely covered with bi-, tri-, or (rarely) quadricellular microhairs, globose, obovoid, 40–70 μm long, 19–30 μm wide. *Lower palea* ovate-lanceolate, 1.9–2.4 mm long, 0.4–0.7 mm wide, membranous, hyaline, glabrous; male flower absent. *Upper antherium* ellipsoid, 2.8–3.2 mm long, 1.1–1.2 mm wide, smooth, shining, pale, covered with evenly distributed dumbbell-shaped silica cells, the apex of the lemma with numerous hooks and dense bicellular microhairs. *Caryopsis* obovoid, 1.8–2 mm long, 1.4–1.8 mm wide; hilum linear, half as long as the caryopsis or a little longer; embryo half the length of the caryopsis.

DISTRIBUTION.—Southern Brazil, Paraguay, and northwestern Argentina, in shaded and humid habitats where it forms dense clumps beneath trees.

ADDITIONAL SPECIMENS SEEN.—**ARGENTINA.** **CORRIENTES:** Garapé stream, mouth of Paraná River, 45 km E of Ituzaingó, *Schinini et*

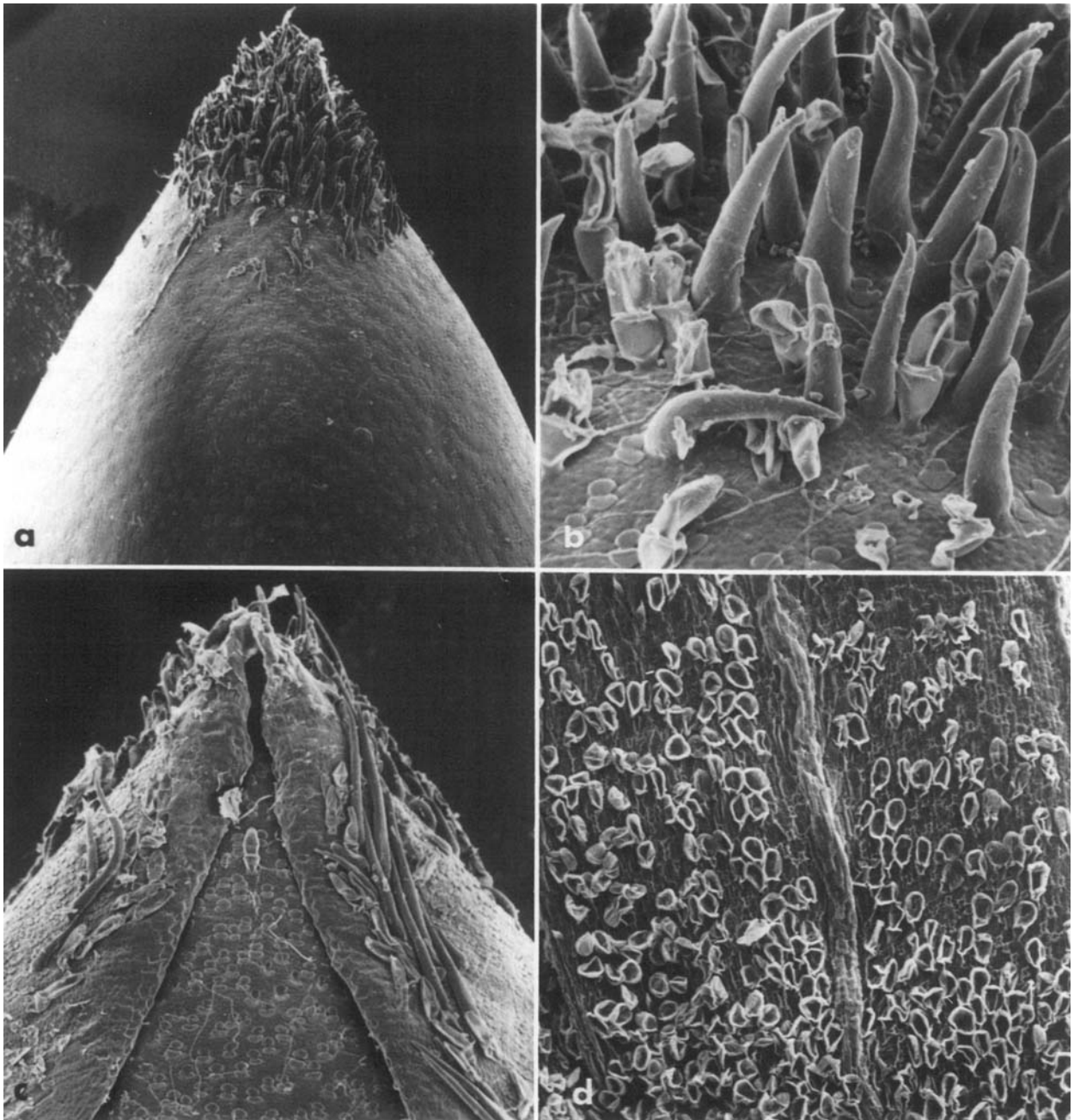


FIGURE 10.—*Homolepis villaricensis*, new combination: *a*, upper antherium, lemma side ($\times 100$); *b*, detail of *a* showing prickly hairs, bicellular microhairs, and suborbicular silica cells ($\times 300$); *c*, upper antherium, palea side, showing macrohairs, bicellular microhairs, and suborbicular silica cells ($\times 200$); *d*, lower lemma, showing glandular microhairs, mostly collapsed ($\times 140$). Photomicrographs *a*–*c* based on *Rojas 3410* (US), and *d* on *Schwindt 3266* (US).

al. 11096 (CTES), *Quarín et al.* 3375 (CTES); Estancia Santa Teresa, *Pedersen* 35 (US); Loreto, *Ahumada & Giberti* 67 (SI, US). MISIONES: Loreto, *Gruner* 764 (BAA), *Novat* 78 (BAB); San Pedro, *Parodi* 5609 (BAA, US); Yabebyrí, *Montes* 747 (LP); San Ignacio, *Giambiagio s.n.*, 1914 (SI 13499), *Quiroga s.n.*, 3 Apr 1914 (NY); San Antonio, *Cabrera, Gebhard & Corte* 108 (BAA); Campo Grande, *Montes* 15357 (SI, US); Salto Encantado, *Schmidt* 4555 (LIL); ruta 14, km 304, *Schwindt* 3266 (LIL, US); Teyucuaré, *Montes* 2110 (US).

BRAZIL. PARANÁ: Guarapuava, *Swallen* 8909 (US).

PARAGUAY. Villa Elisa, *Pedersen* 5902 (Pedersen, US); Villarica, *Jorgensen* 4094 (BAA, F, US), *Ramírez* 828 (BAA); Carobeni Nuevo, *Rosengurttt* B5895 (F, US); Carobeni Nuevo-Itapé, *Ramírez* 676 (BAA); Ipacaray Lake, *Hassler* 12469 (US), 12537 (MO); Alto Paraná, Ñacunday, *Montes* 10906 (US); Santiago, Estancia La Soledad, *Pedersen* 5948 (Pedersen, US); Alto Paraguay, Primavera, *Woolston* 69 (SI); Asunción, Jardín Botánico, *Rojas* 12565 (BAA); Colonia Independencia, *Rosengurttt* 5939 (BAA); Carapeguá, *Rojas* 3410 (BAA, US); Caaguazú, *Hassler* 8919 (BAA, NY); Puerto Bertoni, Alto Paraná, *Rojas* 7951 (BAA), *Bertoni* 3644 (US), 4701 (US); Tobatí, Cerro Tobatí, *Arenas* 1145 (CTES), *Hassler* 500 (NY).

DISCUSSION.—Parodi (1925) considered this species to be conspecific with *Panicum glutinosum*, believing that the smaller size of the plants was the result of logging and of trampling by cattle.

Ichnanthus

Stieber, in his revision of *Ichnanthus* (1982), divided the genus into two sections, *Ichnanthus* and *Foveolatus*, including in the first those species with prominent appendages attached to the base of the upper lemma and in the second those with scars at the base of the upper lemma. He noted that other authors (Zuloaga, 1981; Shaw and Webster, 1981) had demonstrated a common origin for appendages and scars.

The size of the scars varies among the species in *Foveolatus*, from prominent as in *Ichnanthus pallens* to hardly apparent in *I. camporum*, *I. minarum*, and *I. procurrens*. Stieber pointed out that the species in this section are further characterized by a dense aggregation of silica cells at the apex of the upper lemma.

Our study of *Panicum grandifolium* has shown that a pair of diminutive scars is present at the base of the upper lemma, suggesting an alliance with species of *Foveolatus*. An SEM analysis of the upper antheridium has also revealed the presence of numerous silica cells at the summit of the upper palea and lemma, densely aggregated on the palea, sparser and more evenly arranged on the lemma. Additional characters that indicate a relationship to *Ichnanthus* include the keeled condition of the glumes and lateral compression of the spikelets. Because this species is so unlike any other within *Panicum*, instead sharing many characters with *Ichnanthus*, it seems appropriate to include it within this latter genus. Interestingly, Stieber (1982) removed *Ichnanthus nervosus* from the genus and made it synonymous with *Panicum grandifolium* Doell.

Ichnanthus grandifolius (Doell) Zuloaga & Soderstrom, new combination

FIGURE 11

Panicum grandifolium Doell in Martius, 1877:195. [Type: "Habitat in sylvis ad Itahypé fluvium et Camacorum vicum S. Pedro d'Alcantara provinciae Bahiensis (Martius)." Holotype, M, not seen; fragment of the type, US.]
Ichnanthus nervosus Swallen, 1964:147. [Type: "Brazil, Pernambuco, Tapera, in a woods, 24 Apr. 1935, *Pickel* 3855." Holotype, US sheet no. 1645512.]

Cespitose perennials, 60–200 cm tall. *Culms* ascending, cylindrical to compressed, simple, short-pubescent below the nodes, otherwise glabrous; internodes solid, short at the base, becoming longer above, 7–18 cm long. *Nodes* obscure, glabrous to short-pubescent. *Sheaths* 11–15 cm long, the lower ones longer than the internodes, the upper ones shorter, villous at the base and around the collar, the remaining sparsely pubes-

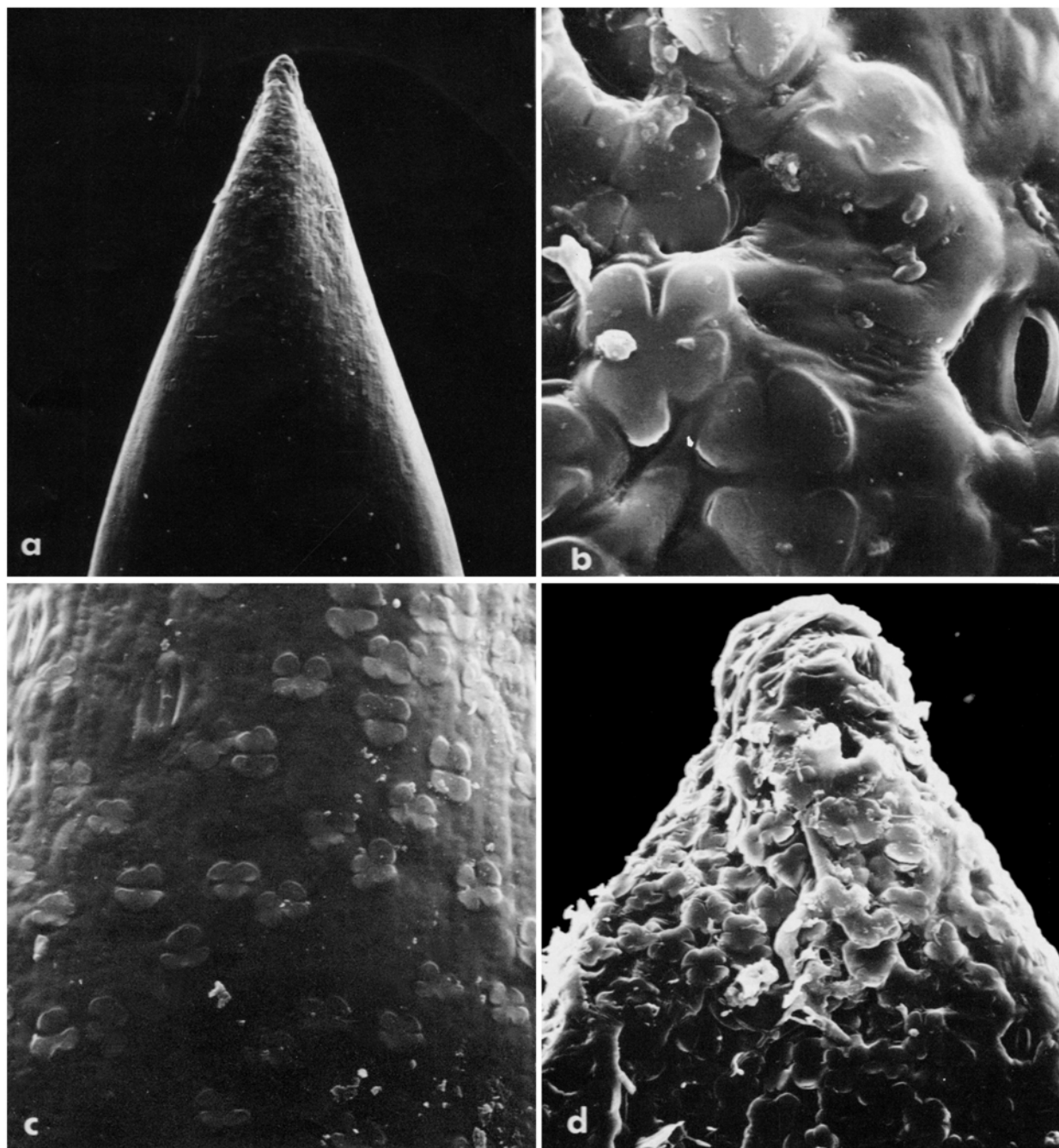


FIGURE 11.—*Ichnanthus grandifolius*, new combination: *a*, upper antheridium, lemma side ($\times 100$); *b*, detail of *a* showing silica cells and stoma ($\times 2000$); *c*, upper antheridium, lemma side ($\times 500$); *d*, detail of upper palea ($\times 500$). All photomicrographs based on *Pickel 1629* (US).

cent to glabrous. *Ligule* membranous-ciliate, 0.7–1.1 mm long, with long hairs adaxially toward the base of the blade; collar dark brown, glabrous to pubescent. *Blades* lanceolate, acuminate, 22–31 cm long, 3.5–6 cm wide, flat, pseudopetiolate, with an asymmetric apex and base, the lower margins glabrous to long-pubescent, with thin, non-tuberculate hairs, otherwise glabrous, the midnerve prominent; pseudopetiole 0.3–2 cm long, short-pilose to glabrous. *Panicles* lax, exerted, diffuse, pyramidal, many-flowered, 15–50 cm long, 5–14 cm wide; axis angular, scabrous to hirsute, the branches alternate to subopposite, diverging, triquetrous, the axils long-pilose, the spikelets in pairs and appressed along both sides of the branches, one sessile, the other shortly pedicellate; pedicels scabrous to hirsute, claviform. *Spikelets* long-ellipsoid, 4–4.5 mm long, 1–1.4 mm wide, greenish, shining, laterally compressed, pubescent only at the apex of the lower glume, otherwise glabrous, glumes and lower lemma rigid and with prominent nerves; upper glume and lower lemma subequal in length. *Lower glume* ovate-lanceolate, acute, 2.6–3.4 mm long, $\frac{2}{3}$ to $\frac{3}{4}$ as long as the spikelet, its margins broadly enclosing the upper glume, 3-nerved, the midnerve scabrous toward the apex and with thick long whitish hairs, scabrous at the apex of the inner surface. *Upper glume* acute, 3.7–4.4 mm long, 5-nerved, both midnerve and inner surface scabrous. *Lower lemma* glume-like, acute, 3.6–4.3 mm long, 5-nerved, scabrous on the inner surface, completely embracing the upper antherium at the base. *Lower palea* lanceolate, 3.1–3.6 mm long, 0.6–1 mm wide, membranous, pubescent along the edges, otherwise glabrous; male flower usually present with 3 stamens, the anthers 1.6 mm long. *Upper antherium* fusiform, 3.3–3.7 mm long, 1 mm wide, laterally compressed, smooth, shining, membranous, the lemma enclosing the palea with its wide margins, the lemma and palea with numerous silica cells and stomata at the apex; silica cells rounded, with 2–4 sinuses, more or less evenly distributed over the upper lemma and densely so on the apex of the palea; small scars present at the base of the antherium on both

sides of the lemma. *Caryopsis* not seen.

DISTRIBUTION.—Occurring from sea level to 300 m elevation in eastern Brazil—from Pernambuco to Espírito Santo—in moist places within or at the edges of woodlands or forests.

