

Revision of the
South American Genus *Otachyrium*
(Poaceae: Panicoideae)

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and *Thomas R. Soderstrom*



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ABSTRACT

Sendulsky, Tatiana, and Thomas R. Soderstrom. Revision of the South American Genus *Otachyrium* (Poaceae: Panicoideae). *Smithsonian Contributions to Botany*, number 57, 24 pages, 7 figures, 1984.—A review of this genus of seven species is provided with descriptions and illustrations of each. Of these species, four are described as new: *O. aquaticum*, *O. grandiflorum*, *O. piligerum*, and *O. seminudum*. Two, *O. pterigodium* and *O. versicolor*, are already known in the literature, and one, *O. succisum*, is a new combination. In addition to its short, subequal glumes, remarkable peculiarities of this panicoid genus are the enlarged palea of the lower staminate floret and the chartaceous, dark and shining or sometimes opaque and greenish, upper hermaphrodite floret, both of which are united at maturity.

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Tatiana Sendulsky and Thomas R. Soderstrom

Introduction

One of the largest and most widespread tribes of grasses is the Paniceae whose principal genus, *Panicum*, comprises some 600 species distributed throughout the world's tropics and subtropics. This genus and related genera are characterized by spikelets that contain two florets, a lower one that is typically more or less chartaceous and staminate or empty, and an upper one, which is hermaphrodite and usually indurate.

In 1826 Trinius described a species of *Panicum* that had been collected in the state of Minas Gerais on the Serra do Espinhaço, a range that extends into the state of Bahia. The peculiar winged nature of the palea of the lower floret must have inspired the author to name the grass after the orchid, *Pterygodium*, whose florets have winglike structures and whose name is derived from the Greek word *pteryx* (wing). In this species the young spikelets are of a papery texture and light green or pale in color. As the fruit develops in the upper floret the palea of the lower one becomes expanded and appressed to the upper palea. At maturity the caryopsis is thus protected

by a complex encasement, which consists of the upper lemma along with the adherent paleas of both florets.

While the peculiar features of the spikelet in this new grass, which prompted Trinius to describe it as a new species, were quite unlike those of any other species of *Panicum*, it was Nees von Esenbeck who recognized the novelty as generically distinct from *Panicum*. Unaware that Trinius had already described the species three years earlier, Nees in 1829 named it *Otachyrium junceum*, the type of his new genus *Otachyrium*. He based the generic name on the Greek words, *ous*, *otos* (ear) and *achyron* (chaff), again in reference to the winged condition of the lower palea at maturity. By modern rules of nomenclature, a species must retain the earliest name, so we have in *Otachyrium pterigodium* the correct name incorporating the contributions from two early and renowned agrostologists, Carl Bernhard Trinius and Christian Nees von Esenbeck. Appropriately both parts of the epithet refer to the winged nature of the lower palea at maturity.

While Nees accorded generic status to the new taxon, many investigators since his time have considered *Otachyrium* to be no more than a section or subgenus of *Panicum*. Pilger (1931) and Henrard (1941), however, were two exceptions, and both made nomenclatural changes in the genus. More recently, Butzin (1970) has

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made the genus the basis of a separate subtribe, Otachyriinae, far removed in his system from the subtribe Panicinae.

In addition to its short, subequal glumes, remarkable peculiarities of this panicoid genus are the enlarged palea of the lower staminate floret and the chartaceous, dark and shining or sometimes opaque and greenish, upper hermaphrodite floret, both of which are united at maturity. This unique combination of characters, shared by the seven species of the genus that we recognize in the present paper, leave little doubt that we are indeed dealing with a genus distinct from *Panicum*.

The species of *Otachyrium* are widely distributed in South America, extending from Trinidad to Argentina but exhibiting their fullest diversity in central and northern Brazil where all are to be found. The plants generally inhabit wet, marshy ground or margins of streams, but sometimes they grow affixed to stones in running water. *Otachyrium versicolor* sometimes occurs in open and drier sandy habitats.

The color of the hermaphrodite floret and degree of expansion of the lower palea depend on the state of maturity of the spikelet. At the time of flowering the spikelet is usually stramineous or ivory-colored, rather loose and resembling an empty shell; at this stage the paleas are not fully expanded. Presumably once fertilization has occurred, the lemma and palea of the upper floret become dark and rigid and the palea of the lower floret becomes expanded. The central, hyaline part of the palea frequently splits lengthwise in the middle, and its margins extend broadly outward from the sides of the upper floret.

The species fall into two readily distinguishable morphological groups. One consists of those with hard, gibbous, beaklike upper lemmas that are generally dark and shining; in the other the lemmas of the upper florets are not indurate and are opaque, stramineous or greenish. Members of the former group—*O. succisum*, *O. piligerum*, *O. seminudum*, and *O. versicolor*—are generally medium to robust and have broad, linear leaves. Plants of *Otachyrium aquaticum*, *O. grandiflorum*,

and *O. pterigodium*, which comprise the second group, are small in stature and have narrow, nearly cylindrical, inrolled or acicular leaves.

In two species, *O. piligerum* and *O. succisum*, the enlarged paleas have no hyaline wings but do have large, firm, carinate margins that tightly embrace the hermaphrodite florets. In other species these firm margins correspond to the lateral nerves that form large, carinate, ribbon-like rims along their length.

In the present paper we present a key to the seven species and a description and illustration of each, the latter drawn by the first author. Of the seven species, four are new to science (*O. aquaticum*, *O. grandiflorum*, *O. piligerum*, and *O. seminudum*) and one has been transferred from *Panicum* (*O. succisum*).

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We both owe appreciation to Alasdair G. Burman for his revisions of the descriptions in Latin, to Dr. Fernando O. Zuloaga, who gave us so much time and assistance during final preparation of the manuscript, and to our young colleague, Andrew Phillips, for his kindnesses and cheerful assistance.

Otachyrium Nees von Esenbeck

Otachyrium Nees von Esenbeck, 1829:273[271].

Spikelets two-flowered (rarely with a 3rd rudimentary, terminal floret in *O. grandiflorum*),

from ovoid and rather laterally compressed to strongly plano-convex, broadly ovate, orbicular in outline, the sides convex with a gibbous, ovate, dark, mostly shining, otherwise opaque, gray-greenish central part (lemma of the upper floret) and broadly ovate to orbicular encircling, hyaline, mostly purplish or light-colored wings (palea of the lower floret); shape of the spikelet and consequently its size depending on the stage of development of the palea margins of the lower floret; spikelets falling entire from the unequal pedicels, generally borne in pairs at the base or along the branches in open or contracted panicles without a definite orientation toward the axis. *Glumes* short, subequal, $\frac{1}{3}$ to $\frac{1}{4}$ the length of the spikelet, membranous, 1–7-nerved.

Lower floret staminate, ovoid-lanceolate, inconspicuously greenish or light-colored, as long as or sometimes longer than the upper floret. *Lemma* oblong-ovate, boat-shaped, membranous, opaque, 3-nerved. *Palea* broad, hyaline, purplish or light-colored, at maturity widely expanding beyond the spikelet and adhering to the upper hermaphrodite floret, otherwise folded. The central, generally hyaline part of a palea frequently splits lengthwise in the middle and its margins extend broadly at the sides of the upper floret, increasing the spikelet in size and changing its shape; nerves 2, forming ribbon-like, opaque, rather dark, firm, alate-carinate rims, mostly finely denticulate or ciliate at the keels. *Lodicules* 2, broadly cuneate, with thinner, gen-

erally slightly raised median and distal margins. Stamens 3.

Upper floret hermaphrodite (probably only female or cleistogamous in *O. pterigodium* and in *O. aquaticum*), ovoid-lanceolate or oblong, strongly plano-convex, sometimes gibbous, from papery to strongly crustaceous, shining, smooth or opaque, rarely finely papillose, pale yellow or greenish or dark purplish brown, nearly black. *Lemma* convex or gibbous, obscurely 3–5-nerved, acute, loosely embracing the margins of the palea. *Palea* flat, rather concave, more or less similar in texture and color to the lemma. *Lodicules* 2, broadly cuneate, mostly with a wide, concave apical area and with median and distal margins expanded into fine wings. Stamens 3, styles distinct, stigmas feathery. *Caryopsis* ovoid, rather compressed; embryo about half the size of the caryopsis; hilum ovate, subbasal.

Rhizomatous perennials (except *O. succisum* and *O. piligerum*) of various habits and sizes. *Leaf-blades* from long-lanceolate or linear to rather convolute, filiform or acicular. *Ligule* membranous, truncate with a ciliate apex (incomplete in *O. piligerum*).

Chromosome number $2n = \sim 18$, reported only once for the genus *Otachyrium* from Brazilian material cited as *Panicum versicolor* Doell, Irwin & Soderstrom 5796 (Gould and Soderstrom, 1967).

TYPE SPECIES.—*Otachyrium pterigodium* (Trinius) Pilger.

Key to the Species of *Otachyrium*

1. Spikelets 4.5–8.5 mm long, panicles few-flowered, with 5–15 spikelets ***O. grandiflorum***, new species
- Spikelets 2–4 mm long, panicles many-flowered, with 50 or more spikelets 2
2. Spikelets with the upper floret strongly crustaceous, shining, dark brown or black 3
- Spikelets with the upper floret not crustaceous, stramineous or greenish, generally opaque, sometimes finely papillose (if slightly shining then only on the lower half of the lemma) 6
3. One pedicel of the paired spikelets 5–10 times longer than the other 4

- One pedicel of the paired spikelets 1.5–2 (2.5) times longer than the other 5
4. Plants leafless at the base and slightly decumbent, strongly rooting at the 2nd to 4th nodes, branching at all subsequent upper nodes; axis of the inflorescence pilose *O. piligerum*, new species
Plants with a leafy, more or less semi-rosette type of base, never rooting at the nodes, if branching, at the base only; axis of the inflorescence glabrous *O. succisum*, new combination
5. Panicles open with spreading branches *O. versicolor*
Panicles narrowly contracted with the branches adherent to the main axis *O. seminudum*, new species
6. Leaf-blades acicular, almost cylindrical *O. aquaticum*, new species
Leaf-blades flat, narrow, convolute *O. pterigodium*

Otachyrium aquaticum
Sendulsky & Soderstrom, new species

FIGURE 1

TYPE COLLECTION.—BRAZIL. BAHIA: Serra do Rio de Contas, ~2 km N of the town of Rio de Contas, in flood plain of the Rio Brumado. Alt. ~980 m. Approx. 41°50'W, 13°35'S, 25 January 1974, R.M. Harley, S.A. Renvoize, S.M. Erskine, S.A. Brighton & R. Pinheiro 15498 [holotype, US, sheet no. 2777098; isotypes, CEPEC, K, NY].