ADDITIONAL SPECIMENS SEEN.—BRAZIL. BAHÍA: 23 km [E] of Ibirataia, on side road connecting with BR-101, Fazenda Macedonia, *Calderón et al.* 2362 (US); Fazenda Uruguayana and vicinity, 8 km S of Santa Cruz da Vitoria, *Soderstrom et al.* 2109 (US); 6 km E of Ubaira city: Rio Jequirica, *Calderón & Pinheiro* 2249 (US); rodovia Itabuna-Uruçuca, *Belém & Aguiar* 1248 (US). ESPÍRITO SANTO: Reserva Biológica de Sooretama, *Soderstrom & Sucre* 1894 (US). PERNAMBUCO: Nazaré da Mata, *Moraes* 1103 (US); Tapera, *Pickel* 1629, 1928, 2347, 3543, 3545 (US).

DISCUSSION.—The sheaths of one specimen, *Soderstrom & Sucre* 1894, are distinctive in their purplish mottling.

Taxonomic Position of *Panicum aristellum*

In an unedited key to South American species of *Panicum*, Chase considered *P. aristellum* to have little relationship to any other species of the genus, because of the presence of awns on both glumes. She placed it next to the only other species with awned glumes, *Panicum najadum* Hackel, which was later transferred to *Oplismenus najada* by Parodi. In fact, Chase later agreed with other authors in regarding *Panicum* as a genus with unawned glumes. Awned glumes are, however, characteristic of several other panicoid genera, such as *Chaetium*, *Echinochloa*, and *Oplismenus*.

The thin and membranous upper antherium of *P. aristellum* resembles that of *Hymenachne* (Figure 13), which was described by Beauvois in 1812 in the following manner (as translated from the Latin):

Panicle simple, spiciform: branches dense. - Glumes unequal, herbaceous, acute: the lower much shorter than the upper. Lower antherium sterile: Lower lemma acute, the palea very short, membranous, hyaline. Upper antherium hermaphrodite: the lemma and palea membranous, acute.

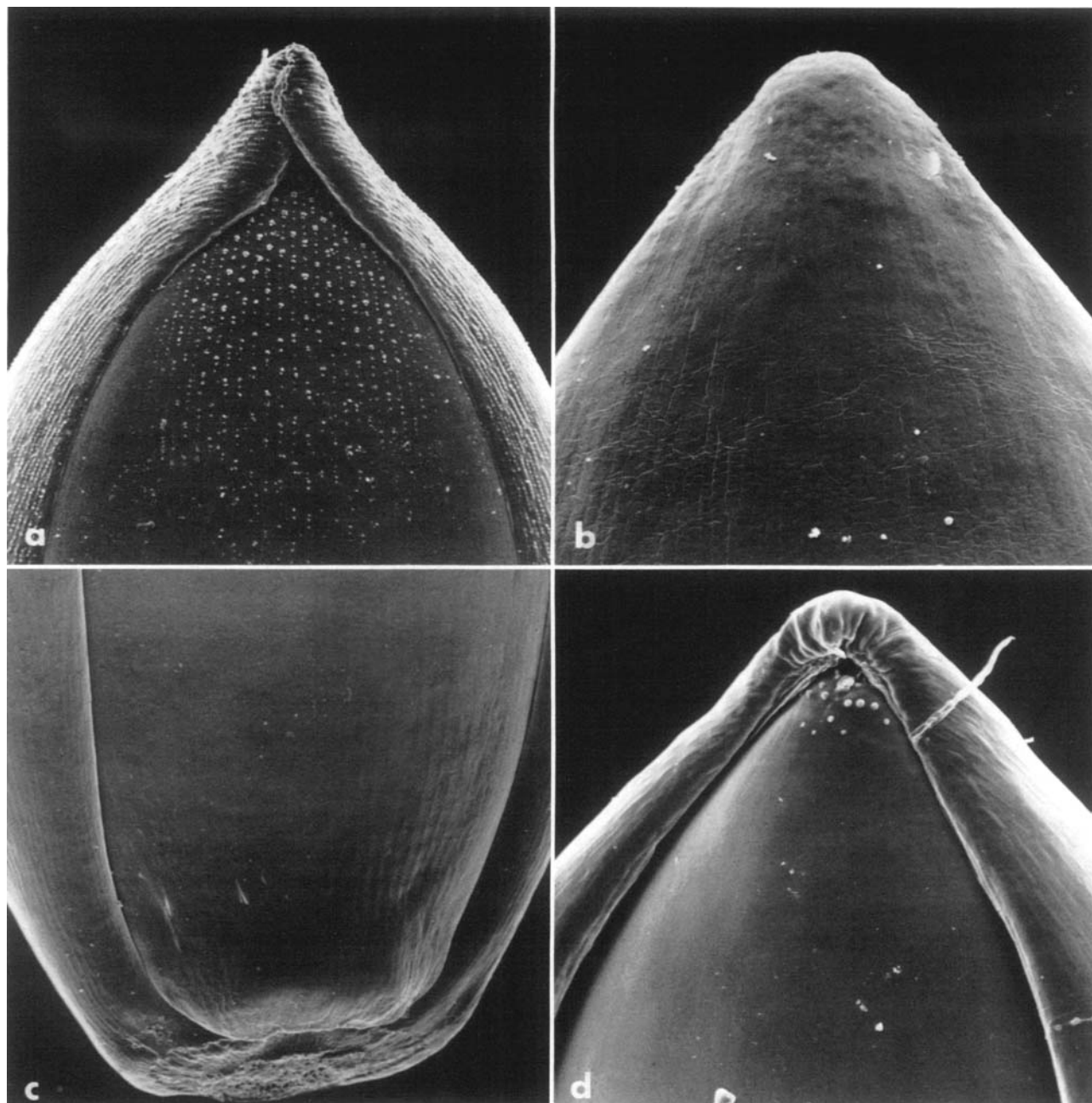


FIGURE 12.—*Panicum* species: *a*, upper antherium of *P. vaseyanum*, palea side ($\times 100$); *b*, upper antherium of *P. quadriglume*, lemma side ($\times 200$); *c*, base of upper antherium of *P. hispidifolium* ($\times 100$); *d*, upper antherium of *P. diffusum*, palea side ($\times 200$). Photomicrograph *a* based on Pringle 1415 (US), *b* on Chase 8897 (US), *c* on Valerio Rodríguez 1981, and *d* on Eggers 76 (US).

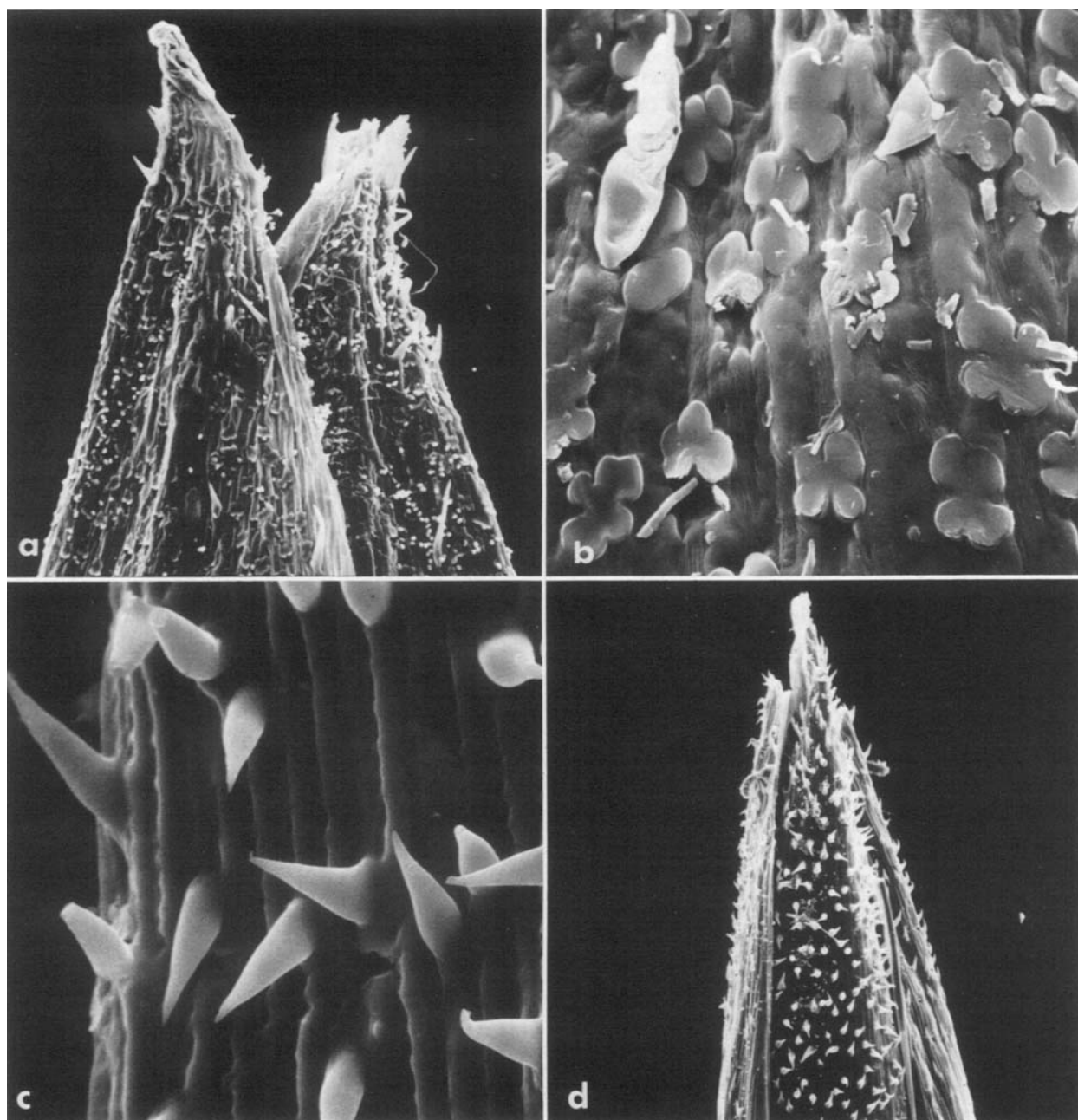


FIGURE 13.—*Hymenachne* species: *a*, upper anthercium of *H. hemitoma* showing the thin lemma and palea ($\times 200$); *b*, detail of upper anthercium, palea side, of *a* showing bicellular microhairs and silica cells ($\times 1000$); *c*, detail of upper anthercium of *H. amplexicaulis* showing prickly hairs ($\times 1000$); *d*, upper anthercium of *H. donacifolia* ($\times 100$). Photomicrographs *a* and *b* based on Tracy 8847 (US), *c* on Rosengurt 6175 (US), and *d* on Ule 883 (US).

Chase (1908) and later Pilger (1940, 1954) considered the distinguishing character of *Hymenachne* to be the membranous consistency of the upper lemma and palea, which is the basis of the generic name (*hymen*, membranous, plus *achne*, scale). In *Panicum* the upper antherium is commonly indurate with the margins of the lemma inrolled over the palea (Figure 12). Chase included in *Hymenachne*, *H. amplexicaulis*, a species with spike-like panicles, and *H. donacifolia*, a species with long and narrow panicles whose branches sometimes diverge from the axis.

Panicum aristellum differs from *Hymenachne* mainly in the laxness of the panicle, the aristate condition of the glumes, and the presence of a palea and male flower in the lower antherium. Some species of the Laxa group of *Panicum* (*P. pernambucense* and *P. grumosum*) share with *Hymenachne* and *P. aristellum* a membranous upper antherium. In these species the spikelets are short-pedicellate and form dense racemes, which are more or less divergent from the axis and not much different from *H. donacifolia* or *H. condensata*. In *Hymenachne* and *P. aristellum* the glumes are acuminate or aristate, whereas in the other species of *Panicum* cited above, the glumes and lower lemma are acute. The palea of the lower floret is usually absent in *P. pernambucense* but is present in *P. grumosum*.

A similar habitat and geographical distribution

are shared by *Hymenachne*, *P. aristellum*, and the above species of *Panicum*. *Panicum pernambucense* occurs from Bahía to the north of Argentina and *P. grumosum* from Santa Catarina to the province of Buenos Aires, Argentina. All of these species are characteristic of river or lake margins and habitats periodically covered by water.

Panicum, *Panicum aristellum*, and *Hymenachne* may be distinguished by the characters listed in Table 2.

If the consistency of the upper antherium is accepted as a character of generic importance to differentiate *Hymenachne* from *Panicum*, then *Panicum aristellum* and species of the Laxa group would be congeneric with *Hymenachne*. In order to test this hypothesis, a study should be made of all of the species in *Hymenachne* as well as those of the Laxa group of *Panicum*. Because we have not made such a study we are not transferring *P. aristellum* to another genus at this time.

Panicum

Panicum aristellum Doell

FIGURES 14, 15

"*Panicum Aristella*" Doell in Martius, 1877:221. [Type: "In provincia Minarum a cl. Widgren lectum (herb. Holm.)." Type, S, not seen; isotype, US sheet no. 702302; fragment of the type, US sheet no. 80468.]

Cespitose or shortly rhizomatous perennials, 1–2 m tall. Culms erect, many-noded, simple,

TABLE 2.—Comparison of *Panicum*, *Panicum aristellum*, and *Hymenachne*.

Character	<i>Panicum</i>	<i>Panicum aristellum</i>	<i>Hymenachne</i>
Upper antherium	indurate or membranous, lemma covering the palea at the apex	membranous, lemma covering the palea at the apex	membranous, lemma not covering the palea at the apex
Lower antherium	palea present or absent and sometimes a male flower	palea and male flower present	palea and male flower absent
Glumes I and II	obtuse, acute or acuminate, not awned	awned, the awns of equal length to the body of the glumes	acuminate, not awned
Inflorescence	panicle lax to contracted	panicle lax, diffuse	panicle spike-like to contracted

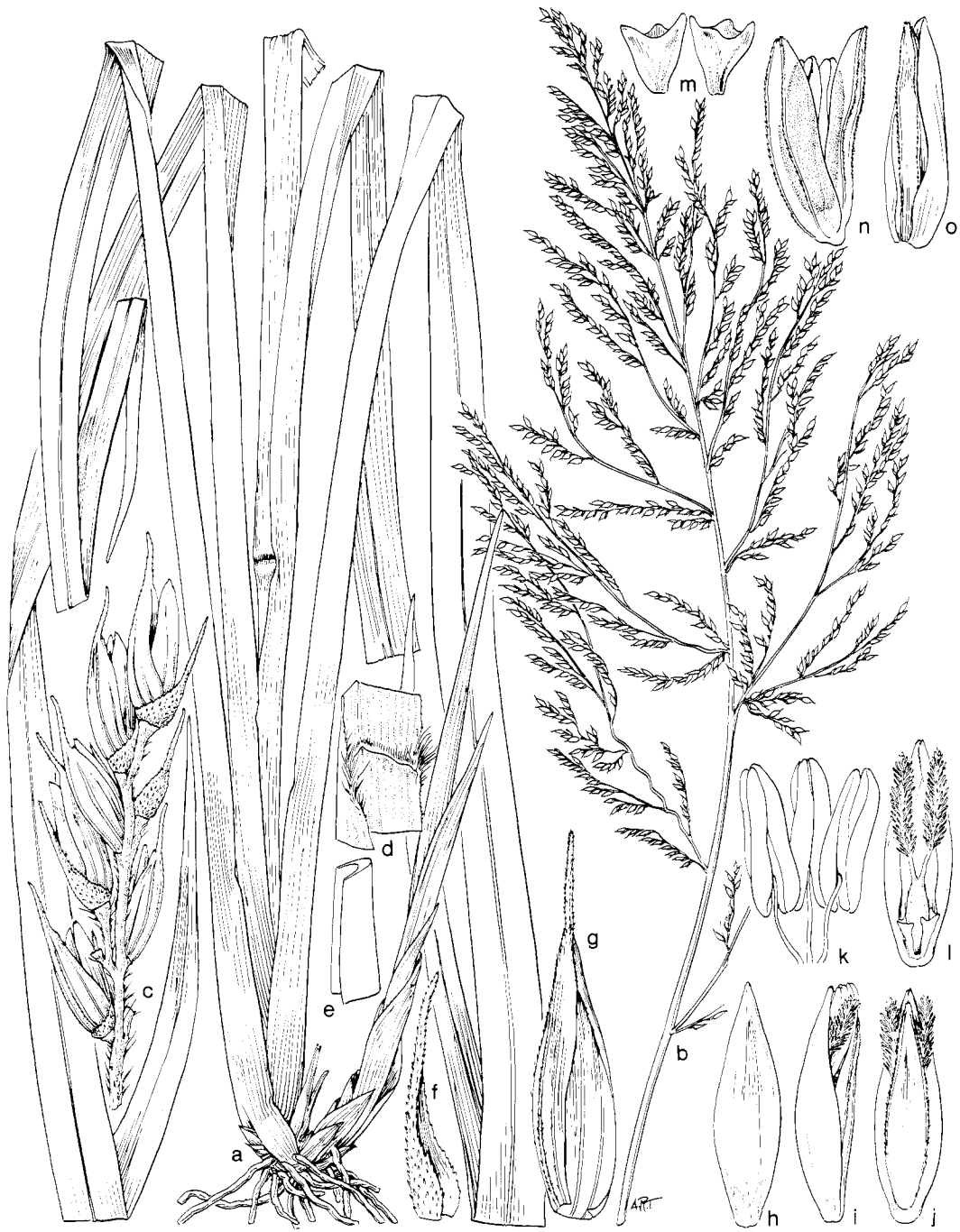


FIGURE 14.—*Panicum aristellum*: a, habit ($\times 1$); b, panicle ($\times 1$); c, branch of the panicle ($\times 12$); d, ligule ($\times 3$); e, scheme of sheath in cross section; f, lower glume ($\times 25$); g, upper glume ($\times 25$); h, upper antherium, lemma side ($\times 25$); i, upper antherium, lateral view ($\times 25$); j, upper antherium, palea side ($\times 25$); k, stamens ($\times 25$); l, upper palea with gynoecium and lodicules ($\times 25$); m, lodicules of the upper antherium ($\times 40$); n, lower antherium, lateral view ($\times 25$); o, lower antherium, palea side ($\times 25$). Drawing a based on *Hatschbach 28413* (US), b–o on *Hatschbach 28413* (US), *Kuhlmann 2774* (US), and *Widgren 924* (US).

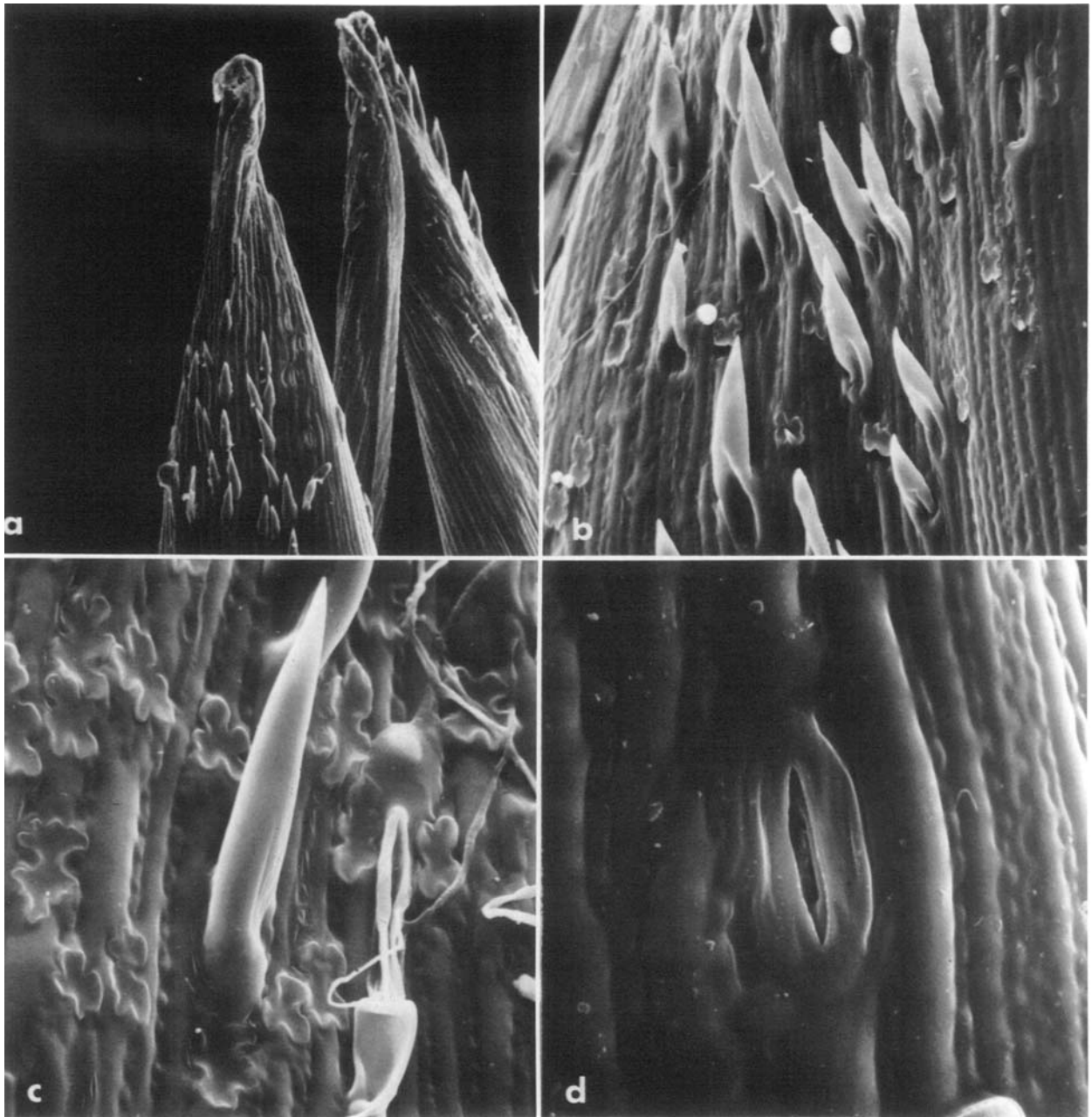


FIGURE 15.—*Panicum aristellum*: *a*, upper antherium, lateral view showing thin lemma and palea ($\times 150$); *b*, detail of palea in *a* showing prickles, silica cells, and stomata ($\times 500$); *c*, detail of upper antherium, lemma side, showing bicellular microhair, prickles, and sinuous silica cells ($\times 1000$); *d*, detail of upper palea showing stoma ($\times 1500$). Photomicrographs *a* and *d* based on Widgren 924 (US), *b* and *c* on Hatschbach 14888 (US).

cylindrical, glabrous to hirsute; internodes solid or with a small lumen, 15–40 cm long. *Nodes* obscure, compressed, glabrous. *Sheaths* shorter than the internodes solid or with a small lumen, 10–25 cm long, keeled, rigid, overlapping at the base, glabrous or papillose-pilose along the margins. *Ligule* membranous-ciliate, 0.5–0.7 mm long; collar inconspicuous. *Blades* linear-lanceolate, acuminate, 45–75 cm long, 1–1.8 cm wide, narrow and involute toward the base, becoming flattened and wider, sometimes with the margins involute, rigid, pubescent toward the base on the adaxial surface, otherwise glabrous, the margins scabrous, the midnerve prominent. *Panicles* lax, diffuse to contracted, pyramidal to oblong, many-flowered, 20–40 cm long, 7–20 cm wide, the branches diverging from the axis with the spikelets congested along secondary racemes; axis cylindrical, scabrous, the branches alternate, triquetrous, markedly scabrous, densely to sparsely hirsute, the axils glabrous to pubescent; pedicels short, scabrous or occasionally hirsute. *Spikelets* fusoid, 3.8–5.7 mm long, 0.7–1 mm wide (3.1–3.9 mm long without the awns), brown, somewhat compressed laterally, glumes and lower lemma herbaceous, weak, prominently scabrous on the nerves. *Lower glume* ovate-lanceolate, 2.3–3.6 mm long with an awn 0.9–1.8 mm long, about as long as the lower lemma, 1–3-nerved, the midnerve and awn as well as the margins markedly scabrous, the inner surface scabrous toward the apex. *Upper glume* 3.7–5.7 mm long, markedly scabrous at the apex on the inner surface, 5-nerved, the nerves scabrous, the midnerve extending into an awn 0.7–2 mm long, this twisted or not. *Lower lemma* oblong, acute, 2.8–3.6 mm long, awnless, 3–5-nerved, the midnerve scabrous. *Lower palea* conspicuous, lanceolate, 2.3–3.1 mm long, 0.5–0.7 mm wide, hyaline, glabrous, with scabrous, denticulate margins; male flower present with 3 stamens. *Upper anthercium* fusiform, 2.3–3.1 mm long, 0.5–0.8 mm wide, membranous, smooth, pale to brown, with prominent hooks toward the apex of the lemma and palea and on the margins of the lemma, also with silica cells, bicellular microhairs and stomata at the apex of both lemma and palea;

lemma 5-nerved; lodicules 2, flat, covering the base of the gynecium; stamens 3, stigmas 2 with the styles united at the base. *Caryopsis* dark brown with an oblong hilum; embryo $\frac{1}{3}$ the length of the caryopsis.

Note: In some specimens the rachilla is prolonged in the form of a small point above the upper anthercium.

COMMON NAME.—“Canarana.”

SPECIFIC EPITHET.—This species was described by Doell under the name of *Panicum Aristella* instead of *aristellum*, which would be the correct neuter agreement. Commenting on this, Smith and Wasshausen (1978) felt that the epithet *Aristella* should be retained and argued that the specific epithet had been taken from a genus named *Aristella* as it appeared in this form in the index to the *Flora Brasiliensis* of Martius (1877:347–348). However, that index contains a number of specific epithets that are capitalized, none of which corresponds to the name of a genus; *Arnacites*, *Aturense*, and *Longispicula* are examples. The index is therefore not helpful and we feel there is no strong argument to retain *Aristella*.

DISTRIBUTION.—Southern Brazil, from the state of Rio de Janeiro to Rio Grande do Sul. A hygrophytic species inhabiting marshes or seasonally inundated lowlands at elevations up to 1000 m. According to Smith and Wasshausen (1982) it is a common species in fields of the central planalto of Santa Catarina, where it is associated with *Hypogynium virgatum* and *Andropogon lateralis*.

ADDITIONAL SPECIMENS SEEN.—BRAZIL. PARANÁ: Foz do Rio Taquaral, *Hatschbach 3337* (US); Guarapuava, Rio das Pedras, *Pereira & Hatschbach 8004* (US); Prainha, *Hatschbach 28413* (US); Mallet, *Hatschbach 15371* (US); Rio das Cinzas, Barra do Perdizes, *Hatschbach 8491* (US); road to Porto Vitoria, *Hatschbach 14888* (US); Piraquara, ~22 km E of Curitiba, *Tessmann s.n.*, 1 Jan 1949 (US); Rio das Pedras, *Hatschbach 10615* (US). RIO DE JANEIRO: without locality, *Glaziou 20576* (US). RIO GRANDE DO SUL: Tupacretan, *Araujo 338* (US). SANTA CATARINA: 6 km E of Porto União, *Smith & Klein 15279* (US);

Bom Retiro, *Reitz & Klein 5500* (US); 10 km E of Poço Preto, *Smith & Klein 15736* (US); Porto União, *Reitz & Klein 13671, 13680* (US); Valões, *Reitz & Klein 3706, 13571* (US); Fazenda Frei Rogerio, Porto União, *Reitz & Klein 13613* (US); Morro do Campo Alegre, São Francisco do Sul, *Reitz & Klein 10062* (US); Campo do Areão, Santa Cecília, *Reitz & Klein 14150* (US). SÃO PAULO: Boraceia, margem do Rio Claro, *Kuhlmann 2774* (US).

Taxonomic Position of *Panicum killipii*

This species displays no apparent affinity to any other species of *Panicum*, as Hitchcock himself pointed out in the original description. However, its affinities to *Paspalum*, to which we are transferring it, become clear in the following enumeration of characters:

1. The spikelets are arranged on unilateral racemes, with one sessile and the other short-pedicellate. Although both spikelets are usually sessile and appressed to the rachis in *Paspalum*, some members, such as *Paspalum flavum* Presl and *P. corcovadense* Raddi, have pedicellate spikelets like *Panicum killipii*.

2. The spikelets are plano-convex and obtuse, characters that are particularly noticeable in the upper anthecium (the presence of a lower male flower obscures this in certain cases). Indeed, the spikelets of *Panicum killipii* and those of *Paspalum flavum* show a great deal of similarity.

Paspalum

Paspalum killipii (Hitchcock) Zuloaga & Soderstrom, new combination

FIGURE 16

Panicum killipii Hitchcock, 1930b:383. ["Type in the U. S. National Herbarium no. 1357803, collected in thickets, Aina, between Huanta and Río Apurimac, Dept. Ayacucho, Peru, alt. 750 to 1000 meters, May 1929, by E. P. Killip and A. C. Smith (no. 22804)."] Holotype, US.]

Perennials 80–160 cm tall with thick adventitious roots at the base. Culms erect, rarely decumbent and rooting on the lower nodes, branching,

cylindrical, glabrous; internodes hollow, 12–28 cm long. Sheaths 12–17 cm long, long-ciliate on the margins, otherwise glabrous. Ligule membranous, lacinate, with long whitish hairs toward the base of the adaxial surface of the blade, brown. Blades lanceolate, acuminate, 20–35 cm long, 2–3.8 cm wide, flat, the upper ones cordate, the lower ones with a pseudopetiole up to 3 cm long, the abaxial surface glabrous, adaxial glabrous to sparsely pubescent, the margins scabrous to short-ciliate, the basal ones long-ciliate; upper blades small. Panicles lax, diffuse, pyramidal, 15–33 cm long, 10–17 cm wide, the branches divergent, alternate, widely separated; axis angular, scabrous, the branches flattened, scabrous, the axils short-pubescent, the spikelets in pairs and arranged more or less unilaterally on the racemose branches, one sessile, the other short-pedicellate; pedicels shorter than the spikelet, scabrous. Spikelets ovoid, plano-convex, 2–2.4 mm long, 0.8–1 mm wide, purplish, glabrous or occasionally with some hairs toward the summit of the upper glume and lower lemma. Lower glume ovate, acute, 0.2–1 mm long, nerveless, short-pubescent. Upper glume and lower lemma subequal, obtuse, herbaceous, 5-nerved, glabrous or pubescent. Lower palea elliptical, 1.8–2.2 mm long, 0.5–0.8 mm wide, hyaline, glabrous, the upper margins short-ciliate; male flower present, with 2 lodicules and 3 stamens, the anthers 1.3 mm long. Upper anthecium ovoid, 2–2.3 mm long, 0.8–1 mm wide, plano-convex, pale, shining, papillate throughout, scabrous at the apex of the lemma. Caryopsis 1.4 mm long, 0.7 mm wide; hilum punctiform, the embryo about half as long as the caryopsis.

DISTRIBUTION.—This species is known only from the Peruvian departments of Ayacucho, Cuzco, and Huancavelica, at 750 to 1200 meters elevation.