Gramen perenne, culmis gracilibus, erectis, 30–40 cm altis. Foliorum laminae aciculatae vel cylindricae, adscendentiae, 8–16 cm longae, 1 mm latae, glabrae. Paniculae oblongae, 6–14 cm longae, sparsim ramosae, ramis effusis, adscendentibus vel appressis, ad apicem brevissimis vel absentibus, spiculis per $\frac{2}{3}$ superiores longitudinis ramorum congestis. Spiculae ovatae oblongae, hiantes, 2.2–2.4 mm longae, glabrae; gluma prima ovata, $\frac{1}{3}$ longitudinis spiculae aequans, 1-nervia; gluma secunda ovata, $\frac{1}{2}$ longitudinis spiculae aequans, 1–3-nervia. Flosculus inferus ♂; lemma ovato oblongum, spiculum aequans, 3-nervium; palea evoluta, binervia, bicarinata; carinis scaberulis vel puberulis et firmis, marginibus membranaceis, latissimis, reflexis. Flosculus superus probabiliter ♀ vel cleistogamus, oblongo

convexus, opacus; lemma et palea obscure papillosa.

Erect, slender, light green, tufted, aquatic perennials, 30–40 cm tall, with scales covering the basal internodes, rather shiny and variable in size; basal internodes 3 or 4, short, the nodes closely approximate with salient, dark, sharp, encircling rims sometimes growing into rigid, long, wiry, glabrous, rather angular, ascending stolons ~2.5 cm long, each consisting of a single long internode, these again growing into a series of approximate nodes similar to those from which they first developed, the last short nodes subsequently giving rise to the culms and branches. *Roots* long, strong, densely covered with root-hairs. *Culms* filiform, terete, simple, glabrous, sulcate, 1–2 mm in diameter. *Nodes* dark, constricted, glabrous. *Leaf-sheaths* of the lower nodes open, wide, loose, with wide hyaline margins, those of the uppermost nodes strongly carinate with the keel area half as wide as the sheath; margins less hyaline; auricles small with a few hairs on the margins; adaxial surface of the sheath bearing numerous, conspicuous transverse veins. *Ligule* with a short, truncate, membranous base, up to 0.25 mm long, long-ciliate at the apex. *Leaf-blades* ascending, acicular, glabrous, sulcate, 8–16 cm long, ~1 mm wide, almost cylindrical in transverse section, the adaxial

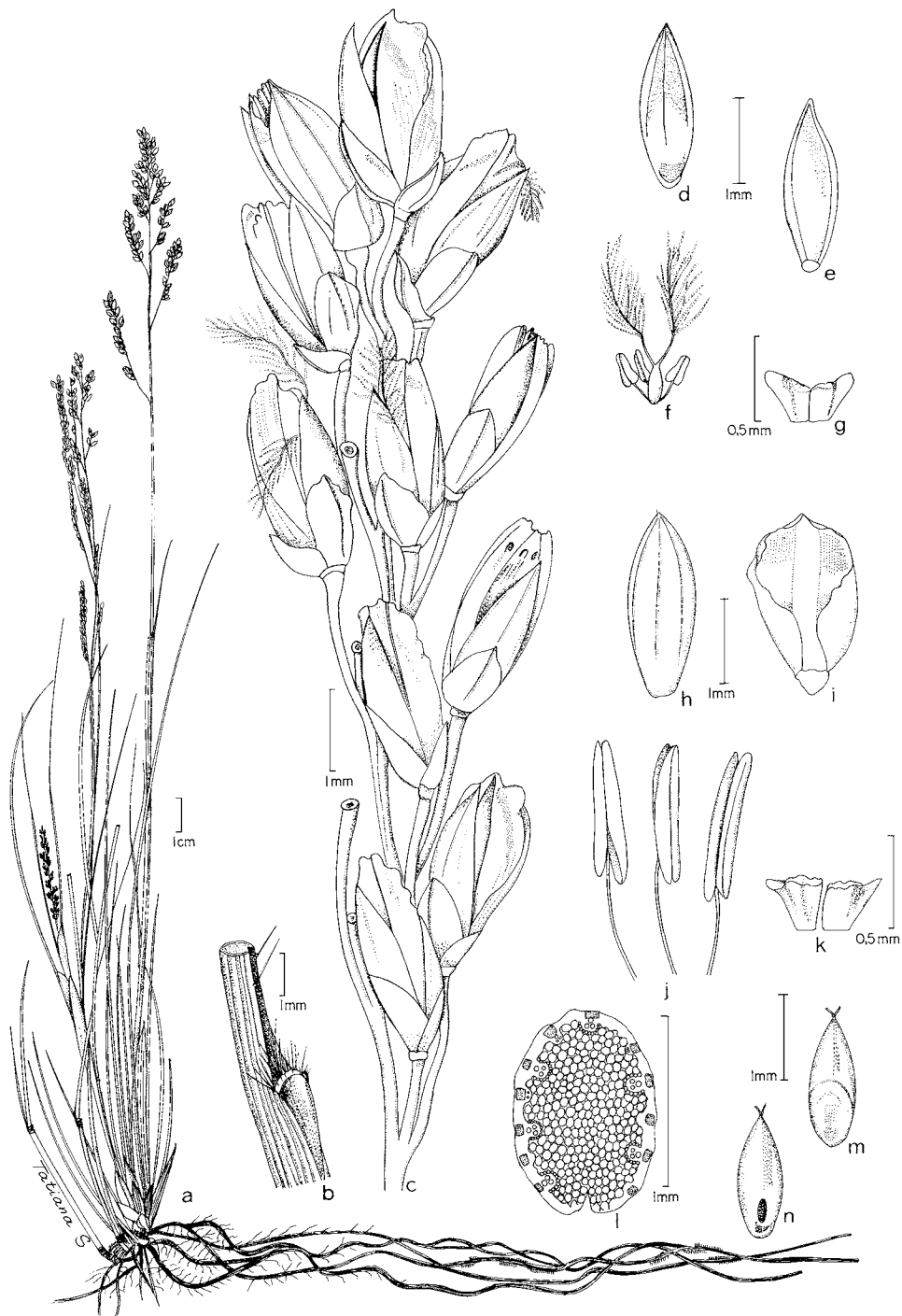


FIGURE 1.—*Otachyrium aquaticum*: *a*, habit of plant; *b*, leaf midregion, showing ligule and part of acicular leaf; *c*, branch of the panicle; *d*, upper floret, lemma side; *e*, upper floret, palea side; *f*, hermaphrodite flower of upper floret, showing reduced anthers; *g*, lodicules of upper floret; *h*, lemma of lower floret; *i*, broad palea of lower floret; *j*, andrecium of lower floret; *k*, lodicules of lower floret; *l*, transverse section of the blade; *m*, caryopsis, embryo side; *n*, caryopsis, hilum side. All drawings based on *Harley et al. 15498* (US).

surface with only a shallow groove, the basal part rather constricted, sometimes with long cilia along the margins.

Panicles 6–14 cm long, 3–4 cm wide, oblong, more or less pyramidal in outline, with sparse, rather few, raceme-like, contracted or spreading, many-flowered branches, the axis sulcate, glabrous; lower branches 2.5–3.5 mm long, diminishing upwards into short clusters of spikelets, bearing no spikelets near the base nor on the lower $\frac{1}{3}$. *Pedicels* unequal, mostly borne in pairs along the branches, with cup-shaped tips.

Spikelets ovoid to oblong-ovoid, 2.2–2.4 mm long, 1.2 mm wide, often somewhat gaping and with a rather truncate apex, gray-greenish or dark purplish, glabrous, opaque, crowded on the racemes. *Glumes* subequal, short, keeled, finely denticulate along the keels. Lower glume $\frac{1}{3}$ the length of the spikelet, 1-nerved. Upper glume $\sim\frac{1}{2}$ the length of the spikelet, 1–3-nerved.

Lower floret staminate. *Lemma* ovate-oblong, navicular, convex and rounded on the back, papery, 1.8 mm long, \sim 1 mm wide, 3-nerved, the margins rather hyaline. *Palea* \sim 2 mm long, 1.5 mm wide, broadly ovate, roundly navicular, with wide, hyaline, undulate, reflexed margins, embracing its flower, at maturity adhering only to the upper floret and not expanding throughout, 2-keeled, producing greenish or purplish, firm longitudinal lines along the keels; keels finely denticulate, the median hyaline area not splitting lengthwise in the middle. *Lodicules* cuneate, truncate, with a wide, concave, horizontal area, the distal margins wing-like and protruding behind the rather swollen adaxial sides.

Upper floret female or cleistogamous? (andrecium reduced to 3 tiny, transparent anthers), narrowly ovoid, 1.8–2 mm long, 0.8 mm wide, plano-convex, acute. *Lemma* ovate, plano-convex, acute, papery or finely crustaceous, opaque, finely papillose, not tightly embracing the palea, firmer in texture than the lemma of the lower floret, nerveless or finely 3-nerved. *Palea* rather flat, of the same texture as the lemma, with narrow hyaline margins and apex, nerveless or finely 2-nerved. *Lodicules* smaller but similar to

those of the staminate floret. *Caryopsis* 1.5 mm long, narrowly ovoid, light brown; embryo half the length of the caryopsis; hilum oblong-ovate, subbasal.

DISTRIBUTION.—Besides the type collection from Bahia, an additional gathering at Kew (*Glaziou 20113*) is labeled as coming from Minas Gerais. This specimen, which we have not seen, was examined and confirmed by Stephen A. Renvoize of the Royal Botanic Gardens, Kew, England.

PARATYPES.—BRAZIL. BAHIA: Municipio de Livramento do Brumado, km 5 da Rodovia Livramento do Brumado-Rio de Contas, *Mori et al. 12251* (MO); Municipio de Rio de Contas, 9–11 km ao N de Rio de Contas, na estrada para o povoado Mato Grosso, *Mori et al. 12348* (MO).