ADDITIONAL SPECIMENS SEEN.—PERU. CUZCO: without locality, *Bues s.n.*, Jun 1930 (F, US). AYACUCHO: Aina, between Huanta and Río Apurimac, *Killip & Smith 22803* (US); Ocarra, between Huanta and Río Apurimac, *Killip & Smith 22491* (US). HUANCAVELICA: Vuelo-Pata,

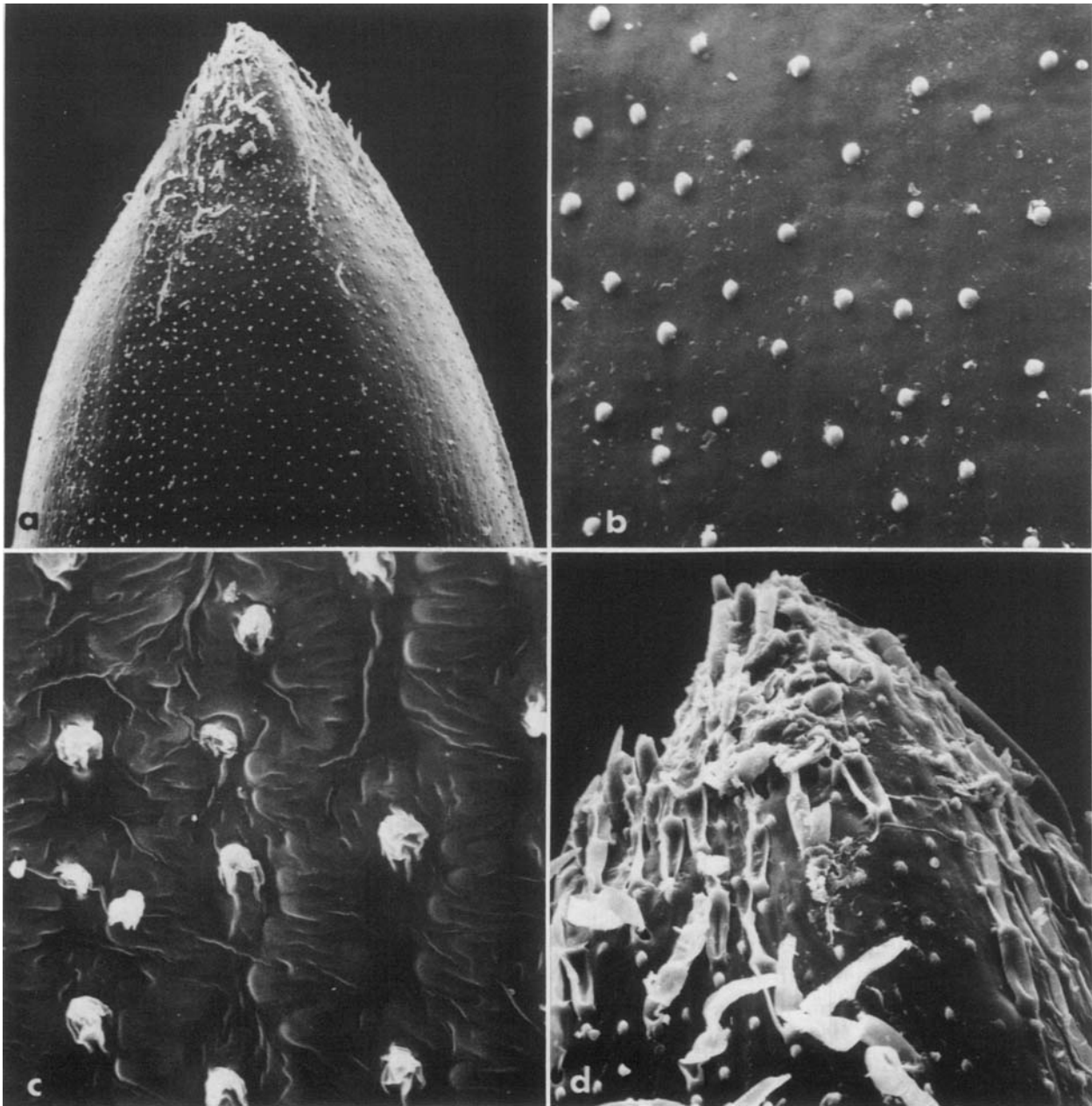


FIGURE 16.—*Paspalum killipii*, new combination: *a*, upper antheridium, lemma side ($\times 100$); *b*, detail of *a* showing simple papillae ($\times 500$); *c*, detail of immature upper antheridium, lemma side ($\times 500$); *d*, upper antheridium, lemma side, showing bicellular microhairs ($\times 500$). All photomicrographs based on *Tovar 4615* (U.S.).

arriba de Virgen-Pampa, al SE de Tintay, *Tovar 4615* (US).

DISCUSSION.—The species exhibits great variation in the length of the lower glume, from spikelets in which it is almost absent to those in which it attains about half the length of the spikelet.

The species is endemic to Peru, a distribution that fits well with *Paspalum*, in which genus more than 25 species occur exclusively in the Andean region of Colombia, Ecuador, Peru, and Bolivia. On the other hand, the only species of *Panicum* that are found here are those of wide distribution.

One specimen, *Bues s. n.*, differs from the others in its smaller panicles with densely hirsute axis and branches and densely hispid sheaths and foliage. The specimen consists only of the upper, densely branched, part of a culm.

Taxonomic Position of *Streptostachys*

A.N. Desvaux established *Streptostachys* in 1810 with a single species, *S. asperifolia*, which he described as monoecious and with spikelets of both sexes intermixed. He further described the female spikelets as having 18–20 glumes. The name was based on the Greek *streptos* (twisted) plus *stachys* (spike), in reference to the twisted disposition of the racemes. Unfortunately, the type material was a sterile monstrosity and neither the description nor generic name reflected the true nature of the genus. In a footnote to the description, Desvaux noted that the disposition of the flowers was quite unusual and served to separate the genus from any other known grass.

After examining specimens that were part fertile and part sterile, Palisot de Beauvois (1812) emended the original description of the genus. Although he described the sterile racemes in the same manner as had Desvaux, he added a description of the fertile panicle and normal spikelets and illustrated both types of inflorescence together with details of the spikelet, lodicules, and ovary of a normal panicle. At the same time he changed the name of the species to *S. hirsuta*, pointing out that the leaves were pubescent

rather than asperous. In the following year Desvaux (1813) redefined the genus and followed the modifications made by Beauvois. Trinius (1820) accepted the genus and also used the name of *S. hirsuta*.

In 1825 Sprengel transferred the species to *Panicum* and called it *P. streptostachys*, and Trinius (1826), Kunth (1829), Steudel (1855), and Doell (in Martius, 1877) followed his lead. Doell additionally listed several synonyms: *P. balanites* Trinius, *P. perfoliatum* Nees, *P. vaginaeflorum* Steudel, *P. rohri* Nees ex Steudel, *S. asperifolia* Desvaux, and *S. hirsuta* Beauvois, and listed *P. macrophyllum* Raddi as doubtful. Bentham (1883) was the first to indicate the position of the species in the genus by assigning it to section *Grandiflora* with *P. macranthum* and *P. zizanioides*. Hitchcock (1922) accepted the species as valid in *Panicum* but effected the combination *P. asperifolium* (Desvaux) Hitchcock.

It was not until 1931 that the original genus was re-established by Pilger. For the first time since its inception 121 years earlier, *Streptostachys* was described on the basis of several natural characters: the oblong shape of the lower glume, which reaches $\frac{3}{4}$ – $\frac{4}{5}$ the length of the spikelet, absence of a sterile palea, and linear hilum. Pilger further pointed out that the base of the spikelet is flat and strongly thickened with recurved margins. In 1940 and 1954 the same author emphasized the generic characters of long lower glume, thickened and flattened base, and the prominently thickened margins.

Butzin (1970a) grouped together a whole series of genera of Paniceae on the basis of leaves with tessellate venation, adding that all of these possessed a syndrome of characters that he considered primitive: the “bamboo habit”; diffuse panicles; presence of a lower, usually many-nerved glume; elongation of the rachilla between the lower glume and the upper antherium; presence of a developed lower flower; and indurate upper antherium. He cited genera that “prove” that the Paniceae were derived from ancestors with many-flowered spikelets, including among these *Streptostachys*, for which he cited teratological panicles in which the spikelets demonstrate a

multiplication of glumes and absence of fertile flowers. Butzin regarded this as an extreme case of spikelet dimorphism that could be interpreted as a link between putative many-flowered ancestors and the genera that presently comprise the tribe.

Butzin related *Streptostachys* phylogenetically to *Acroceras*, enumerating the following shared characters: amplexicaul leaves, panicles with spikelets arranged in pairs in racemose branches, and caryopses with a linear hilum. He distinguished *Acroceras* by its laterally compressed spikelets and presence of a rudimentary lower flower. (Although the spikelets of *Streptostachys* are indeed dorsally compressed, a lower flower is frequently present. Along with *Oplismenus*, these two genera are further distinguished by a linear hilum. *Homolepis* belongs here as well, although Butzin included it with genera having a punctiform hilum.)

In another paper Butzin (1970b) published a systematic treatment of the *Panicaceae* and divided it into 11 subtribes, giving to the group already mentioned the rank of subtribe, which he called *Microcalaminae*, characterized by leaves with tessellate venation. Curiously, he placed *Panicum* in another subtribe even though many of its species share the character assigned to his *Microcalaminae*.

In spite of monstrous material and his misinterpretations of it, Desvaux's recognition of a new genus, *Streptostachys*, has been validated by the years. To the type-species we are adding a new one and transferring yet another from *Panicum*. The observations that follow refer to the genus of three species as we now recognize it.

Rachilla: This is manifest with the internodes prominent between the lower glume and upper anthercium. At the same time it is thickened and gives the spikelet a particular aspect at its base. As a consequence of this peculiar type of rachilla, the glumes and lower and upper anthercia are strongly adnate to it and do not break apart easily, for which reason the spikelet falls at maturity with all of its parts together. In *S. asperifolia* the rachilla is recurved at the base and covers the upper part of the pedicel, but in *S.*

macrantha and *S. ramosa* it is erect and prominently thickened.

Caryopsis: The hilum is linear and as long as the caryopsis. *Streptostachys* shares this particular character with few genera of *Panicaceae*, including *Acroceras*, *Echinochloa*, *Homolepis*, *Mesosetum*, *Oplismenus*, and *Tatianyx*.

Upper Anthercium: Round papillae are evenly distributed over the lemma and palea. The anthercium is generally densely pubescent at the apex and sparsely so or glabrous toward the base, varying in the three species. The hairs are unicellular, long and wavy in *S. macrantha* and *S. ramosa*, whereas in *S. asperifolia* they are bicellular and shorter with the distal cell elongated.

Lower Lemma: In different specimens variation in the consistency of the lower lemma may occur; in some spikelets it is membranous, whereas in others the median portion is hard and the edges membranous. There are also spikelets with the lower lemma indurate throughout and with an ornamentation similar to that of the upper anthercium, i.e., with abundant hairs and evenly distributed papillae.

Ligule: This may be ciliate—formed by a line of whitish hairs—to absent, with all variations between these extremes occurring within a single specimen.

We do not consider the two following characters, which were enumerated by Pilger, to be of taxonomic value:

Lower Glume: Pilger pointed out that the lower glume is generally about $\frac{3}{4}$ to $\frac{4}{5}$ the length of the spikelet and utilized the character to separate *Streptostachys* from the remaining genera of *Panicaceae*. When *S. macrantha* and *S. ramosa* are included in the genus, the length of the lower glume varies from $\frac{1}{3}$ to $\frac{4}{5}$ the length of the spikelet. In *Panicum* itself the length of the lower glume varies considerably; for example, in the groups *Parviglumia* and *Dichotomiflora*, it reaches $\frac{1}{5}$ to $\frac{1}{3}$ the length of the spikelet, $\frac{1}{2}$ to $\frac{3}{4}$ in *Panicum*, *Rudgeana*, *Sarmentosa*, *Laxa*, *Penicillata*, and approximately $\frac{3}{4}$ in *Dura* and *Parvifolia*. In species such as *P. obtusum* and *P. longipedicellatum*, the lower glume is about as long as the upper glume and lower lemma. Al-

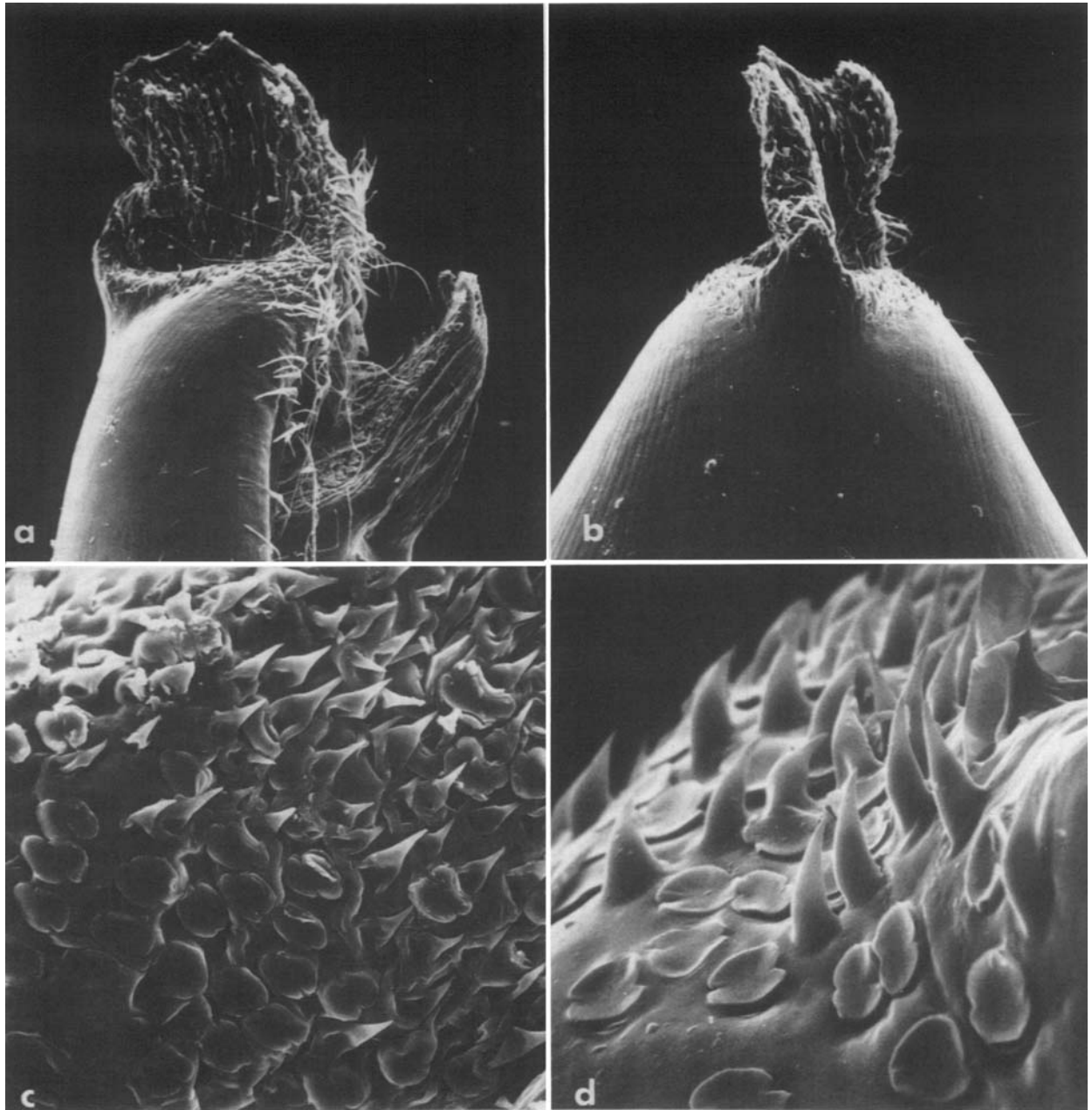


FIGURE 17.—*Acroceras zizanioides*: *a*, upper antheridium, lateral view, showing thin and crested summits of lemma and palea ($\times 100$); *b*, upper antheridium, lemma side, showing the crested summit ($\times 100$); *c*, detail of apex of upper lemma, showing prickly hairs and rounded silica cells ($\times 500$); *d*, same as *c* but at higher magnification ($\times 1000$). All photomicrographs based on *Gillett 16486* (US).

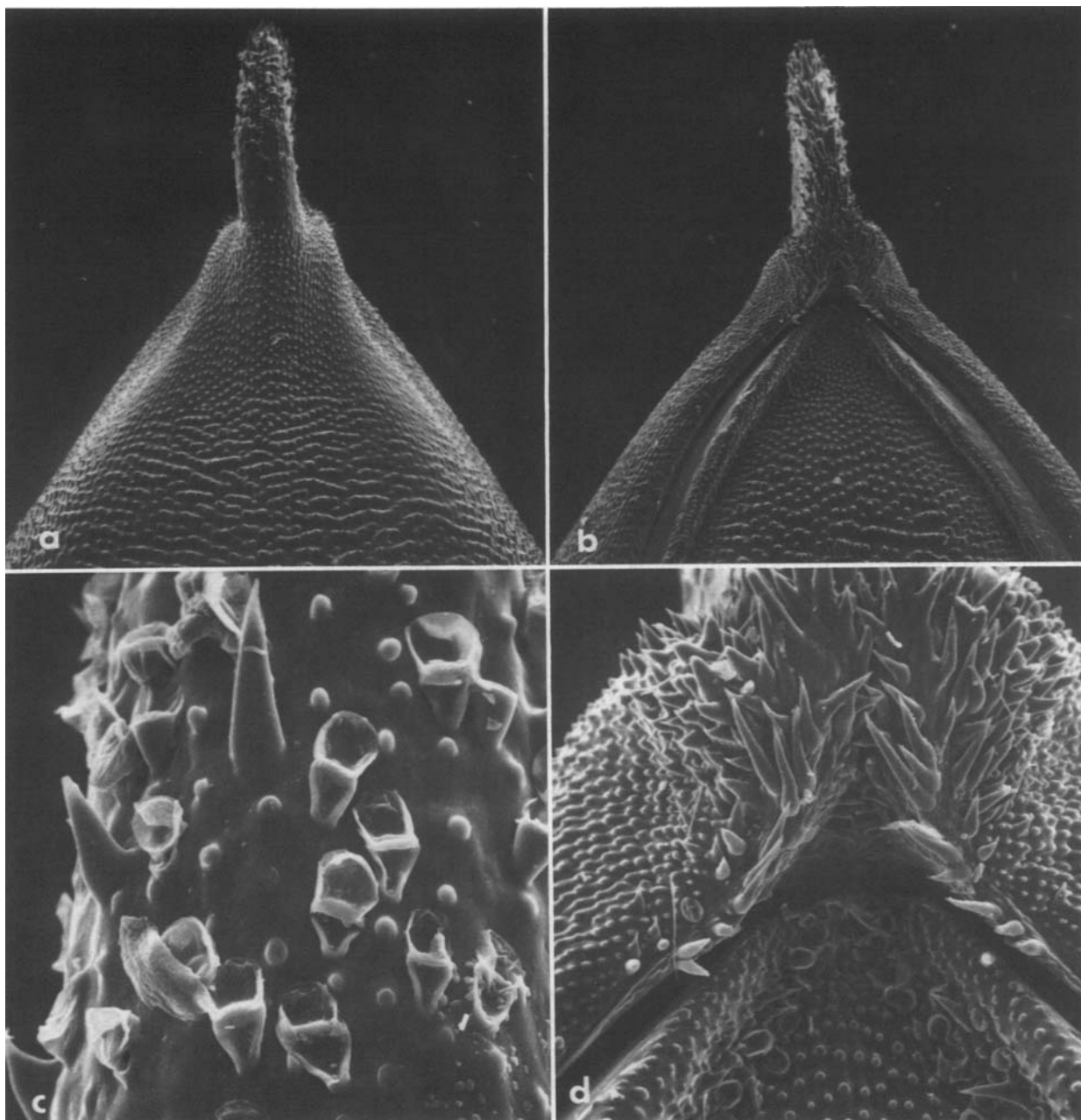


FIGURE 18.—*Acroceras paucispicatum*: *a*, upper anthercium, lemma side, showing the crested summit and rugose surface ($\times 50$); *b*, upper anthercium, palea side, showing crested summit and rugose surface ($\times 50$); *c*, detail of summit of lemma showing bicellular microhairs, rounded papillae, and prickly hairs ($\times 500$); *d*, detail of apex of upper anthercium, palea side, showing same structure as in *c* ($\times 200$). All photomicrographs based on *Hassler 12914* (US).

though this character generally remains constant within each group, it is not considered to be of generic value.

Lower Palea: Contrary to published accounts, a lower palea is developed in some specimens of *S. asperifolia*. Although rudimentary or reduced in some cases, it reaches half the length of the lower lemma in others. In *S. macrantha* and *S. ramosa* the lower palea is conspicuous, attaining the same size as its lemma and sometimes enclosing a male flower. In *Panicum* the lower palea is absent in the groups Parviglumia and Cordovensia and in some species of the groups Panicum, Laxa, and Penicillata.

***Streptostachys* Desvaux, 1810, emended
Zuloaga & Soderstrom**

Streptostachys Desvaux, 1810:190.

Plants perennial, cespitose or with short rhizomes. *Culms* decumbent or ascending, simple or branched; internodes hollow. *Ligule* ciliate, formed by a line of whitish hairs, or lacking. *Blades* ovate-lanceolate, flat, subcordate to cordate, amplexicaul. *Panicles* lax, diffuse to contracted, the spikelets short-pedicellate, aggregated in racemes diverging from the rachis.

Spikelets oblong, compressed dorsiventrally, di-

sarticulating below the glumes, caducous, blunt, glabrous to shortly hirsute; rachilla thickened between the lower glume and upper anthercium and with conspicuous internodes. Glumes 2, herbaceous, pale to purplish, unequal (the lower glume rarely equalling the upper). *Lower glume* oblong to ovate, $\frac{1}{3}$ to $\frac{4}{5}$ as long as the spikelet, 1–7-nerved. *Upper glume* 5–7-nerved, obtuse to acute, frequently not covering the upper anthercium. *Lower lemma* 3–5-nerved, acute. *Lower palea* conspicuous, lanceolate, equal in size to the lemma or reduced to absent; male flower sometimes present. *Upper anthercium* fusoid to narrowly-ellipsoid, pale, shining, indurate, papillose-pilose over the entire surface (more so toward the summit), and with round papillae distributed evenly, margins of the upper lemma enclosing the palea; lodicules 2, conduplicate; stamens 3, styles 2, stigmas plumose. *Caryopsis* fusoid, pale to light brown; hilum linear; embryo less than half the length of the caryopsis.

A New World genus, occurring in Trinidad and South America and favoring open places, savannas, or cerrados with sandy soils; less frequent in margins of forests or woods.

TYPE-SPECIES.—*Streptostachys asperifolia* Desvaux.

Key to the Species of *Streptostachys*

1. Spikelets 3.9–5.1 mm long; lower glume obtuse, $\frac{3}{4}$ – $\frac{4}{5}$ as long as the spikelet; rachilla forming a thick, recurved disc around the pedicel; lower palea small, ovate, $\frac{1}{3}$ as long as the lemma or absent; upper anthercium with bicellular hairs toward the apex, the basal cell short, the distal cell elongated; papillae encircled by a raised process; axillary panicles present, usually reaching the length of the terminal panicle; leaves amplexicaul, 2–4.3 cm wide ***S. asperifolia***
1. Spikelets 5.9–9.3 mm long; lower glume acute, $\frac{1}{3}$ – $\frac{1}{2}$ as long as the spikelet; rachilla thickened, not recurved at the base; lower palea conspicuous, lanceolate, equal in size to the lemma; upper anthercium with long unicellular hairs throughout; papillae not encircled by a raised process; axillary panicles absent; leaves subcordate, not amplexicaul, 0.7–1.3 cm wide 2
2. Panicles 5–10 cm long, 2–4 cm wide; axils of the racemes glabrous or occasionally sparsely pubescent; plants 50–70 cm tall; blades 7–12 cm long, 0.7–1.3 cm wide
. ***S. macrantha***, new combination
2. Panicles 30–45 cm long, 15–30 cm wide; axils of the racemes densely pubescent with long whitish hairs; plants 1.5–2 m tall; blades 35–55 cm long, 1–1.2 cm wide
. ***S. ramosa***, new species

Streptostachys asperifolia Desvaux

FIGURE 19

Streptostachys asperifolia Desvaux, 1810:190. [Type: "Habitat in America calidiore." Holotype, P, not seen; fragment of the type, US.]

Streptostachys hirsuta Beauvois, 1812:50, pl.10: fig. 11. [Type: The same as that of *Streptostachys asperifolia* Desvaux.]

Panicum streptostachys Sprengel, 1825:316.

Panicum perfoliatum Nees, 1829:142. [Type: "Habitat in sylvaticis umbris ad flumen Amazonum ejusque confluentes provinciae Paraensis et Fluminis Nigri passum." Holotype, M, not seen.]

Panicum balanites J.B. Trinius, 1836:297. [Type: "Colarea ad ost. fl. Amaz (America calidiores, Poeppig)." Holotype, L.E., not seen; isotype, US sheet no. 1126919.]

Panicum vaginaeflorum Steudel, 1855:80. [Type: "Guiana." Holotype, P, not seen; fragment of the type, US.]

Panicum streptostachys f. *paleacea* Doell in Martius, 1877:231. [No type cited.]

Panicum asperifolium (Desvaux) Hitchcock, 1922:489.

Perennials, 30–100 cm tall, shortly rhizomatous. Culms geniculate, decumbent and sometimes rooting at the lower nodes, then becoming erect, simple or branching, cylindrical to compressed, sparsely hirsute to glabrous, many-noded; internodes hollow, 4–20 cm long, pale to purplish. Nodes purplish, compressed, glabrous to pubescent. Sheaths 5–10 cm long, densely hirsute to glabrous, with long tuberculate hairs toward the margins. Ligule in an arc, shortly ciliate or lacking with long whitish hairs toward the base of the blade; collar hirsute to glabrous. Blades ovate-lanceolate, acuminate, 14–28 cm long, 2–4.3 cm wide, flat, cordate, amplexicaul, commonly tessellate, densely hirsute on both surfaces to glabrous, the margins ciliate with long tuberculate hairs, the midnerve prominent on the abaxial surface. Panicles lax, oblong to pyramidal, 6–16 cm long, 1–9 cm wide, the branches often diverging from the axis, spikelets short-pedicellate and aggregated in pairs on the branches; axis angular, scabrous to hirsute, the branches alternating, flattened, glabrous to sparsely pubescent, the axils pubescent; pedicels scabrous, angular, sometimes bearing whitish hairs; axillary panicles numerous, similar to the terminal one and borne on long peduncles, these

15–35 cm long. Spikelets fusoid, 3.9–5.1 mm long, 1.5–1.9 mm wide, glabrous to hirsute with a truncate and prominently thickened base. Lower glume oblong, obtuse, 3.2–4.7 mm long, $\frac{2}{3}$ – $\frac{4}{5}$ as long as the spikelet, 5–7-nerved, the nerves anastomosing toward the apex. Upper glume 3.5–4.7 mm long, 5–7-nerved, the nerves anastomosing toward the obtuse apex. Lower lemma acute, 3.4–4.6 mm long, 5-nerved, glabrous to sparsely pubescent at the base and central zone, hirsute at the apex, membranous to indurate (in which case the midnerve and adjacent nerves not manifest), its margins enclosing the upper antherium. Lower palea lanceolate, 1.3–1.9 mm long, 0.4–0.9 mm wide, brown or whitish, hyaline, glabrous, frequently absent; male flower absent. Upper antherium oblong to narrowly ellipsoid, acute, 3.1–4.1 mm long, 1.3–1.6 mm wide, pale, shining, finely papillose throughout with the papillae distributed evenly, pubescent toward the apex; lodicules 2, conduplicate. Caryopsis oblong, 2.4–2.8 mm long, 1.2–1.3 mm wide, pale or brown; hilum linear; embryo less than half the length of the caryopsis.

DISTRIBUTION.—Inhabiting forests in shaded spots or more frequently in savannas or cerrados, in sandy soils and among shrubs, from Trinidad to Venezuela, the Guianas, and northern Brazil.

ADDITIONAL SPECIMENS SEEN.—BRAZIL. Without locality, Burchell 9291 (US), Gardner 6108 (US); Granjeiro, Luetzelburg 25974 (F, US). AMAPÁ: Matapi, Pires & Silva 4799 (US); Porto Platon, Mattos 10120 (US); Mapati, km 116, Black & Lobato 50-9676 (US); 2 km from Rio Araguari, along road from Porto Platon to Macapa, Pires et al. 51084 (US); road to Amapá, km 108, beginning of Rio Pedreira, Pires & Cavalcante 52179 (F, NY); Calcoene, frequent at roadside, road to gold mines, Pires & Cavalcante 52520 (NY). BAHÍA: without locality, Zehntner 3758 (US); Cruz das Almas, Pinto 139 (US); Serra do Apora, Muritiba, Pinto 256 (US); road Maracas-Contendas do Sincorá (BA 026), km 2, Mattos Silva et al. 213 (NY); Road BR 330, trecho Jequié-Ipiaú, 4 km de Jequié, Mori & King 12200 (NY); on road to Abaira, ~8 km N of the town of Rio de Contas, Harley et al. 15235 (NY); 31

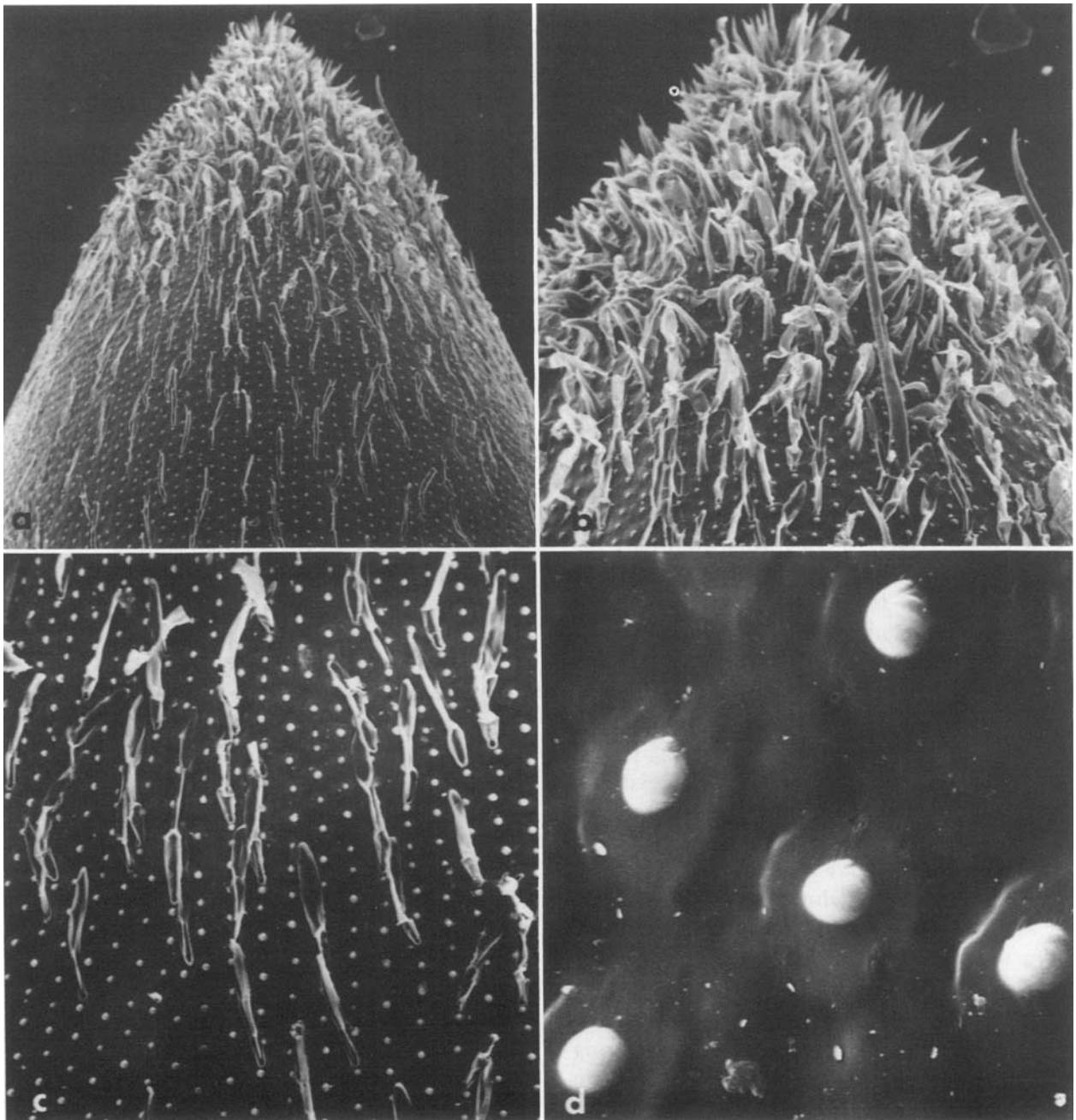


FIGURE 19.—*Streptostachys asperifolia*: *a*, upper anthercium, lemma side ($\times 100$); *b*, detail of *a* showing macrohairs, bicellular microhairs, and rounded papillae ($\times 200$); *c*, detail of upper palea showing bicellular microhairs and simple papillae ($\times 200$); *d*, detail of simple, rounded papillae of upper palea ($\times 2000$). All photomicrographs based on *Swallen 4898* (US).

km S of Olindina, along highway BR-116, *Davidse et al.* 11750 (NY); 16 km NW of Lagoinha, on side road to Minas do Mimoso, *Harley et al.* 16642 (NY). CEARÁ: Serra de Baturite, *Eugenio* 287 (US); Campo Salles to Crato, *Swallen* 4317 (US); Campo Grande, *Swallen* 4517 (US); Camocim to Granja, *Swallen* 4631 (US); Baturite to Guarimirango, *Swallen* 4431 (US). GOIÁS: 2 km N of Araguaina, *Irwin et al.* 21133 (F, NY, US). MARANHÃO: São Luís to São José, *Swallen* 3463 (US); Caxias to Barra do Corda, *Swallen* 3485 (US); 39 km NE of city of Grajaú, on old road to Barra do Corda, *Eiten & Eiten* 10266 (US); Carolina to São Antonio de Balsas, *Swallen* 4144 (US); about 25 km S of Loreto, between the Rios Balsas and Parnaíba, *Eiten & Eiten* 4143 (US); Ilha de Balsas, region between the Balsas and Parnaíba rivers, Santa Barbara, 55 km SSE of Loreto, *Eiten & Eiten* 10704 (US). PARÁ: without locality, *Spruce* 95 (US); Marapanim, estrada para Igarapé Grande, *Silva* 496 (US); Marajó Island: Caracara river, in plantations, *Goeldi* 99 (F, US), near Soure, *Goeldi* 299 (F, US); Ilha de Mosqueiro, near Pará, *Killip & Smith* 30482 (US); Ilha de Marajó, Salvaterra, *Kauffmann* 4 (F, US); Soure, *Black* 50-9071 (US), *Swallen* 4975 (US); Fazenda Camburupy, near Soure, *Swallen* 4956 (US); Rio Moju, Fabrica, *Black* 54-16242 (US); estrada João Coelho-Vigia, km 40, *Black et al.* 52-14200 (US); Santarém, *Kuhlmann* 1740 (US), *Swallen* 3267, 3293 (US); near Santarém, *Spruce* 15, 606, 697 (US); Boim, Tapajós, *Kuhlmann* 1922 (US); Mosqueira, *Swallen* 4898 (US); Breu Branco, km 40 S of Represa Tucuruí along highway BR 422, *Plowman et al.* 9659 (NY); 36 km SE of Vigia, along highway PA-140 to Belém, *Davidse et al.* 17597 (NY); Campo de Matapiquara, ~1 km E of Matapiquara, 73 km NNE of Castanhal by road, *Davidse et al.* 17896 (NY); ~73 airline km NE of Castanhal; savanna adjoining the village of Martins Pinheiro, *Davidse et al.* 17960 (NY). PARAIBA: Areia, *Coelho de Moraes* 854, 1156 (US). PERNAMBUCO: Dois Irmãos, vicinity of Recife, *Chase* 7728 (F, US); Olinda, *Pickel* 2273 (US); João Pessoa, *Pickel* 3852 (US). PIAUÍ: without locality, *Lutzelburg* 5544, 5547 (US), *Ule* 7425 (US), *Gardner* 2341 (US); Oeiras,

Martius s.n. (US); 32.8 km along road S of Amarante, 25 km S of Piauí river, *Eiten & Eiten* 10371 (US). RIO GRANDE DO NORTE: Pedro Velho, *Emygdio* 1655 (US); Natal, *Swallen* 4675 (US); Nova Cruz to Montanhas, *Swallen* 4811 (US).