DISCUSSION.—Only a few plants of this species were available for study. It is apparently closely related to *O. pterigodium* since both species share a similar overall aspect, similar type of inflorescence and spikelets, and habitat. Both species occur in marshy, wet ground or on the stream banks; but sometimes they grow attached in tufts to the stones in strong stream currents. A feature observed only in these two species is the presence of a reduced andrecium in the upper hermaphrodite floret (which may also be only female or cleistogamous). In spite of the similarity in several features between these species, the vegetative and the sexual organs of *O. aquaticum* are obviously more adapted to conditions of running water as evidenced by the reinforcement of strength in the basal stolons, which show an alternation of a few abbreviated internodes with long ones.

The increase of the plant's resistance to water pressure can also be observed in the transverse veins, which form air chambers in the tissue of the adaxial surface of the sheath, a feature known in other grasses such as *Paspalum millegrana* Schrader. The acicular leaves are filled with a uniform spongy parenchyma, which is also found in the upper part of the leaf-sheath. The adaxial side of the blade can be ascertained only by a minute groove that occurs on that surface of the

cylinder. This represents an extreme example of the acicular mode of specialization in grass leaves, according to Metcalf (1960).

Otachyrium grandiflorum
Sendulsky & Soderstrom, new species

FIGURE 2

TYPE COLLECTION.—BRAZIL. GOIÁS: Chapada dos Veadeiros, 24 km NW of Veadeiros, road to Cavalcante, 14°S, 47°W, 22 October 1965, H.S. Irwin, R. Souza & R. Reis dos Santos 9515 [holotype, US, sheet no. 2528885; isotypes, MO, sheet no. 2400649, UB, sheet no. 10691].

Gramen perenne, culmis gracilibus, erectis, 20–50 cm altis, egregie usque ad 1 m. Foliorum laminae involutae vel aciculatae, non cylindricae, adscendentiae, 3–20 cm longae, ~1 mm latae, glabrae. Paniculae gracilae, pauciflorae, 2–5 (13) cm longae, ramulis vel pedicellis distantibus, tenuibus. Spiculae 4–7.5 (8.5) mm longae, 2–7.5 mm latae, rotundato-ovatae, pilosae vel glabrae, (sub maturitatis tempus diverso glumarum valvularumque colore plus minus palido-purpureo-centes); gluma prima ovata, $\frac{1}{4}$ longitudinis spiculae aequans, 1–5-nervia; gluma secunda late ovata, semiglobosa, acuminata, spiculae basin einges, $\frac{1}{3}$ longitudinis spiculae aequans, irregulariter 5–7-nervia. Flosculus inferus ♂; lemma ovatum, oblongum, spiculum aequans, irregulariter 3–7-nervium; palea alata, ovata, vel orbiculata, binervia, bicarinata, marginibus membranaceis, latissimis, undulatis, pallido-purpureis, pilosis vel glabris, secus carinas longeciliatis. Flosculus superus ♀, plano-convexus; lemma herbaecum, pallidum, oblongo-ovatum, acutiusculum, hyalinum, glabrum; palea hyalina, tenuis, plana.

Erect, slender, slightly tufted perennials, 20–50 cm (exceptionally up to 1 m) tall, with short, sympodial rhizomes and small cataphylls at the base of new shoots; roots whitish, thick. *Culms* simple, terete, glabrous, striate, 1–1.5 mm in diameter. *Nodes* constricted, yellow or sometimes purplish, with dense, antrorsely appressed, whit-

ish, thick, short hairs; adjacent prenodal zone rather swollen, smooth, stramineous. *Leaf-sheaths* shorter than the internodes, loose around the culms, striate, glabrous, with 2 small auricles at the summit; margins membranous, glabrous or densely ciliate; auricles with a tuft of dense, white hairs at the apex. *Ligule* membranous, truncate, 0.4 mm long, finely denticulate at the apex, occasionally with a hairy line extending on the abaxial side of the sheath from the hairy auricle downwards to the midnerve and forming a V-shaped, hairy abaxial collar. *Leaf-blades* 3–20 cm long, usually ~1 mm wide, glabrous, with prominent nerves, strongly infolded or acicular, with a narrow adaxial furrow less than half the width of the blade, leaving free inconspicuous margins only, rarely flat, up to 7 mm wide; midnerve not prominent.

Panicles few-flowered, 2–5 (13) cm long, ~2–3 (7) cm wide, with a few short, spreading branches or pedicels borne along the glabrous axis. *Pedicels* unequal, mostly in pairs, discoidal or shallowly cup-shaped at the apices.

Spikelets 4–7.5 (8.5) mm long, 2–7.5 mm wide, mostly 2-flowered (rarely with a 3rd rudimentary terminal floret consisting of only 2 scales ~3.5 mm long, 0.5 mm wide), when mature, broadly ovate to orbicular in outline, bi- or plano-convex, with an ovate, salient, light-colored central part (lemma of the lower or of the upper floret, depending on the side exposed) and of broadly ovate, light-colored, hyaline, pilose, encircling wings (palea of the lower floret), otherwise ovate or oblong. *Glumes* subequal, membranous, convex, nearly subglobose, glabrous or with a few white hairs. *Lower glume* ~ $\frac{1}{4}$ the length of the spikelet, broadly ovate, acute, 1–3(5)-nerved. *Upper glume* broader and longer than the first, acute, irregularly 5–7-nerved.

Lower floret staminate. *Lemma* narrowly ovate, 4–6.5 (7.5) mm long, 1–1.8 mm wide, navicular, convex, somewhat keeled, papery, glabrous, greenish, opaque, irregularly 3–7-nerved, often longer than the lemma of the upper floret; margins papery. *Palea* broad, sometimes up to 8.5 mm long, 7 mm wide, membranous, hyaline,



FIGURE 2.—*Otachyrium grandiflorum*: *a*, habit of plant; *b*, androecium of upper floret; *c*, gynecium of upper floret; *d*, lodicules of upper floret; *e*, branch of the panicle; *f*, caryopsis, hilum side; *g*, caryopsis, embryo side; *h*, leaf midregion, showing ligule; *i*, upper floret, lateral view; *j*, upper floret, lemma side. All drawings based on Irwin *et al.* 9329 (US).

white or light purplish, pilose or glabrous, with wide, undulate margins, expanding broadly beyond the lemma; nerves 2, forming along their length a ribbon-like, rather dark, alate-carinate, densely ciliate rim, the central canaliculate part of the palea splitting lengthwise in the middle and forming two broad wings that embrace the upper floret. *Lodicules* less differentiated than those of the upper floret, ~0.3 mm long, cuneate, truncate, with a more or less wide apical area and rather raised median and distal margins, otherwise a rather amorphous mass.

Upper floret hermaphrodite, 4–7 mm long, 1–2 mm wide, narrowly ovoid, plano-convex, pale or greenish, rather shiny. *Lemma* strongly convex, acute, papery, semitransparent, 3-nerved, not tightly embracing the margins of the palea. *Palea* flat, 2-nerved, thin, with convexly reflexed margins, narrowing towards the base. *Lodicules* cuneate, ~0.3 mm long, with a wide, deep, funnel-shaped, horizontal area and with slightly raised median margins, the distal margins wing-like, protruding behind the swollen ridges of the abaxial sides. *Caryopsis* 2.5 mm long, 1.5 mm wide, obovoid, pale; embryo half the length of the caryopsis; hilum prominent, dark, subbasal.

DISTRIBUTION.—Northern and central Brazil, Venezuela.

PARATYPES.—BRAZIL. AMAZONAS: parte baixa ou pe da Serra Araca, arredores da pista de pouso, *Rosa & Cordeiro 1603* (NY). GOIÁS: Chapada dos Veadeiros, ~12 km NW of Veadeiros, *Irwin et al. 9329* (MO, UB, US); ~20 km N of Veadeiros, *Irwin et al. 12593* (NY, US); Municipio Alto Paraiso, *Heringer et al. 2381* (IBGE, SP). RORAIMA: Rio Anaua, afluente do Rio Branco, *Pires et al. 14448* (US; sheet numbers 2781363, 2781364, and 2781372). VENEZUELA. AMAZONAS (Territorio Federal): Canaripo, lado sur del Río Ventuari, *Steyermark et al. 113821* (MO). ATABAPO: W de la cabecera del Cano Cotua (Yapacana), *Huber 1801* (MO); alrededores de Canaripo, margen izquierda (Sur) del bajo Río Ventuari, a unos 20 km al E de la confluencia con el Río Orinoco, *Huber 1879* (MO); cabecera del Cano Cotua hasta el pie occidental del Cerro Yapacana, *Huber 1542* (MO),

1680 (MYF); southeastern bank of the middle part of Cano Yagua, at Cucurital de Yagua, *Davidse et al. 17392* (MO), 17420 (MO); lower part of Cano Yagua, Chipital, *Davidse et al. 17312* (MO); area between the western base of Cerro Yapacana and the headwaters of Cano Cotua, *Davidse et al. 17212, 17234, 17254* (MO); upper portion of Cano Caname, *Davidse et al. 17125* (MO); Cucurital de Caname, south bank of the middle part of Cano Caname, *Davidse et al. 16890* (MO); Cano Caname (afluente derecho [oriental] del medio Río Atabapo), *Huber et al. 3641* (MO). CASQUIARE: al W del medio Río Temi, aprox. a unos 5 km del río, *Huber 3409* (MO).

DISCUSSION.—This species is placed in the morphological group characterized by opaque, yellowish, not indurate lemmas, and is close to *O. aquaticum* and *O. pterigodium*. Most of the Brazilian material examined has flowered after burning and the flowering culms generally arise from a short burnt stock. The plants are weak and small, with one or two fine culms.

None of the specimens that we have examined from Venezuela, except *Davidse et al. 17234*, show signs of having been burned. The plants are mostly all more robust, some up to 1 m tall, and with more developed basal parts, larger inflorescences and occasionally with some flat, wide leaves. In these specimens the leaves vary from plant to plant; even within the same individual there may be flat or somewhat involute or nearly acicular leaves.

The size and general aspect of the spikelet depend considerably on its state of maturity; unfortunately nearly all of the material that we studied was immature. The few mature spikelets that we observed look remarkably like real petaloid flowers with their light purplish, transparent wings.

Otachyrium piligerum
Sendulsky & Soderstrom, new species

FIGURE 3

TYPE COLLECTION.—BRAZIL. GOIÁS: Municipio Formosa, 24 km ao norte da Vila JK, no km 147 da RB-020, 15°02'S, 47°04'W, alt. 500

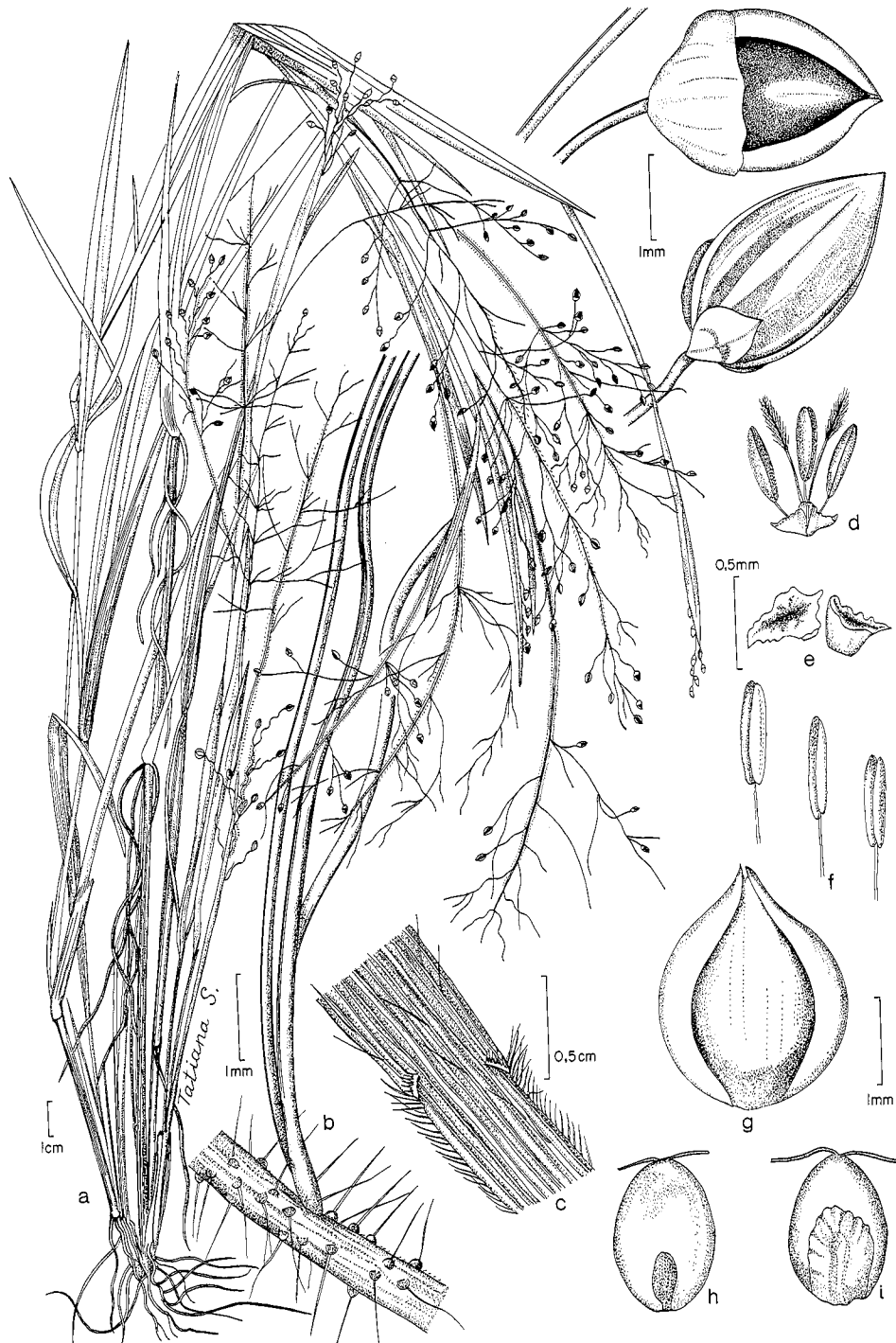


FIGURE 3.—*Otachyrium piligerum*: a, habit of plant; b, section of axis with branch, showing papillose hairs; c, leaf midregion, showing incomplete ligule; d, hermaphrodite flower of upper floret; e, lodicules of upper floret; f, andrecium of lower floret; g, palea of lower floret, showing large folded margins; h, caryopsis, hilum side; i, caryopsis, embryo side. All drawings based on Valls et al. 6009 (CEN).

m, *J.F.M. Valls, R.F.A. Veiga & G.P. Silva 6009* [holotype, CEN; isotypes, K, RB, SP, US].

Gramen perenne?, 25–55 cm altum, culmis gracilibus, fasciculatis, erectis, laxe caespitosis; culmus unus inter alios geniculatus et ad nodes non radicans; culmi ceteri erecti, non geniculati, 2° et 3° nodis valde radicanes et ramificantes, rami novi necnon ramificantes. Foliorum laminae anguste lanceolatae, (3)8–15 cm longae, 4–8 cm latae, acutae, glabrae vel sparsim pilosae. Ligula foliorum superiorum incompleta, pars mediana carens. Panicula multae, axillares, moderate ramosae, pauciflorae, laxa, 3–15 cm longae, 4–12 cm latae; axis primarius dense pilosus, pilis tuberculatis, ~1 mm longis. Spiculae 2.5–3 mm longae, 1.8–2.2 latae, ovatae, glabrae, gibboso planiusculae, chartaceae, margine implicato albo cincta. Gluma prima ovata, longitudine $\frac{1}{4}$ spiculae aequans, acuta, angusta, obscure 1–3-nervia; gluma secunda late ovata, truncata, obscure 5–7-nervia, longitudine $\frac{1}{3}$ spiculae aequans. Flosculus inferus ♂, lemma flosculum superum aequans, ovatum, oblongum, 2.2–2.5 mm longum; palea 2.8–3 mm longae, 2.2 mm latae, late ovata, marginibus conduplicatis, chartaceis, opaco-albidis, flosculum superiorem cingens. Flosculus superus ♀, plano-convexus; lemma chartaceum, ovatum, gibbosum, acutiusculum, nigrescente castaneum, nitentum, subnervium; palea minus chartacea, plana.

Erect, slender, nonrhizomatous perennials? (25) 42–55 cm tall, branching from the second or third node and all subsequent nodes and at each axil, giving rise to one or two branches and an axillary inflorescence. *Roots* dense, fascicled. *Culms* terete, rather grooved, sparsely pilose when young, afterwards glabrous, 1–3 mm in diameter; usually one of the culms somewhat geniculate at the first, never-rooting, node, the other culms always straight and mostly with long internodes and strongly rooting at the first, second, and third nodes. *Nodes* constricted, usually light-colored, glabrous to finely pilose, the adjacent prenodal zone rather swollen, pilose, the hairs antrorse, appressed, whitish. *Leaf-sheaths*

generally shorter than the internodes, loose, striate, densely ciliate on the margin, glabrous or sparsely pilose, the hairs fine, simple or papillose. *Ligule* of the lower leaves a short membrane, ~0.5 mm long, finely denticulate at the apex, asymmetrically arcuate; of the upper leaves incomplete and present only as two short, ciliate, asymmetrically situated membranes at the sides of the sheath, absent from middle part. *Leaf-blades* lanceolate, (3) 8–15 cm long, 4–8 mm wide, attenuate, opaque, glabrous or sparsely pilose; hairs long, fine, stiff, whitish, the mid-nerve differentiated on the abaxial side only.

Panicles numerous, axillary, open, sparsely flowered, 3–15 cm long, 4–12 cm wide, the axis usually sinuous, the surface finely denticulate and pilose; hairs persistent, ~1 mm long, white, stiff, papillose; branches glabrous, dark, ascending or spreading, distichous or somewhat verticillate, fascicled or solitary. *Pedicels* very unequal, sinuous, occurring mostly in pairs or in three's at the base or along the branch, the longer ~20 mm long, the shorter 2–5 mm long, with the apices minutely discoid.

Spikelets ovoid, 2.5–3 mm long, 1.8–2.2 mm wide, glabrous, with an ivory to dark brown, shining, convex central part (lemma of the upper floret), with external, thick, light-colored, tightly encircling margins, ~0.5 mm wide (palea of the lower floret). *Glumes* short, membranous. *Lower glume* ovate, acute, slightly keeled, ~ $\frac{1}{4}$ the length of the spikelet, much narrower than the second glume, obscurely 1–3-nerved. *Upper glume* broad, truncate, ~ $\frac{1}{3}$ the length of the spikelet, with 5–7 obscure nerves.

Lower floret staminate. *Lemma* equal in length to the upper floret, oblong-ovate, naviculate, 2.2–2.5 mm long, 1 mm wide, crustaceous, whitish, inconspicuously 3-nerved, with two prominent, opaque, rather thick, longitudinal ridges and a canaliculate, membranous median part; margins membranous, convexly reflexed. *Palea* broad, without hyaline wings, 2.8–3 mm long, 2.2 mm wide, 2-nerved, the nerves bearing firm, glabrous, strongly reflexed ribbon-like margins along their length, the central part hyaline. *Lod-*

icules ~0.5 mm long, cuneate, irregularly truncate, with a rather wide horizontal area and raised median and distal margins.

Upper floret hermaphrodite, 2.6–2.8 mm long, ~1.5 mm wide, crustaceous, strongly plano-convex, light or dark brown. *Lemma* convex, beak-like, shining, obscurely 3-nerved, embracing the margins of the palea. *Palea* thinly crustaceous, flat, with convexly reflexed margins narrowed toward the base. *Lodicules* similar to those of the staminate floret but with a wider and more concave horizontal area. *Caryopsis* 1.8–2 mm long, 1 mm wide, broadly ovate, plano-convex, brownish; embryo more than half the size of the caryopsis; hilum prominent, dark, ovate, subbasal.

DISTRIBUTION.—Known only from the type collection made in Goiás, Brazil.

DISCUSSION.—*Otachyrium piligerum* bears a superficial resemblance to *O. succisum* but is readily distinguished by the pilose axis of the inflorescence, the continuously branching habit, wider and thicker margins of the palea of the lower floret and unique incomplete ligule of the uppermost leaves.

Otachyrium pterigodium (Trinius) Pilger

FIGURE 4

Otachyrium pterigodium (Trinius) Pilger, 1931:239.

Panicum pterigodium Trinius, 1826:227 [type: Brazil, Minas Gerais, inter Villa Fanado et Contendas, in campis S. Philippi; holotype, LE, not seen; fragment of the type, US ex LE].

Pterigodium junceum Nees ex Trinius, 1826:228 [nomen nudum].