FRENCH GUIANA. Without locality, *Sagob* 1395 (US), *Leprieur s.n.* (US). CAYENNE: St. Madeleine road, vicinity of Cayenne, *Broadway* 745 (US).

GUYANA. Without locality, *Schomburgh* 774 (F, US). Waranawa Ranch, *Harrison* 1047 (US).

SURINAM. Kayser airstrip, 25 km above confluence with Lucie River, *Maguire et al.* 53953 (US); Zuid River, Kayser airstrip, *Irwin et al.* 55991 (F); Kaysergebergte airstrip, *Freund R-34-B* (US).

TRINIDAD. Chaguasamas, *Broadway s.n.*, 12 Jul 1927 (US).

VENEZUELA. BOLIVAR: between Los Castillos de Guayana and Piacoa, *Steyermark* 86270 (US); Morichal, Santa Isabel, *Cardona* 655 (US). MONAGAS: 17 km NNW of San Felix and Río Orinoco along hwy 10, *Davidse* 4604 (NY).

DISCUSSION.—The pubescence in this species is quite variable, both on the vegetative parts and in the inflorescence, with hirsute to totally glabrous specimens encountered. The panicle of *Swallen* 4431, for example, contains both hirsute and glabrous spikelets.

The lower lemma is frequently indurate with a consistency similar to that of the upper; in such examples the midnerve and adjacent nerves are not manifest. In other cases the lower lemma is membranous and similar to the glumes. Even though the lower palea is generally lacking or poorly developed, it occasionally reaches half the length of its lemma, as in *Pires* 4799. Axillary panicles are frequent and numerous in this species and reach the same length as the terminal one.

The upper antherium is sparsely pubescent toward the apex with bicellular hairs on the lemma and palea. Sparse long unicellular hairs and numerous hooks also occur on the the apex of the lemma, as revealed by SEM. Except toward the margins of the lemma the entire surface of the antherium is evenly covered with rounded

papillae, each of these centered on a swelling of the antherium.

A ligule is generally absent. When it does occur it consists of a line of short hairs.

Brown (1977) reported the species to be C₃, or non-Kranz, with a ¹³C/¹²C index of -27.0.

***Streptostachys macrantha* (Trinius)
Zuloaga & Soderstrom, new combination**

FIGURE 20

Panicum macranthum Trinius, 1826:209. [Type: "V. spp. Brasil. (*Langsd.*)."] Holotype, LE, not seen; fragment of the type, US sheet no. 974708.]

Panicum vaginatum var. *alpha* et *beta* Nees, 1829:156. [Type: "Habitat in Brasilia meridionali (*Sellow*). Vidi in Herb. Reg. Berol." Holotype, B, not seen; fragment of the type, US s.n.]

Short-rhizomatous perennials, 50–70 cm tall, covered at the base by densely villous cataphylls. Culms compressed, simple, glabrous; internodes hollow, 5–15 cm long. Nodes pilose to glabrous, compressed, dark; basal leaves persistent, curling. Sheaths 6–14 cm long, pale to purplish, glabrous to short-pubescent, the basal ones short, overlapping, the upper elongated. Ligule ciliate, 0.5–1 mm long, lacking in the lower leaves; collar pale to purplish, short-pubescent to glabrous. Blades ovate-lanceolate, acuminate, 7–14 cm long, 0.7–1.3 cm wide, flat, occasionally with involute margins, cordate and sometimes amplexicaul, densely hirsute to glabrous, the margins ciliate, the midnerve not differentiated; upper blades commonly small or absent. Panicles lax, open, 5–10 cm long, 1.5–4 cm wide, long-exserted, peduncles 16–35 cm long, the spikelets more or less spread along the branches; axis angular, glabrous, the lower branches verticillate, opposite or alternate above, flexuous, glabrous, smooth, without spikelets at the base, diverging from the axis, axils of the lower branches glabrous to sparsely pubescent; pedicels scaberulous, claviform. Spikelets fusiform, 5.9–6.8 mm long, 2.1–2.5 mm wide, glabrous to hispid on the apex of the upper glume and lower lemma, greenish to purplish, the rachilla thickened between the lower glume and upper antherium and

with manifest internodes. Lower glume ovate, acute, 2.3–3.5 mm long, 1/3–1/2 the length of the spikelet, 1–3-nerved, the midnerve scabrous or not toward the apex. Upper glume 5–5.8 mm long, not completely enclosing the upper antherium, sparsely hispid to glabrous at the obtuse apex, 5–7-nerved, the nerves anastomosed toward the apex. Lower lemma 5.4–6 mm long, acute, 3–5-nerved, the nerves anastomosed toward the apex, densely hispid to glabrous, membranous to indurate. Lower palea lanceolate, conspicuous, 4.3–5.1 mm long, 1–1.4 mm wide, hyaline, glabrous; male flower sometimes present, with 2 lodicules, and 3 stamens. Upper antherium ovoid, 5.1–5.9 mm long, 1.8–2.1 mm wide, pale, shining, pubescent, covered with long, thin unicellular macrohairs, glabrescent toward the base, finely papillose throughout, the papillae rounded and distributed evenly; lemma 5-nerved. Caryopsis fusiform, 3.6 mm long, 1.7 mm wide; hilum linear; embryo less than half the length of the caryopsis.

DISTRIBUTION.—Occurring in the Brazilian cerrados of Goiás and Mato Grosso between 400 and 1200 m elevation and reported from the Amambay range of Paraguay.

ADDITIONAL SPECIMENS SEEN.—BRAZIL. Without state: Rio de San Francisco, *Pohl 329* (US); Lagoa Santa, *Warming s. n.* (NY). DISTRITO FEDERAL: 20 km S of Brasília on road to Goiania, near Rio Melchior, *Irwin et al. 8658* (US); Rodovia DF6-Brasília, *Allem & Vieira 1087* (MO). GOIÁS: without locality, *Glaziou 22526* (US); 33 km S of Caiaponia on road to Jataí, *Irwin & Soderstrom 7131* (MO, US); Serra do Caiapó, 30 km N of Jataí on road to Caiaponia, *Irwin & Soderstrom 7307* (US); ~20 km S of Brasília on road to Goiania, near Rio Melchior, *Irwin et al. 8658* (NY). MINAS GERAIS: Serra do Cipó, 110 km NE of Belo Horizonte, *Chase 9297* (US); Morro do Cruzeiro, Lagoa Santa, 42 km N of Belo Horizonte, *Chase 9018* (NY, US); 38 km de Parnaopeba, *Ferreira 1463* (MO).

PARAGUAY. Sierra de Amambay, Estrella, *Hassler 10115* (BAA), *Rojas 6298* (BAA).

DISCUSSION.—As in *S. asperifolia* this species is

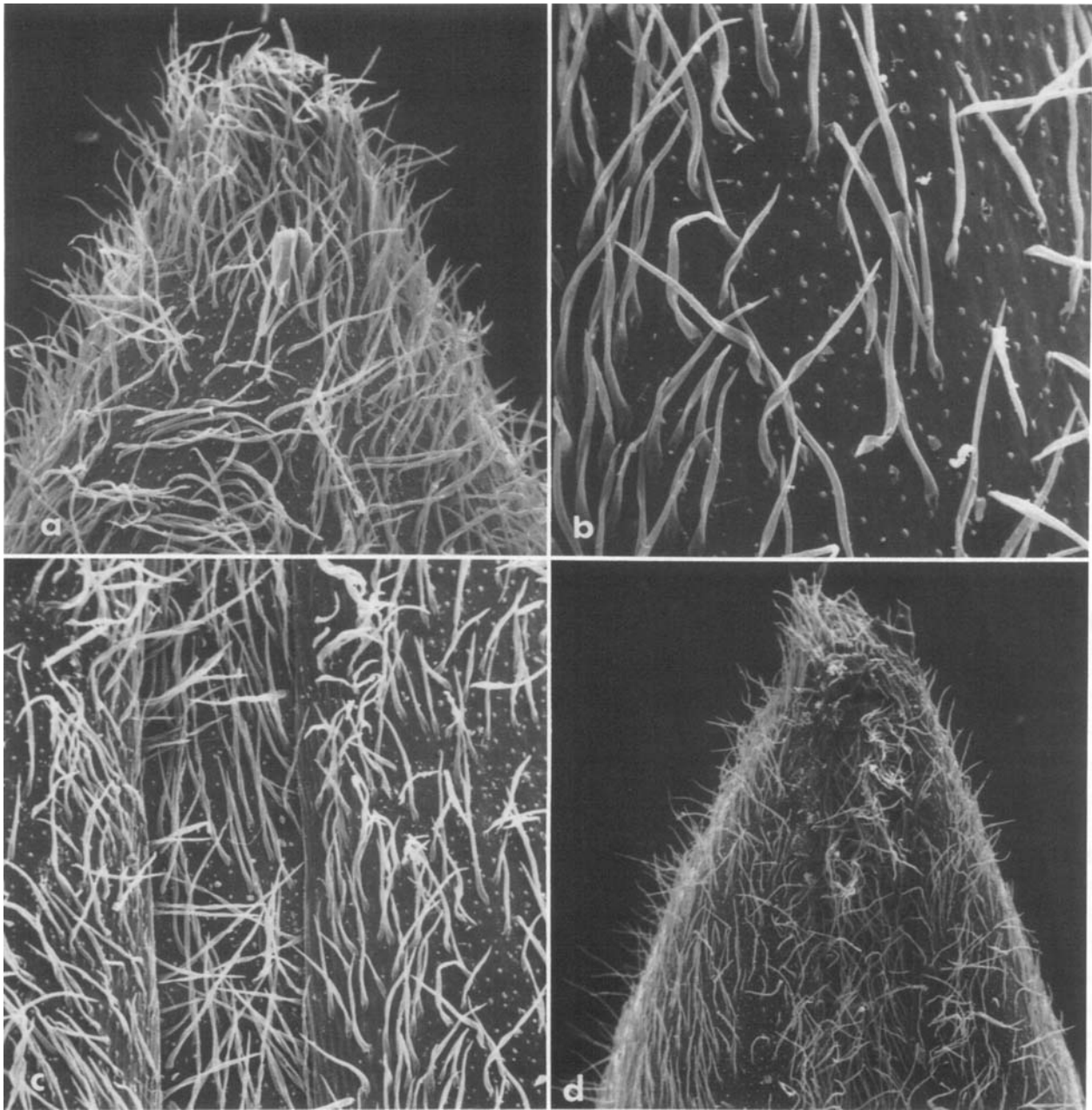


FIGURE 20.—*Streptostachys macrantha*, new combination: *a*, upper antherium, lemma side ($\times 100$); *b*, detail of *a* showing macrohairs and simple rounded papillae ($\times 200$); *c*, upper antherium, palea side ($\times 100$); *d*, upper antherium, palea side ($\times 50$). All photomicrographs based on *Glaziou 22526* (US).

variable in the consistency of the lower lemma, which may be membranous to indurate throughout. In *Irwin et al.* 8658, for example, there are spikelets with the lower lemma totally membranous and similar in aspect to both glumes; in others the central part of the lower lemma is indurate, smooth, shining, pale, and densely pubescent toward the apex, bearing rounded papillae as well and not distinguishable from the upper antherium. In this latter case the midnerve and lateral nerves are not manifest. The lower lemma remains membranous and purplish toward the margins and here the nerves are visible.

Both Kunth (1829) and Doell (in Martius, 1877) made note of the thickened base of the spikelet and also mentioned that the base of the panicle was either pubescent or glabrous. The illustration in the former work agrees exactly with what we here consider to be the species.

The lower sheaths are persistent and completely envelop the culm, giving protection to the plants that are affected by periodic fires.

***Streptostachys ramosa* Zuloaga & Soderstrom,
new species**

FIGURES 21, 22

Type Specimen.—BRAZIL, BAHÍA: 22 km S of the Rio Galheirão along highway BR-020, 8 Apr 1976, 860 m, G. Davidse, T.P. Ramamoorthy & D.M. Vital 12216 (Holotype, MO; isotype, NY).

Gramina perennia rhizomatibus brevibus, 1.5–2 m alta. Culmi erecti, simplices. Foliorum vaginae carinatae, manifeste distichae. Ligula ciliata. Laminae lineari-lanceolatae, 35–62 cm longae. Paniculae laxae, diffusae, 30–45 cm longae, axillis ramorum dense pubescentibus. Spiculae oblongoideae, 6.3–9.3 mm longae, 2.1–2.5 mm latae, glabrae. Gluma inferna acuta, longitudine $\frac{1}{3}$ – $\frac{1}{2}$ spiculae aequans, 3-nervata. Gluma supera obtusa vel acuta, 5-nervata. Lemma infernum subacutum, 3–5-nervatum. Palea inferna lanceolata, 5.3–7.9 mm longa. Anthoecium superum oblongum ad anguste ellipsoideum, 5.4–7.9 mm longum, pubescens, omnino subtiliter papillosum. Caryopsis ellipsoidea, hilo lineari.

Short-rhizomatous perennials, 1.5–2 m tall with densely villous cataphylls. Culms erect, few-noded, simple, cylindrical, glabrous; internodes hollow, 8–20 cm long. Nodes purplish, glabrous to short-pubescent. Sheaths 15–40 cm long, longer than the internodes, overlapping at the base and villous, prominently distichous, keeled, sericeous to glabrous above, the margins short-ciliate. Ligule ciliate, formed by a line of whitish hairs 0.8–2.5 mm long or lacking; collar dark brown to purplish, glabrous to short-pubescent. Blades linear-lanceolate, acuminate, 35–62 cm long, 1–1.4 cm wide, flat or with the margins involute, rigid, cordate, the margins short- to long-ciliate, scabrous, hispid toward the base of the adaxial surface, the remainder glabrous or densely pubescent on both surfaces with long appressed hairs. Panicles lax, diffuse, pyramidal, 30–45 cm long, 15–30 cm wide, spikelets solitary along the branches; subsessile; axis cylindrical, undulate, glabrous, the branches verticillate or opposite, naked at the base, glabrous, wavy, axils densely pubescent, the hairs long, whitish, the pulvini dark brown, pedicels short, angular, smooth, glabrous, thickened at the apex. Spikelets fusoid, 6.3–9.3 mm long, 2.1–2.5 mm wide, glabrous, greenish to brown or purplish, glumes and lower lemma with prominent nerves, pubescent or scabrous toward the apex of the inner surface. Lower glume acute, 2.2–4.4 mm long, $\frac{1}{3}$ – $\frac{1}{2}$ the length of the spikelet, 3-nerved, short-pilose at the apex. Upper glume obtuse or acute, 5.3–8.1 mm long, commonly leaving exposed the apex of the upper antherium, 5-nerved. Lower lemma subacute, 6.2–8.5 mm long, 3–5-nerved. Lower palea conspicuous, lanceolate, 5.3–7.9 mm long, 1–2.2 mm wide, hyaline, glabrous; male flower sometimes present, with 2 lodicules and 3 stamens, the anthers 4.3 mm long. Upper antherium ovoid to narrowly-ellipsoid, 5.4–7.9 mm long, pale to brown, 1.9–2.4 mm wide, shining, pubescent, with thin whitish hairs, more abundant toward the apex, finely papillose throughout; lodicules 2, the stigmas purplish. Caryopsis ellipsoid, 3.8 mm long, 1.9 mm wide, olivaceous; hilum linear; embryo a little less than half the length of the caryopsis.