Otachyrium junceum Nees, 1829:272 [type: presumably the same as that of *Panicum pterigodium* Trinius, above].

Panicum neurophyllum Spruce in Martius, 1877:254 [nomen nudum].

Erect, slightly tufted perennials with slender rhizomes, 30–55 cm high. *Culms* decumbent, branching and rooting at the lower nodes, terete, filiform, glabrous, striate, 1–2 mm in diameter. *Nodes* constricted, brown or nearly black, glabrous or pilose, the adjacent prenodal zone slightly swollen, smooth, glabrous, stramineous

or purplish below; hairs, when present, dense, whitish, rather long, antrorsely appressed. *Leaf-sheaths* longer or shorter than the internodes, striate, glabrous, loose around the culms, ciliate along the upper margins, slightly auriculate; auricles with dense tufts of long hairs on the margins, the hairs ~5 mm long. *Ligules* papery, ~0.5 mm long, truncate, irregularly denticulate and finely ciliate at the apex, with dense, long, white hairs behind. *Leaf-blades* flat, narrow, convolute, 8–17 cm long, 2 mm wide, glabrous, sulcate.

Panicles narrowly contracted, many-flowered, 6–7 cm long, ~0.8 cm wide, the axis glabrous or scaberulous, striate; branches rather long, ascending, adherent to the main axis, the first branch sometimes distant below. *Pedicels* unequal, mostly in pairs, occurring densely at the base of the main branches and more sparsely toward the summit.

Spikelets ovoid, ~2 mm long, 1.3 mm wide, yellowish green or purplish, glabrous, rather opaque. *Glumes* subequal, membranous, ~1/3 the length of the spikelet. *Lower glume* ovate, keeled, acute, 1-nerved, finely denticulate along the keels, smaller than the second glume. *Upper glume* broader, keeled, acute, 3-nerved, finely denticulate along the keels.

Lower floret staminate, more or less laterally compressed. *Lemma* ovate, navicular, ~2 mm long, 0.7 mm wide, keeled, acute, yellowish green, obscurely 3-nerved, finely denticulate on the keels, the margins papery. *Palea* broad, winged, up to 2 mm wide, 2-nerved, keeled along the nerves, the keels slightly firmer and ribbon-like, opaque, finely ciliate, the central part hyaline, canaliculate, sometimes splitting lengthwise at maturity and embracing the margins of the upper floret. *Lodicules* cuneate, ~0.25 mm long, with a rather wide, concave, horizontal area and slightly raised, thin, lateral margins.

Upper floret probably female (anthers present as tiny, open structures less than 0.1 mm long), ~2 mm long, 0.6 mm wide, thinly crustaceous, ovoid, acute, yellow or greenish, nearly equal in length to the lower floret. *Lemma* convex, a little smaller than the lower floret, obscurely 3-nerved,

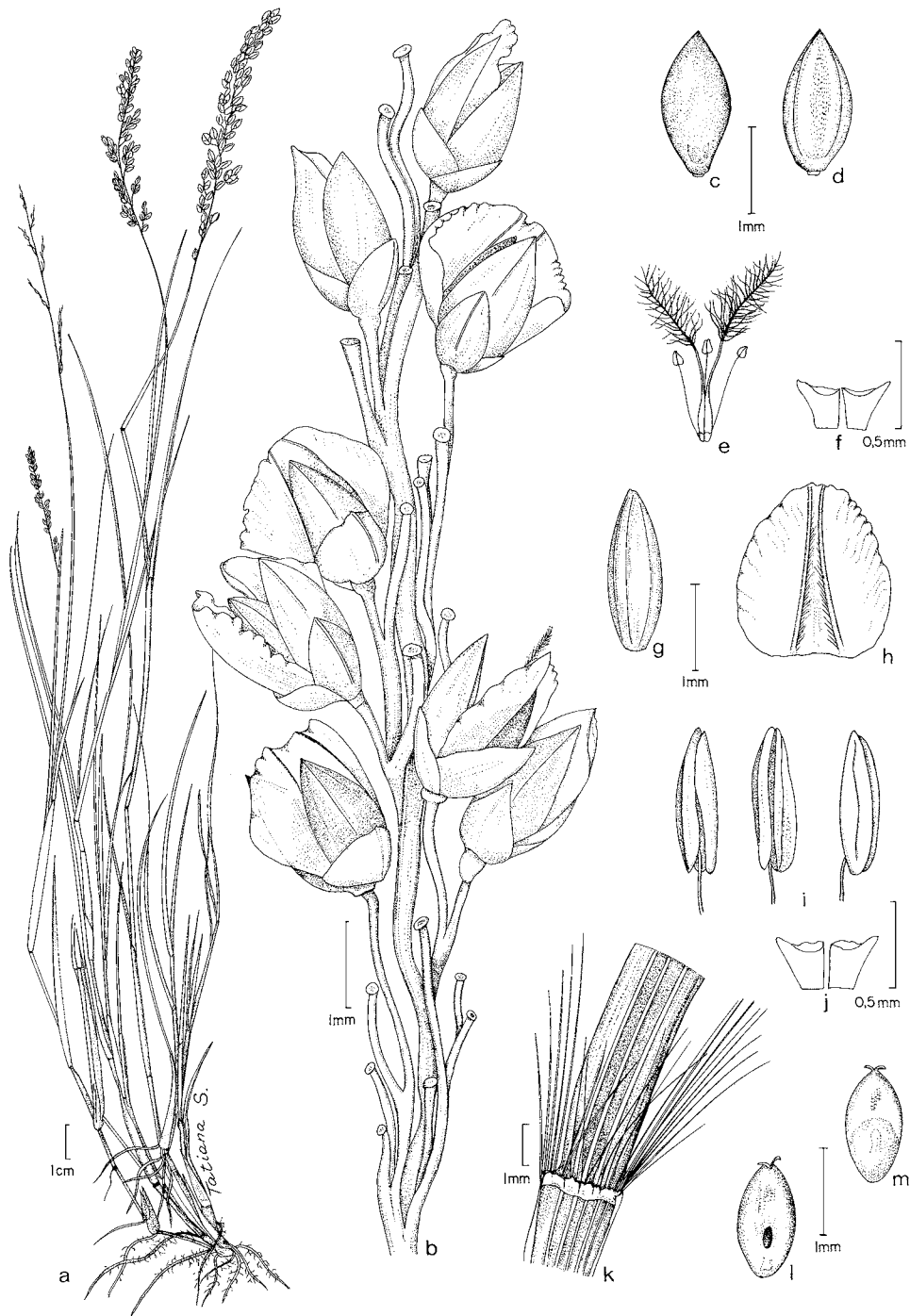


FIGURE 4.—*Otachyrium pterigodium*: *a*, habit of plant; *b*, branch of the panicle; *c*, upper floret, lemma side; *d*, upper floret, palea side; *e*, hermaphrodite flower of upper floret, showing tiny anthers; *f*, lodicules of upper floret; *g*, lemma of lower floret; *h*, palea of lower floret, showing enlarged margins; *i*, andrecium of lower floret; *j*, lodicules of lower floret; *k*, leaf midregion, showing ligule; *l*, caryopsis, hilum side; *m*, caryopsis, embryo side. All drawings based on *E. Pereira 1464* (US).

not tightly embracing the sides of the palea, with a rather shiny basal part, the upper part covered by short, sometimes dark-colored tubercles, the margins membranous. *Palea* membranous, flat, nerveless, the margins reflexed. *Lodicules* similar to those of the lower floret. *Caryopsis* ~1.5 mm long, 0.6 mm wide, ovoid, light brown; embryo ~ $\frac{1}{2}$ as long as the caryopsis; hilum oblong, dark, subbasal.

DISTRIBUTION.—Brazil: Minas Gerais; Amazonas (?).

ADDITIONAL SPECIMENS SEEN.—BRAZIL: AMAZONAS: Rio Negro, inter S. Gabriel et Barcellos, *Spruce 2050* (fragment, US). MINAS GERAIS: Diamantina, *Romariz 0118* (US); Diamantina, Tombador, *Glaziou 20113* (US, sheet numbers 1162988, 1126870, 1715299, 1341373, 1280006); Diamantina, Serra do Rio Grande, *Mexia 5812* (US); Diamantina, Agua Limpa, *E. Pereira 1463* (R, US); 2 km depois de Soupa na estrada para São João de Chapada, *Burman 611* (SP); 5 km de Diamantina, 2 km ao sul da linha ferroviaria a Conselheiro Mata, *Burman 554* (SP); Serra de Santo Antonio, 2–5 km ao leste da cidade de Diamantina, *Burman & Sendulsky 719, 720, 721B, 723* (SP); Serra do Espinhaço, Serra do Cipó, km 120, ~145 km N of Belo Horizonte, *Irwin et al. 20290, 20291* (NY).

DISCUSSION.—The flowering of *O. pterigodium* has been observed in situ by the first author when innumerable purplish, feathery stigmas exerted laterally near the tips of the florets at anthesis gave a light purple coloration to dense tufts of this grass. The plant mostly occupies wet, marshy grounds and margins of streamlets. It also occurs in strong water currents in large tufts affixed to stones.

As all specimens of *O. pterigodium* come from the state of Minas Gerais within a habitat of highland streams and “campos rupestres,” the single collection of *Spruce 2050* from Amazonas is noteworthy.

Brown (1977) reported a non-Kranz type of leaf anatomy for this species, with a $^{13}\text{C}/^{12}\text{C}$ ratio of -27.2 .

Otachyrium seminudum Hackel
ex Sendulsky & Soderstrom, new species

FIGURE 5

TYPE COLLECTION.—BRAZIL: GOIÁS: Serra dos Cristais, 2 km N of Cristalina, 17°S, 48°W, elev. 1250 m, 2 March 1966, *H.S. Irwin, J.W. Grear Jr., R. Souza & R. Reis dos Santos 13321* (holotype, US, sheet no. 2529147; isotype, NY).

Gramen perenne, robustum, 80–150 cm altum, Foliorum laminae lineares, acutae, firmae, scabriusculae. Panícula lineari-contracta, multiflora, 12–30 cm longa, 3–5 cm lata, ramis ascendentibus vel appressis, ad basin ramulis instructis, spiculis ad basin ramorum congestis. Spiculae 2.4–2.7 (3) mm longae, 1–3 mm latae, ovate-alatae vel ovatae, gibboso-planiusculae, sub maturitatis tempus diverso glumarum valvularumque colore plus minus violascentes. Gluma prima ovata, $\frac{1}{3}$ longitudinis spiculae aequans, acuta, 1–3-nervia; gluma segunda late ovata, truncata, 5–nervia, $\frac{1}{3}$ longitudinis spiculae aequans. Flosculus inferus ♂, lemma oblongo-ovatum, spiculum aequans, membranaceo-papyraceum, 3-nervium, palea 3 mm longa, 3 mm lata, rotundado-ovata, latissima, binervia, marginibus membranaceis, undulatis, glabris, pallido-purpureis, carinis inflexis, scaberulis vel puberulis firmisque. Flosculus superus ♀, lemma chartaceum, ovatum, gibbosum, acutiusculum, nigrescenti-castaneum vel fusco-purpureum, nitentum, subnervium, apice pallido; palea minus chartacea, plana.

Erect, robust perennials, 80–150 cm tall, with a well-developed rhizomatous base. Young extravaginal shoots enclosed in short, obtuse, glabrous, aphyllous, yellowish scales arising from the upper part of curved, scaly rhizomes; roots whitish, extremely thick. *Culms* simple or sometimes branching at the nodes, terete, rigid, rather stout, glabrous, striate, up to 1 cm in diameter. *Nodes* with a swollen, shining, yellow to brown, glabrate adjacent prenodal zone grading upward into a wide, densely pubescent ring; the hairs

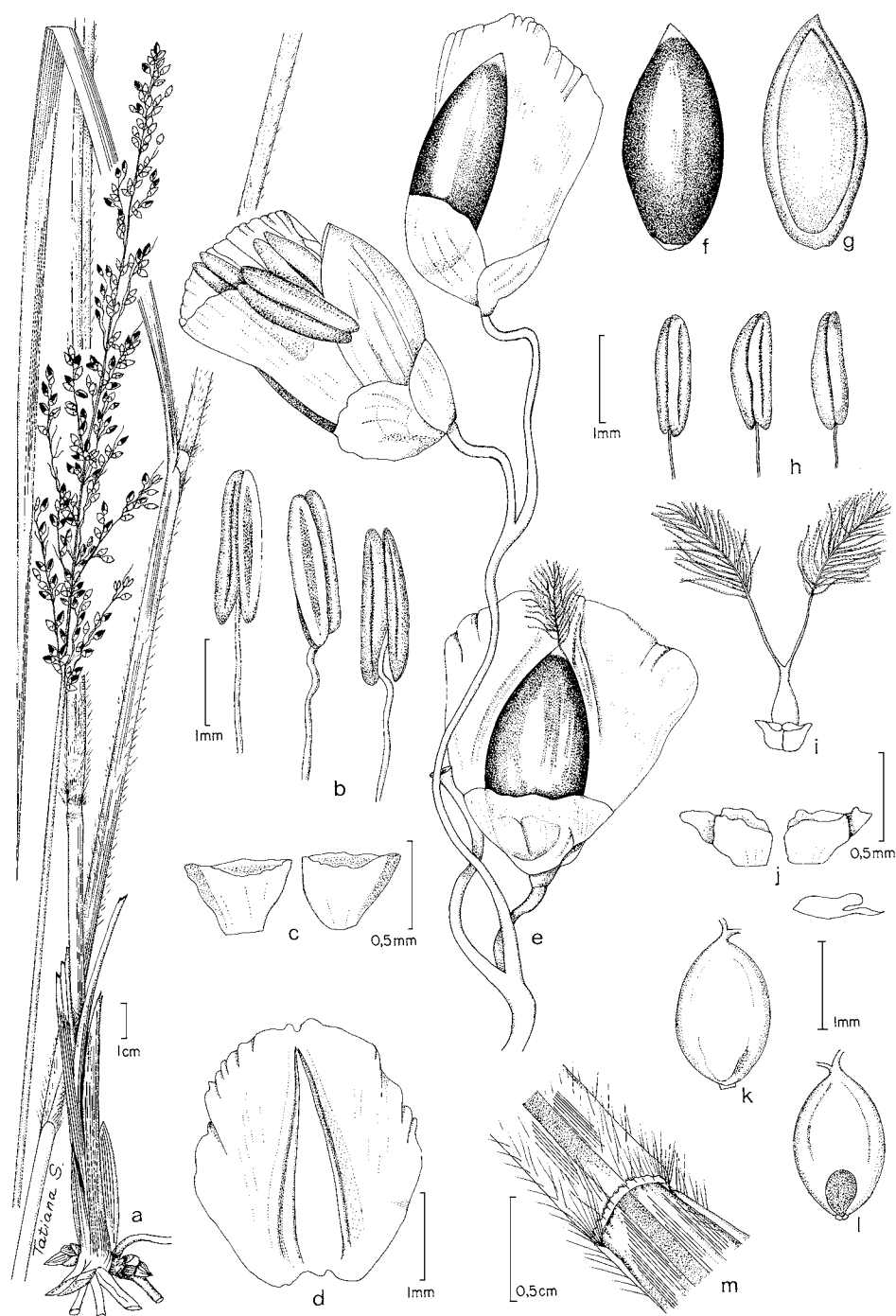


FIGURE 5.—*Otachyrium seminudum*: *a*, habit of plant; *b*, andrecium of lower floret; *c*, lodicules of lower floret; *d*, palea of lower floret, showing enlarged margins; *e*, part of branch of the panicle (enlarged, not to scale); *f*, upper floret, lemma side (enlarged, not to scale); *g*, upper floret, palea side (enlarged, not to scale); *h*, andrecium of upper floret; *i*, gynecium of upper floret; *j*, lodicules of upper floret with schematic transverse section; *k*, caryopsis, embryo side; *l*, caryopsis, hilum side; *m*, leaf midregion, showing ligule. All drawings based on Irwin *et al.* 13321 (US).

long, white, antrorsely appressed, often papillose, mostly straight or sometimes flexuous on the lower part of the node. *Leaf-sheaths* generally shorter than the internodes, loose around the culms, striate, mostly densely pilose at the base; hairs long, sometimes sparse, borne between the nerves, generally antrorsely appressed; margins densely ciliate; adaxial area near the ligule sometimes with dark, brown spots. *Ligules* papery, ~1 mm long, truncate, irregularly denticulate at the apex, split longitudinally, dark yellowish, shining and sometimes with brown spots similar to those of the inner surface of the sheath. *Leaf-blades* linear, (5) 20–40 cm long, 5–10 mm wide, firm, rigid, with inrolled margins, gradually narrowing toward the sharp, hard point, slightly scabrid, with a few long hairs scattered between the nerves and along the margins; midnerve not prominent.

Panicles narrowly contracted, 12–30 cm long, 3–5 cm wide, the axis finely and mostly retrorsely scabrid; branches ascending, fascicled, flexuous, adherent to the axis and held at a more or less uniform angle; each branch consisting of the stout main branch, invariably containing at its base two pairs of shorter, half as thick, sometimes dark-colored, many-flowered supplementary branchlets, one pair on each side, the pair sometimes also consisting of one branchlet and a pair (rarely 3) of short pedicels, arising in place of another supplementary branchlet, the base of the branches thus with many approximate spikelets appearing densely crowded, the first branch sometimes distant below. *Pedicels* unequal, mostly in pairs, borne at the base or along the branch, shallowly cup-shaped at the apices.

Spikelets 2.4–2.7 (3) mm long, 1–3 mm wide, the convex side with a dark brown, almost black, shining, gibbous, ovate-lanceolate central part (lemma of the upper floret) and broadly ovate or recurved, encircling, light-colored, hyaline wings (palea of the lower floret); the opposite side with a papery, whitish scale (lemma of the upper floret). *Glumes* short, subequal. *Lower glume* ~ $\frac{1}{3}$ the length of the spikelet, broad, slightly acute, 1–3-nerved, keeled, finely denticulate along the

keels. *Upper glume* broader and a little longer than the first, truncate, 5-nerved, keeled, finely denticulate along the keels.

Lower floret staminate. *Lemma* oblong-ovate, 1.7–2.5 mm long, 0.8–1 mm wide, navicular, papery, whitish, opaque, 3-nerved, sometimes longer than the upper floret; margins papery. *Palea* broad, up to 3 mm long, 3 mm wide, with membranous, hyaline, white or light purplish margins; nerves 2, forming ribbon-like, rather dark, alate-carinate, finely denticulate rims; the central canaliculate part of the palea at maturity splitting lengthwise in the middle, the margins extending broadly to the sides of the upper floret. *Lodicules* cuneate, truncate, with a wide horizontal area and thin, slightly raised distal margins.

Upper floret hermaphrodite, 1.6–2.2 mm long, 0.8–1 mm wide, ovate, crustaceous, strongly plano-convex, light or dark to almost black. *Lemma* gibbous, smooth, shining, obscurely 3-nerved, loosely embracing the margins of the palea, the apex attenuate to a whitish beaklike point. *Palea* thinly crustaceous, flat or slightly concave, with convexly reflexed margins, narrowed toward the base. *Lodicules* broadly cuneate, truncate, with a wide irregular, horizontal apical area and thin wing-like, adaxial distal lobes protruding behind the swollen abaxial side. *Caryopsis* 1.7 mm long, 1.2 mm wide, ovoid, pale; embryo rather indistinguishable, ~ $\frac{1}{2}$ the length of the caryopsis; hilum prominent, dark, obovate, subbasal.

DISTRIBUTION.—Brazil: Goiás and Mato Grosso.

PARATYPES.—BRAZIL: locality unknown, Glaziou 22587 [must be 22537] (US). DISTRITO FEDERAL: Parque Municipal do Gama, ~20 km S of Brasília, Irwin & Soderstrom 5796 (NY); ~25 km SW of Brasília, Irwin et al. 12993 (NY, SP, US); Brasília, 3 km SE da Reserva Ecológica do IBGE, Heringer et al. 1873 (IBGE); Bacia do Rio São Bartolomeu, Heringer et al. 4329, 4637, 5117, 6134 (IBGE). GOIÁS: locality unknown, 1894-1895, Glaziou 22497, 22537 (fragments, US sheet no. 1126933); Fazenda de Lamarão,

Glaziou s.n. (US sheet no. 1160498); Serra dos Cristais: ~6 km from Cristalina, *Irwin et al.* 9753 (US), 9887 (NY, SP, US); Chapada dos Veadeiros, ~40 km N of Alto do Paraíso, *Irwin et al.* 33111 (SP); Mun. Rio Verde, BR-060, km 172, entre Rio Verde e Acreuna, *Valls et al.* 5144 (CEN, K, SI, SP, US). MATO GROSSO: Rio do Sangue, Linha Teleg., *Kuhlmann* 1753 (US); Margin of Rio Ibo, NW of São Lourenço, *Chase* 11958 (US).