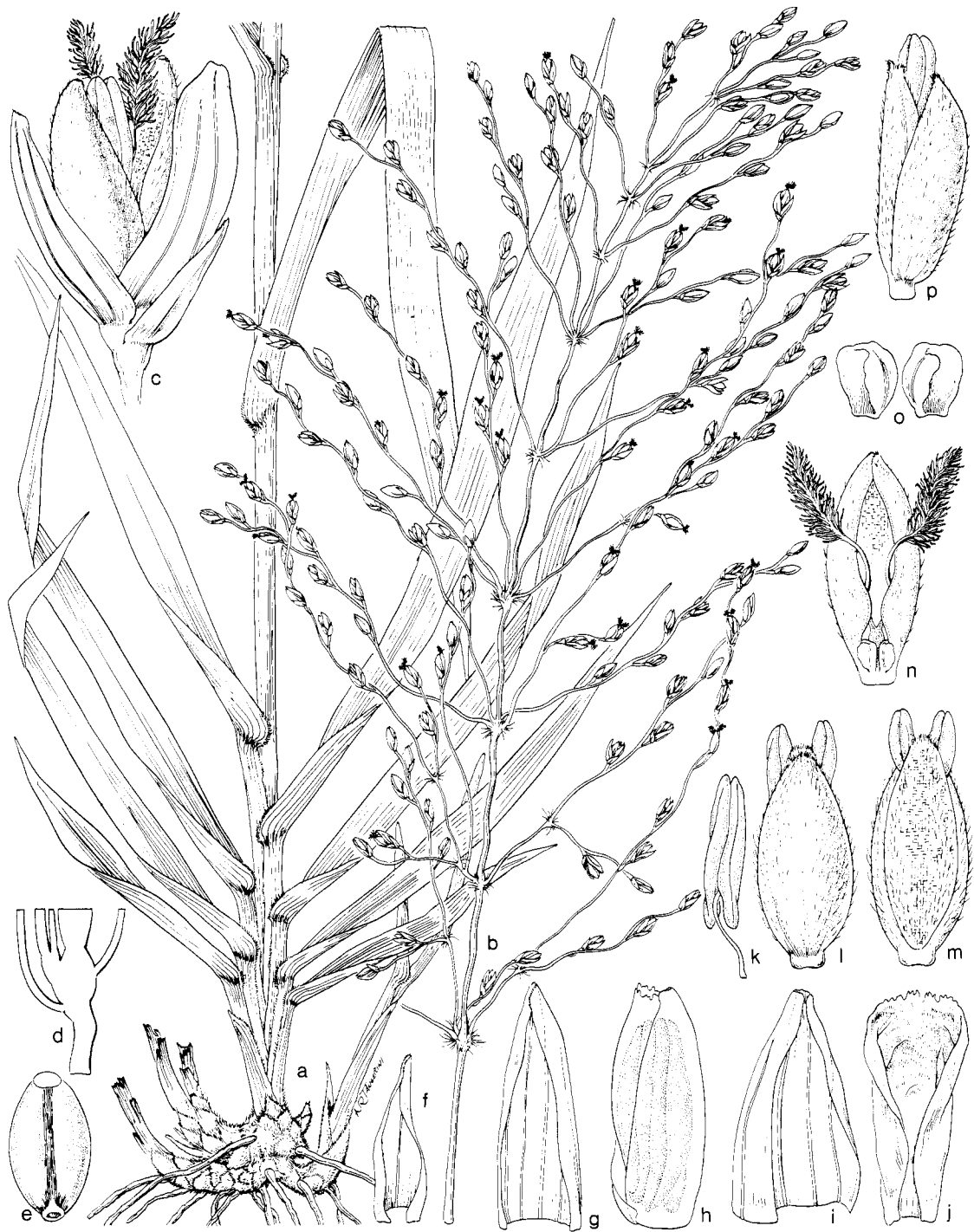


FIGURE 21.—*Streptostachys ramosa*, new species: *a*, habit ($\times 1$); *b*, panicle ($\times 1$); *c*, spikelet, lateral view ($\times 12$); *d*, scheme of longitudinal section through base of spikelet ($\times 12$); *e*, caryopsis, showing linear hilum ($\times 12$); *f*, lower glume ($\times 12$); *g*, upper glume ($\times 12$); *h*, lower antheridium ($\times 12$); *i*, lower lemma ($\times 12$); *j*, lower palea ($\times 12$); *k*, stamen ($\times 12$); *l*, upper antheridium, lemma side ($\times 12$); *m*, upper antheridium, palea side ($\times 12$); *n*, upper palea with gynecium and lodicules ($\times 12$); *o*, lodicules of upper antheridium ($\times 25$); *p*, upper antheridium, lateral view ($\times 12$). Drawing *a* based on *Davidse et al.* 12216 (MO), *b* on *Hatschbach et al.* 36145 (MO), and *c*–*o* on both.

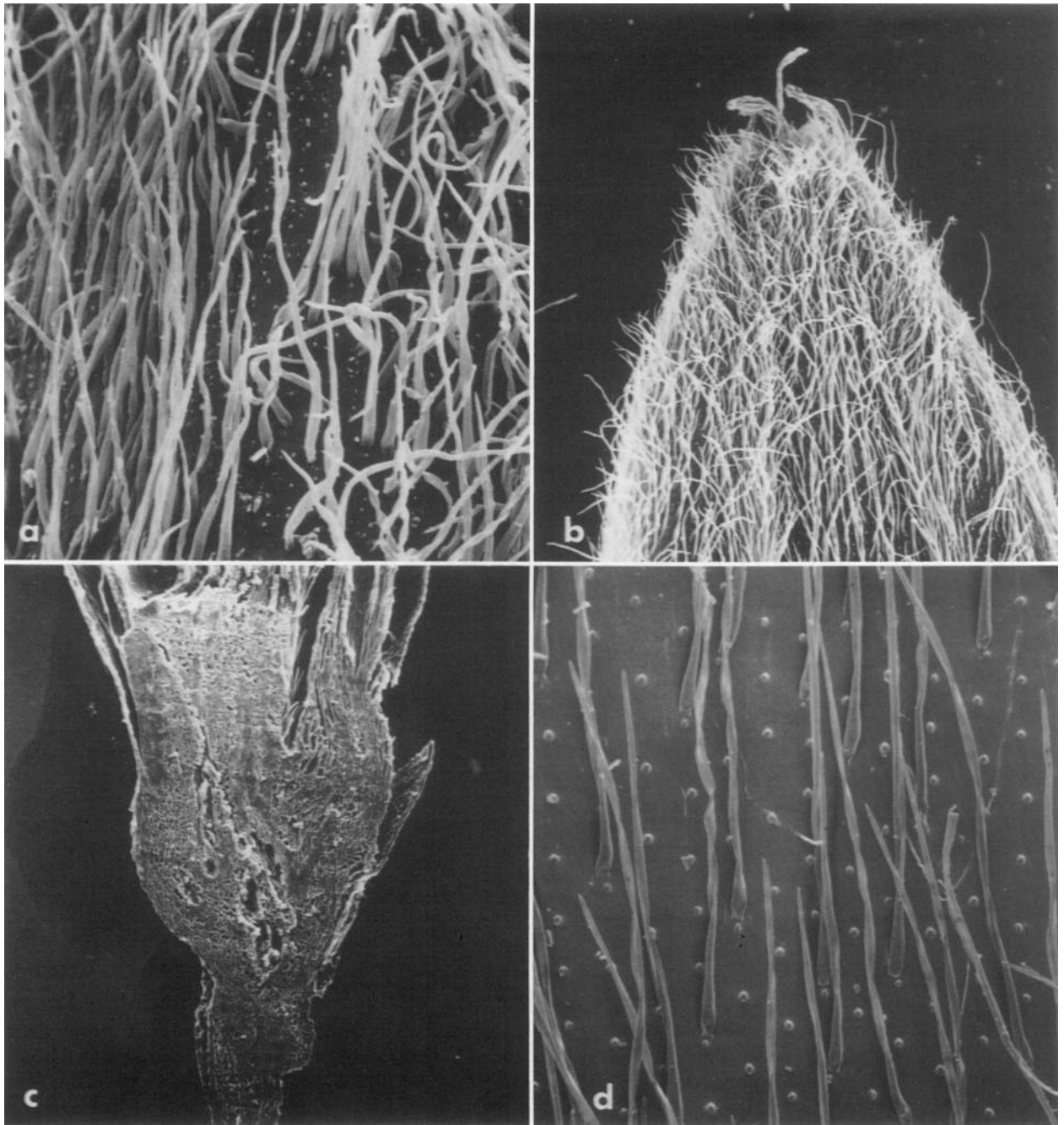


FIGURE 22.—*Streptostachys ramosa*, new species: *a*, detail of upper antherium, lemma side ($\times 200$); *b*, upper antherium, palea side ($\times 40$); *c*, base of spikelet showing thickened internodes ($\times 40$); *d*, detail of upper palea showing macrohairs and simple rounded papillae distributed evenly over the surface ($\times 200$). Photomicrographs *a*, *b*, and *d* based on *Harley 16876* (US), *c* on *Heringer 9590* (NY).

PARATYPES.—BRAZIL. BAHÍA: 15 km S of the intersection of highway BR-020 and the Rio Roda Velha, *G. Davidse et al.* 12085 (MO, NY, US); Serra do Curral Feio, 22 km NW of Lagoinha, on side road to Minas do Mimoso, 6 Mar 1974, *R.M. Harley et al.* 16876 (MO, NY, US); BR 242, km 216, 12 km N of Lençóis, *S. Mori* 13335 (NY); Espigão Mestre, ~100 km WSW of Barreiras, *W. R. Anderson et al.* 36657 (MO, NY). GOIÁS: region of Chapada dos Veadeiros, 38 km N of São João da Aliança, at W long. 47°30', S lat. 14°30', *E. Y. Dawson* 14554 (US). MATO GROSSO: Chapado dos Guimarães, *G. Hatschbach et al.* 36145 (MO, NY); entre Queimada e Rio Verde, without collector (MO sheet no. 2312029). MINAS GERAIS: Tres Marias, 26 Feb 1964, *E.P. Heringer* 9590 (NY); ~20 km S of Alto do Paraíso (formerly Veadeiros), *H.S. Irwin et al.* 24716 (NY); ~33 km NE of Francisco Sá, road to Salinas, *H.S. Irwin et al.* 23126 (NY).

DISTRIBUTION.—Species of the Brazilian cerrados, occurring between 800 and 1100 m elevation.

DISCUSSION.—This species is related to *S. macrantha*, from which it is distinguished by the size of the plants, leaves, and panicles, the branches of the latter much longer and the spikelets borne more distant from one another than in *S. macrantha*. The densely pubescent axils of the panicle branches further distinguish it.

The only basis for assigning *Glaziou 20123a* (US) to this species is a fragment of the panicle with the following annotation by A. Chase:

Specimen in Paris hb. labeled *Panicum grandiflorum* n. sp. agrees with *Glaziou 22526* and Chase collections but is 70 cm tall, the panicle 25 cm long, the ascending-spreading branches to 9–10 cm long.

There is also a fragment of the same specimen from Vienna. The type-locality must be erroneous as given on the label: "Brazil, Rio. *Glaziou 20123a*." Obviously the species does not occur in Rio de Janeiro and the veracity of this label—like so many of *Glaziou*—is open to question.

It is possible that this species was first described by Mez under the name *Panicum mirabile* Mez (1921) not A. Braun (1846) nor Walpers (1848–

1849). In his publication Mez gave very brief descriptions of his new species, making their identification difficult. The author's reference to the large size of the plant and striking similarity of spikelet characters between *P. mirabile* and *S. ramosa* suggest that we may be dealing with the same species. A fragment of the type, which consists of a racemose branch of the panicle, is at US and is labeled "*Panicum mirabile* Mez. Brasil occ. Tamberlik." The holotype from the Berlin Museum consists only of a fragment of the panicle and a leaf and even though the aspect of the panicle matches that described for *S. ramosa*, the absence of fuller material does not allow us to arrive at a definitive conclusion regarding the identity of *P. mirabile*. The point is not critical, however, because the name of this species is invalidated by two earlier epithets.

CHROMOSOME NUMBERS.— $n = 27$ (Davidse and Pohl, 1978, as *Panicum macranthum* Trinius).

Taxonomic Position of *Tatianyx*

Among the most beautiful of panicoid grasses in tropical America is a species that was named *Panicum arnaces* by Trinius for a grass that inhabits the "campo rupestre" of Brazil in the states of Bahia, Pará, Goiás, Minas Gerais, and Mato Grosso. The epithet *arnaces*, which comes from the Greek word for "woolly," aptly describes the long-hairy spikelets of this species.

Our comparison of this *Panicum* with other members of the tribe confirms its unique position. A linear hilum immediately distinguishes it from other species in the genus as does the position of the pedicel relative to the spikelet. The pedicel is falcate at the apex and the spikelet held in an oblique position, behind the upper glume and upper lemma where it forms a pubescent callus. In *Panicum* the hilum is round and basal and the pedicel is truncate at the apex with the spikelet held erect. A linear hilum is found in other panicoid genera such as *Streptostachys*, and a callus is found in *Chaetium* and *Digitariopsis*.

Trinius did not refer to the caryopsis when he described the species nor was the hilum mentioned in the latter references of Trinius (1834),

Steudel (1855), or Doell (in Martius, 1877). The unusual placement of the pedicel and spikelet had apparently also never been considered as an important character to separate this species from others in *Panicum*.

In comparison with other panicoid grasses, *Panicum arnacites* is superficially similar to *Anthaenantiopsis* and *Leptocoryphium*, in which the spikelets are lanate or pilose. In the latter the anthercium is delicate, not rigid, and the margins of the upper lemma are hyaline and do not cover the apex of the palea. The anthercium is open at the summit and the lower glume is diminutive. In the former genus the upper anthercium is also open at its summit and the spikelets are arranged on unilateral racemes rather than in a panicle.

Because *Panicum arnacites* cannot be accommodated in any known genus of the Paniceae, we are establishing a new genus for it, which we are calling *Tatianyx*, in honor of Sra. Tatiana Skvortzov Sendulsky (born 1922, Harbin, Manchuria), of the Instituto de Botânica in São Paulo, an authority on the grasses of Brazil.

***Tatianyx* Zuloaga & Soderstrom, new genus
(Poaceae: Panicoideae)**

Gramen perennis. Culmi erecti, simplices. Ligula ciliata. Laminae lineari-lanceolatae. Paniculae laxae, pyramidales; pedicelli longi, flexuosi, apice falcati, facie dorsali spiculae oblique affixi. Spiculae ellipsoideae, argenteae. Gluma inferna longitudine $\frac{1}{2}$ – $\frac{3}{4}$ spiculae aequans. Gluma supera 5–7-nervata. Lemma infernum 5–7-nervatum. Palea inferna lanceolata, interdum florem masculinum continens. Anthoecium superum ellipsoideum, induratum, papillas compositas superficiarias gerens. Caryopsis ellipsoidea, hilo lineari.

TYPE-SPECIES.—*Tatianyx arnacites* (Trinius) Zuloaga & Soderstrom, new combination.

***Tatianyx arnacites* (Trinius) Zuloaga & Soderstrom, new combination**

FIGURES 23, 24, 25

Panicum arnacites Trinius, 1832:117. [Type: "Figura ad specimen Brasilianum." Holotype, LE, not seen; fragment of the type, US sheet no. 974682.]