DISCUSSION.—*O. seminudum* is the most robust of all species in the genus except for the unusually large form of *O. versicolor*, known only from Paraguay. This species resembles, and has often been confused with, *O. versicolor* but differs mainly in the narrowly contracted panicle, which may sometimes be spike-like, in the rather short upwardly appressed branches and the somewhat crowded disposition of the spikelets along the main axis. When fresh, the mature spikelets are funnel-shaped and flower-like as a result of the fine, transparent and mostly purplish, large paleas of the lower florets.

The earlier herbarium sheets of this species (*Glaziou* 22497 and 22537), of which fragments were examined at US, bear the specific epithet, *seminudum*, given by Dr. E. Hackel to this species for which, however, he never published a description.

In a note on the herbarium sheet of *Irwin et al.* 12993 (US), Brown noted that the leaves have a $^{13}\text{C}/^{12}\text{C}$ ratio of -25.1 and non-Kranz type of anatomy.

***Otachyrium succisum* (Swallen)
Sendulsky & Soderstrom, new combination**

FIGURE 6

Panicum succisum Swallen, 1952:391 [type: the same as that of *P. inaequale* Pilger].

Panicum inaequale Pilger, 1902:133 [type: Brazil, Mato Grosso, Piava, April 1899, *H. Meyer* 499; holotype, B, not seen; fragment of the type, UB ex B; not *P. inaequale* Mueller, 1874:189].

Otachyrium inaequale (Pilger) Pilger, 1931:239.

Erect, stout annuals, leafy at the base, of a

somewhat semirosette type with one terminal inflorescence, rarely with one or two small panicles on the basal lateral branches, 10(45)–60(85) cm tall; roots dense, fascicled. Culms rather flat, glabrous, striate, 3–8 mm in diameter, sparingly branching from the lower nodes. Nodes constricted, stramineous, pilose; hairs white, rigid, antrorsely appressed. Leaf-sheaths generally longer than the internodes, the lower usually dark purplish, loose, striate, prominently nerved, densely pilose; hairs white or dark purplish, thick, sparse, papillose, the margins not differentiated, the inner sometimes thinner and hyaline. Ligules papery, ~0.5 mm long, truncate, finely denticulate at the apex. Leaf-blades long-lanceolate to linear, (2)10–30 cm long, 5–15 mm wide, gradually attenuate toward the apex, glabrous to densely pilose on both surfaces; hairs long, stiff, white, papillose, the midnerve white or sometimes not prominently differentiated.

Panicles open, sparsely flowered, 5–30 cm long, 5–10 cm wide, the axis glabrous, sometimes sinuous, finely denticulate, the branches ascending or spreading, distichous or somewhat verticillate, fascicled or solitary. Pedicels very unequal, borne mostly in pairs at the base or along the branch, the longer ~20 mm long, the shorter 2–5 mm long, the apices minutely discoid.

Spikelets ovoid, 2.2–2.5 mm long, 1.2–1.5 mm wide, glabrous, with an ivory to dark brown, shining, gibbous central part (lemma of the upper floret) and with pale external, narrow, encircling margins ~0.2 mm wide (palea of the lower floret). Glumes short, membranous, ~ $\frac{1}{3}$ the length of the spikelet, usually dark purple. Lower glume ovate, acute, slightly keeled, much narrower than the second glume, obscurely 1–3-nerved. Upper glume broad, nearly embracing the base of the spikelet, nerves obscure, 5–7, distally anastomosing.

Lower floret staminate. Lemma equal in length to the upper floret, oblong-ovate, navicular, 2.2 mm long, 0.8 mm wide, crustaceous, whitish, inconspicuously 3-nerved, with two prominent, opaque longitudinal ridges and a canaliculate, hyaline central part; margins membranous, re-

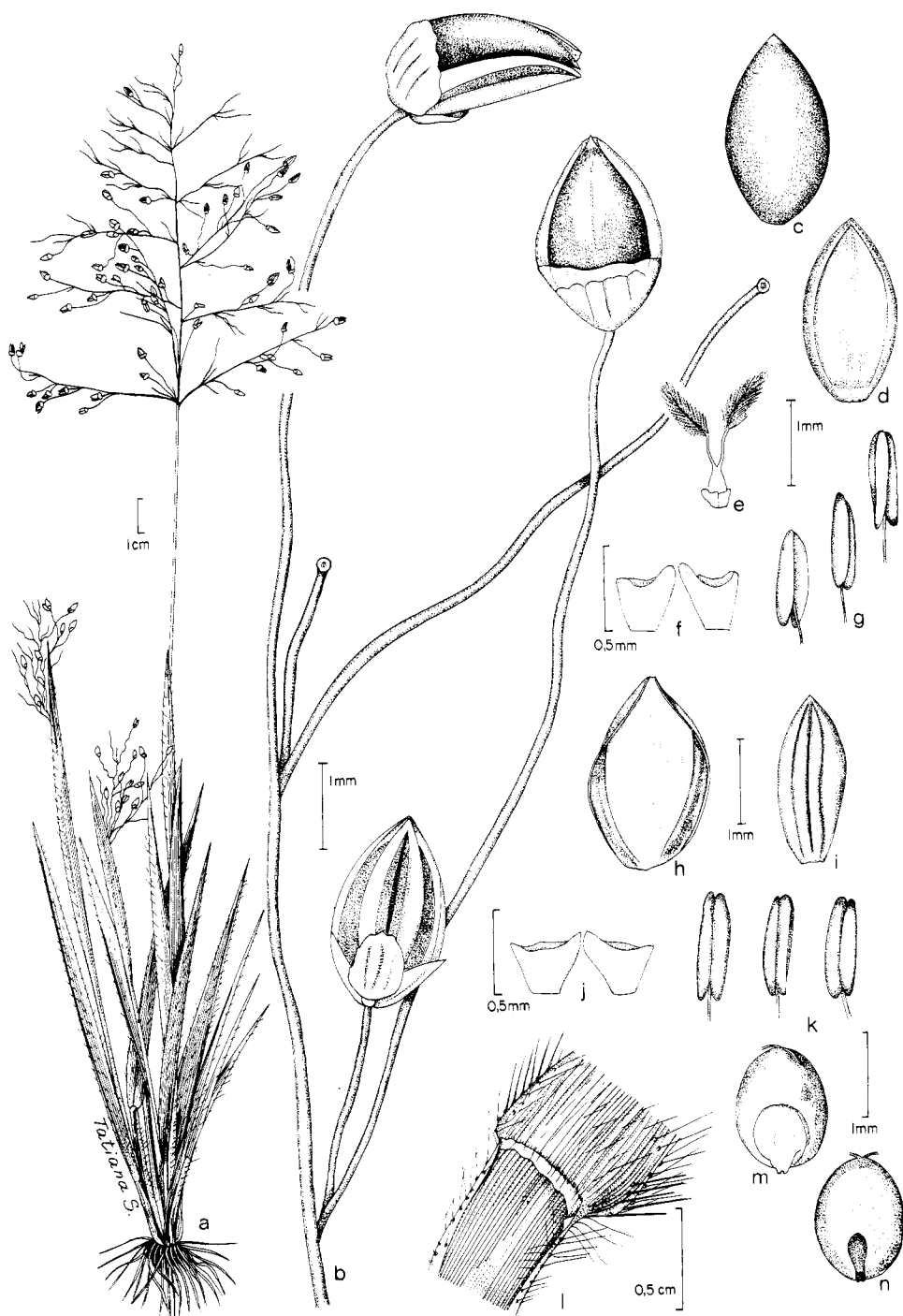


FIGURE 6.—*Otachyrium succisum*: *a*, habit of plant; *b*, part of branch of the panicle, showing long and short pedicels; *c*, upper floret, lemma side (enlarged, not to scale); *d*, upper floret, palea side (enlarged, not to scale); *e*, gynecium of upper floret with lodicules; *f*, lodicules of upper floret; *g*, andrecium of upper floret; *h*, palea of lower floret, showing ribbon-like margins; *i*, lemma of lower floret; *j*, lodicules of lower floret; *k*, andrecium of lower floret; *l*, leaf midregion, showing ligule; *m*, caryopsis, embryo side; *n*, caryopsis, hilum side. All drawings based on Swallen 4944 (US).

curved. *Palea* broad, without hyaline wings, up to 2 mm long, 1.5–1.8 mm wide, 2-nerved, the nerves bearing firm, glabrous, reflexed, ribbon-like margins, the central hyaline part at maturity splitting lengthwise in the middle, with its margins adhering to the upper floret. *Lodicules* 0.3 mm long, cuneate, irregularly truncate, with a broad, concave horizontal area and slightly raised median and distal margins.

Upper floret hermaphrodite, 2.1–2.2 mm long, 1.2 mm wide, crustaceous, strongly plano-convex, light or dark brown. *Lemma* gibbous on the back, beaklike, shining, obscurely 3-nerved, embracing the margins of the palea. *Palea* thinly crustaceous, flat or slightly concave, with convexly reflexed margins narrowed toward the base. *Lodicules* similar to those of the staminate floret. *Caryopsis* 1.5 mm long, 1 mm wide, broadly ovoid, plano-convex, brownish; embryo half the size of the caryopsis; hilum prominent, dark, ovate, subbasal.

DISTRIBUTION.—Guyana, French Guiana, Surinam, northern and central Brazil.