Cespitose perennials 40–100 cm tall with densely villous cataphylls. Culms erect, cylindrical to compressed, glabrous or sparsely pubescent near the nodes, simple; internodes hollow, 4–20 cm long. Nodes purplish, long to shortly pubescent with whitish hairs. Sheaths 5–26 cm long, longer than the internodes, the lower ones enveloping the culm, densely to sparsely pubescent, the upper ones glabrous. Ligule ciliate, formed by an arc of whitish hairs 0.3–0.4 mm long; collar glabrous or short-pubescent. Blades linear-lanceolate, acuminate, 10–36 cm long, 0.2–0.4 cm wide with the margins involute, rarely flat, narrowed at the base, ciliate along the lower margins, the adaxial surface sericeous, the abaxial pubescent; upper blades small, inconspicuous. Panicles lax, diffuse, pyramidal, many-flowered, 6–13 cm long, 4–9 cm wide, exserted, peduncles 15–24 cm long, almost completely included in the upper leaves when young, the spikelets borne on long flexuous pedicels, axillary panicles sometimes present; axis cylindrical or angular, smooth, glabrous, usually purplish, the branches alternate, opposite or verticillate, smooth, thin, glabrous, wavy, the axils densely pubescent to glabrous; pedicels long, glabrous, smooth, flexuous, falcate at the apex, positioned obliquely on the dorsal side of the spikelet. Spikelets ellipsoid, 4–4.5 mm long, 1.2–1.4 mm wide, silvery-villous with long rigid whitish hairs, exceeding the apex of the glumes and lower lemma in length; glumes and lower lemma herbaceous, glumes and anthercia separated by prominent internodes. Lower glume acute, 2.3–3 mm long, $\frac{1}{2}$ to $\frac{3}{4}$ as long as the spikelet, 3–5-nerved, glabrous on the inner surface. Upper glume acute, 2.8–3.5 mm long, leaving exposed the apex of the upper anthercium, 5–7-nerved. Lower lemma acute, 3.2–4 mm long, glume-like, 5–7-nerved. Lower palea lanceolate, 3.2–4.3 mm long, 0.7–1 mm wide, long to short-pilose on the upper margins, otherwise glabrous, hyaline; male flower sometimes present with 3 stamens, the anthers ~3.3 mm long. Upper anthercium ellipsoid, 2.9–3.7 mm long, 1–1.4 mm wide, glabrous, indurate, shining, pale, with long prickle hairs at the apex of the lemma, this and the palea covered by compound papillae distrib-

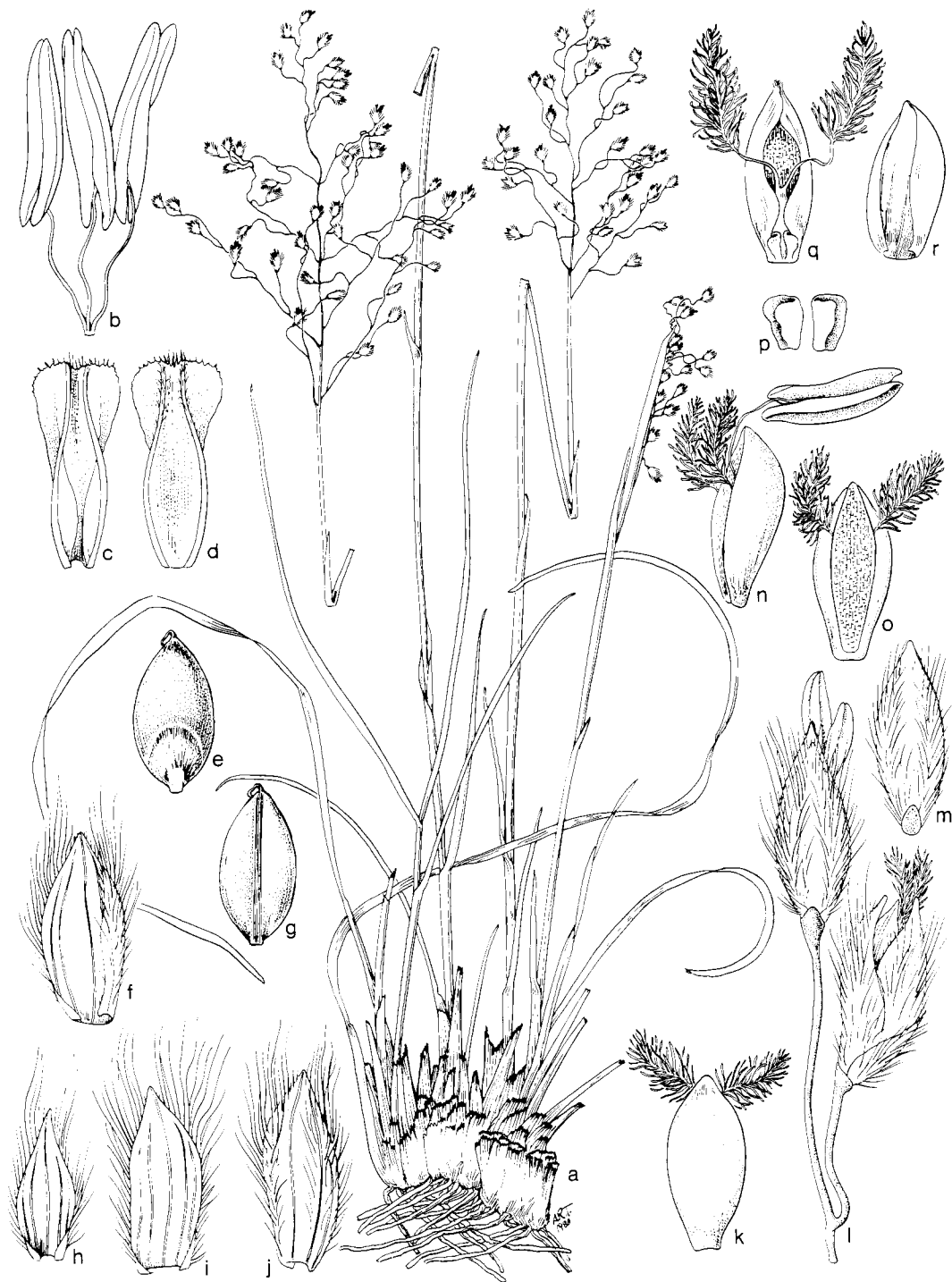


FIGURE 23.—*Tatiyanx arnacites*, new combination: *a*, habit ($\times 1$); *b*, stamens ($\times 18$); *c*, lower palea, inner surface ($\times 18$); *d*, lower palea, outer surface ($\times 18$); *e*, caryopsis, embryo side ($\times 18$); *f*, lower lemma, inner surface ($\times 18$); *g*, caryopsis, showing linear hilum ($\times 18$); *h*, lower glume ($\times 18$); *i*, upper glume ($\times 18$); *j*, lower lemma ($\times 18$); *k*, upper antherium, lemma side ($\times 18$); *l*, pair of spikelets, showing oblique attachment of pedicels ($\times 12$); *m*, spikelet, upper glume side, showing oblique callus ($\times 12$); *n*, upper antherium, lateral view ($\times 18$); *o*, upper antherium, palea side ($\times 18$); *p*, lodicules ($\times 35$); *q*, upper palea showing gynecium and lodicules ($\times 18$); *r*, upper lemma ($\times 18$). All drawings based on Irwin & Soderstrom 6959 (US) except *e* and *g* based on Pires 2947 (US).

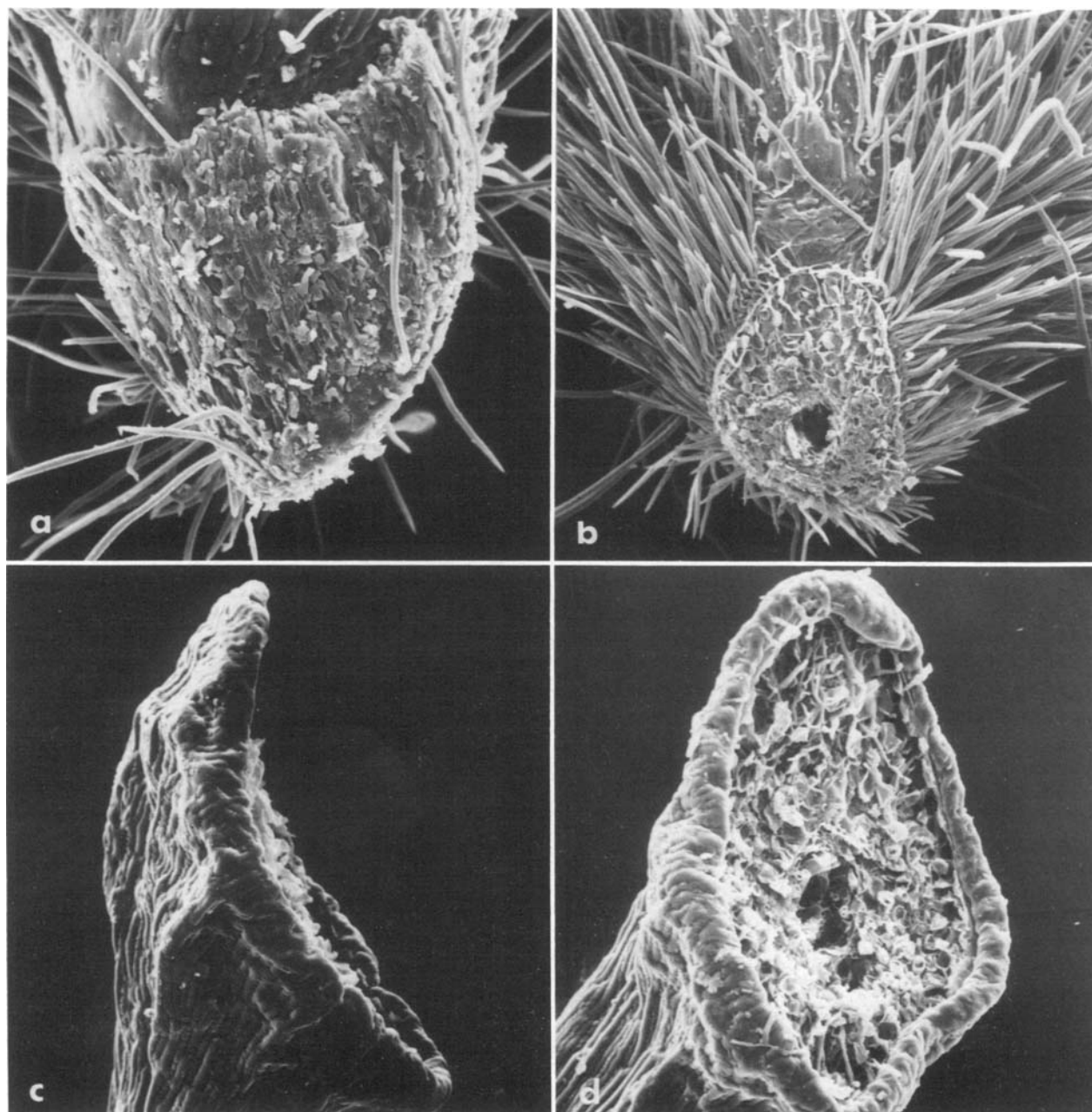


FIGURE 24.—*Tatianyx arnacites*, new combination: *a*, base of spikelet showing oblique callus ($\times 200$); *b*, base of spikelet, upper glume side, showing oblique callus ($\times 150$); *c*, falcate pedicel, lateral view ($\times 200$); *d*, pedicel, locus of attachment with spikelet ($\times 200$). All photomicrographs based on *Eiten* 6752 (US).

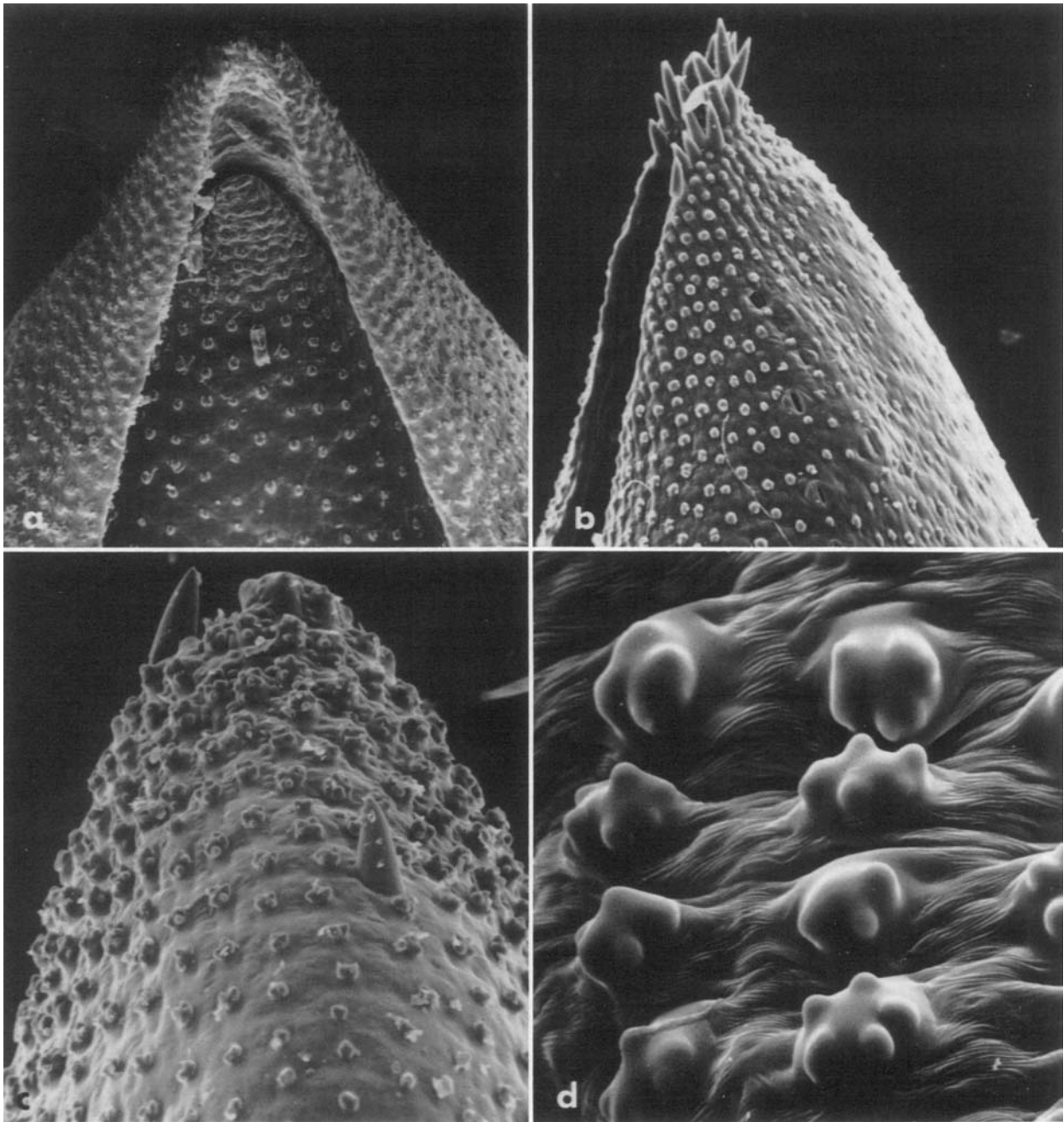


FIGURE 25.—*Tatianyx arnacites*, new combination: *a*, upper antheridium, palea side ($\times 200$); *b*, upper antheridium, lateral view, showing prickly hairs on apex of lemma and stomata below ($\times 200$); *c*, upper antheridium, lemma side ($\times 500$); *d*, detail of upper palea showing compound papillae ($\times 2000$). All photomicrographs based on *Eiten 6752* (US).

uted evenly over the surface. *Caryopsis* ellipsoid, 2.2 mm long, 1.1 mm wide, brown; hilum linear, as long as the caryopsis, embryo $\sim\frac{1}{3}$ as long as the caryopsis.

DISTRIBUTION.—Endemic to the “campos rupestres” of Brazil in the states of Pará, Goiás, Minas Gerais, and Mato Grosso, in rocky or sandy soils at elevations of 800–1400 m; occasionally burned over.

ADDITIONAL SPECIMENS SEEN.—BRAZIL. BAHÍA: near 6 km N of the town of Rio de Contas on road to Abaira, *Harley et al.* 15085 (MO, NY, US). GOIÁS: near 33 km S of Caiaponia on road to Jataí, *Irwin & Soderstrom* 6959 (US). MATO GROSSO: Fazenda Capão da Taquara, *Hatschbach* 32469 (MO); Fazenda Urubu Branco, *Pires & Silva* 11318 (US); 7 Quedas, *Hatschbach* 33145 (MO, NY, US). MINAS GERAIS: Estrada Conceição do Cerro, *Occhioni s/n.*, Dec 1940 (US); Serra do Cipó, perto do Hotel Palacio, *Black & Magalhães* 51-12039 (NY, US); Chapeo de Sol, Serra do Cipó, *Chase* 9191 (US), 9207 (NY, US); Serra

do Cipó, along the road at km 134–135, *Eiten* 6752 (US). PARÁ: Ariramba, *Ducke* 8015 (US).

DISCUSSION.—Although it is most common in *Panicum* for the spikelet to be even on the pedicel, it is sometimes twisted as in the case of *P. hirtum*, *P. cervicatum*, and *P. rudgei*. In these species, however, the pedicel is claviform and truncate at the apex and there is no callus.

In the genus *Plagiantha* Renvoize the pedicel is also truncate and the spikelet lacks a callus at its base, with the spikelets disposed in oblique form in the panicle. The morphology of this genus is therefore similar to that of the species of *Panicum* mentioned above.

Two specimens from Mato Grosso (*Hatschbach* 32469 and 33145) are about 1 m tall, exceptionally robust, possess broad leaves that are flat throughout, and have lax and diffuse panicles. We consider these to represent extremes in the variation of the species, as in smaller specimens (*Irwin & Soderstrom* 6959, for example) small and involute blades occur along with larger flat ones.

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