ADDITIONAL SPECIMENS SEEN.—BRAZIL. GOIÁS: Serra do Morcego, Corrego Estrema, ~38 km NE of Formosa, *Irwin et al.* 15176 (NY, US), Municipio Natividade, proximo a Natividade, a 3 km ao norte, na estrada para Dianopolis, *Valls et al.* 6641 (K, RB, SI, SP, US). MARANHÃO: Porto Franco, *Swallen* 3869 (US); Carolina, *Swallen* 3872 (US), *Pires & Black* 2550 (US); Carolina to São Antonio de Balsas, *Swallen* 3991 (US), *s.n.* (US, sheet no. 1817712). MATO GROSSO: Barra de Garças, Xavantina road, 25 km from Xavantina, *Hunt* 5935 (K, NY, SP, US); 25 km S of Xavantina, *Irwin et al.* 17072 (US). PARA: E of Pará, Meseiaria?, *Huber?* 2330 (US); Curralinho, *Pires* 1227 (US, sheet numbers 2205585, 2487500); Marajó Island: *Swallen* 6966 (US), Estate Gavinho, *Goeldi* 226 (US); Fazenda Camburupy, near Soure, *Swallen* 4944 (US), Soure, *Swallen* 4991 (US), Rio Camara, Fazenda Curupatuba, *Black* 50-9886 (US), Rio Arari, Fazenda Tuiniu, *Black et al.* 52-14241 (US). GUYANA: Rupununi, *Dirven* 220 (US). FRENCH GUIANA: Route de Sinnomary, Chemin Marosipetit pont, *Hook s.n.* (K); Route de Sinnomary,

Pariacobo a Cote, Montayne Carapa, *s.coll.* (NY). SURINAM: Sapaliwini, on Brazilian frontier, *Oldenburger et al.* ON 287 (NY).

DISCUSSION.—Plants of *O. succisum* inhabit wet grounds, flooded fields and margins of ponds and streams. The species most resembles *O. piligerum* but can be distinguished from it and all other species by its annual habit, lack of rooting on the lower nodes, absence of rhizomes or stolons, semirosette habit with a leafy basal part and usually one terminal inflorescence, and the glabrous axis of the panicle. The striking difference in length between the pedicels of each pair is a further characteristic that differentiates *O. succisum* from all species except from *O. piligerum*.

Brown (1977:17) reported this species (as *O. inaequale*) to have a non-Kranz anatomy with a $^{13}\text{C}/^{12}\text{C}$ ratio of -26.8 . This was based on a study of *Goeldi* 226.

Otachyrium versicolor (Doell) Henrard

FIGURE 7

Otachyrium versicolor (Doell) Henrard, 1941:511.

Panicum versicolor Doell in Martius, 1877:254 [new name; type: the same as that of *P. truncatum* Nees].

Panicum truncatum Nees, 1829:215 [type: Brazil, Minas Geraes, fluminis (Rio) Jequitinhonha; holotype M, not seen; fragment of the type, US ex M; not *Panicum truncatum* Trinius, 1826].

Erect, slender to rather robust, variable perennials, usually 20–65, but as much as 195 cm tall, with creeping, well-developed, shiny, scaly rhizomes and strong, thick, spongy roots. *Culms* rigid, terete, striate, glabrous, mostly simple, rarely branching at the second or third node. *Nodes* dark, constricted, glabrous or with white, sinuous, tightly appressed hairs. *Leaf-sheaths* generally shorter than the internodes, open to the base, loosely rolled around the culms, overlapping only at the very base, striate, scabrous, sometimes purplish, from glabrous to slightly hirsute or pilose, with rather long, sparse hairs, the margins glabrous or ciliate. *Leaf-blades* linear, 4–40 cm long, 2–24 mm wide, flat, narrow at the base, gradually tapering above the middle toward the attenuate tip, obscurely nerved, with

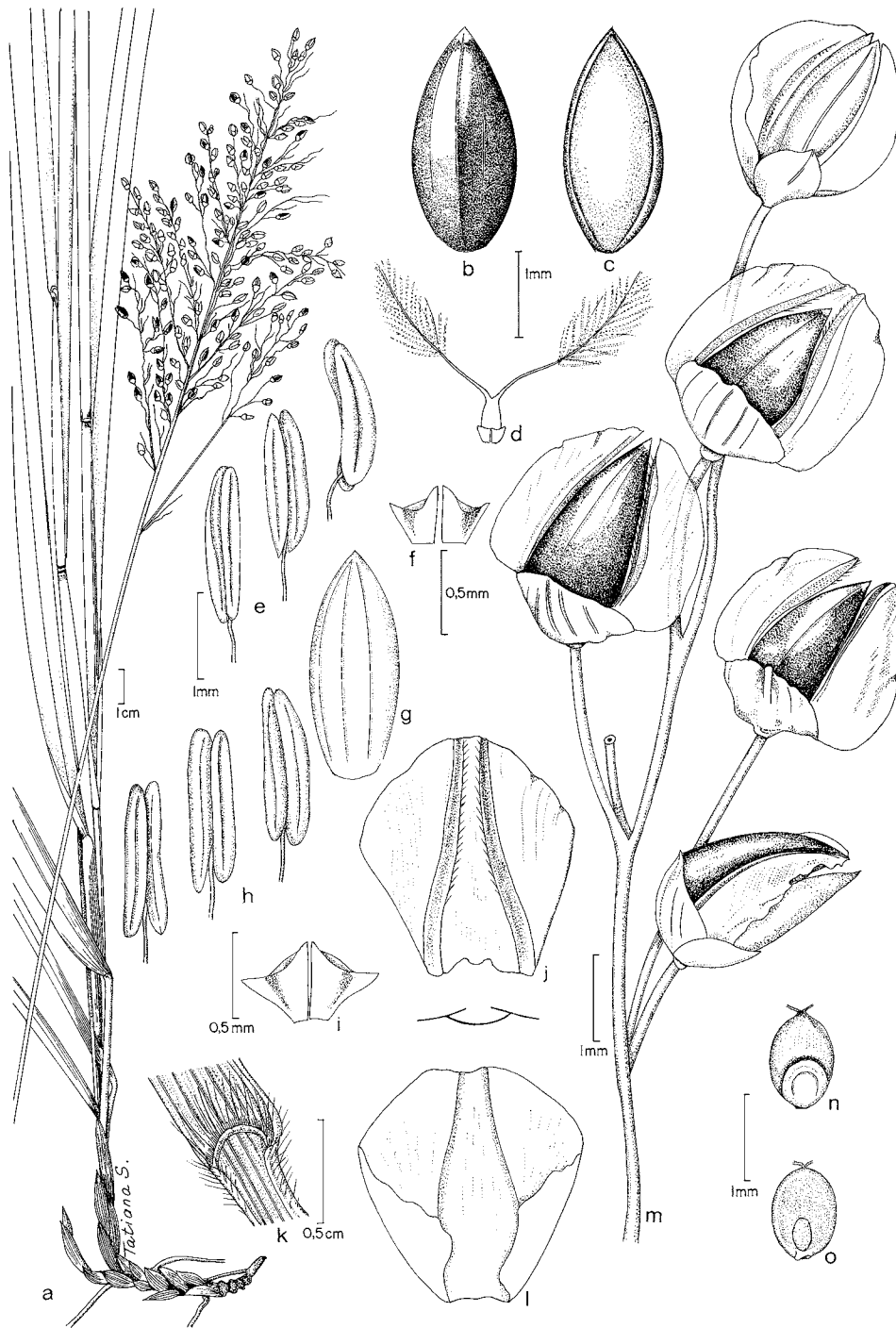


FIGURE 7.—*Otachyrium versicolor*: *a*, habit of plant; *b*, upper floret, lemma side; *c*, upper floret, palea side; *d*, gynecium of upper floret with lodicules; *e*, androgynium of upper floret; *f*, lodicules of upper floret; *g*, lemma of lower floret (enlarged, not to scale); *h*, androgynium of lower floret; *i*, lodicules of lower floret; *j*, palea of lower floret, showing enlarged margins and schematic transverse section (enlarged, not to scale); *k*, leaf midregion, showing ligule; *l*, palea of lower floret, opposite side from that shown in *j*; *m*, part of branch of the panicle; *n*, caryopsis, embryo side; *o*, caryopsis, hilum side. All drawings based on *Hassler 12430* (US).

the midnerve not clearly differentiated, slightly scabrid above and between the nerves, the margins finely denticulate.

Panicles open, many-flowered, 2–30 cm long, 2–15 (24) cm wide, the branches ascending or spreading, flexuous, stramineous or dark purplish, distichous, fascicled or verticillate, the axis light green, sulcate, glabrous, finely denticulate, sparsely pilose, each branch consisting of the stout main branch and invariably bearing at its base two pairs of smaller, half as thick, sometimes dark-colored, supplementary branchlets, one pair on each side, the pair sometimes consisting also of one branchlet and a pair (rarely 3) of pedicels, arising in place of another supplementary branchlet, the lower branch sometimes subtended by a few hairs and a rather long scale on the semi-oval scar. *Pedicels* unequal, mostly in pairs, shallowly cup-shaped at the apices.

Spikelets ovoid, plano-convex, (1.8) 2–3.5 (4) mm long, (2) 2.5–3 mm wide (when immature rather laterally compressed, ~1 mm wide), the convex side with a dark brown, almost black, shining, gibbous, narrowly ovate central part (lemma of the upper floret), and with broadly ovate to rounded, pale, hyaline, encircling wings (palea of the lower floret), the opposite side with a pale, opaque, central part (lemma of the lower floret). *Glumes* short, subequal, sometimes purplish, glabrous, rarely with rather thick, white apical hairs. *Lower glume* ~ $\frac{1}{3}$ the length of the spikelet, ovate, acute, keeled, 1 (5)-nerved, denticulate or with a few hairs along the keel. *Upper glume* broader and a little longer than the lower, truncate at the apex, suborbicular, 5-nerved, keeled.

Lower floret staminate. *Lemma* ovate-lanceolate, navicular, narrowing to the base, membranous, whitish, opaque, sometimes purple, 3-nerved, 2–3.5 mm long, 0.8–1 mm wide, longer than the upper floret, when mature, with firm, brown, wide lines extending from the base to the middle of the lateral nerves, the margins papery. *Palea* membranous, hyaline, white or light purplish, 2–4 mm long, ~2.5 mm wide, with 2 nerves, forming ribbon-like, rather dark, alate-carinate, inflexed rims with finely ciliate margins, the can-

aliculate, hyaline central part of the palea, when mature, splitting in the middle, the halves extending broadly to the sides of the hermaphrodite floret, increasing the size of the spikelet. *Lodicules* cuneate, ~1 mm long, with wide, concave, deep, somewhat funnel-shaped apical areas and with slightly raised median margins, the distal margins wing-like, behind the thicker abaxial sides.

Upper floret hermaphrodite, narrowly ovoid, 2–3.5 mm long, 1.5 mm wide, strongly plano-convex. *Lemma* gibbous, keeled, shining, light to dark brown, almost black, whitish toward the apex, obscurely 5-nerved, loosely embracing the sides of the palea. *Palea* thinly crustaceous, shining, flat or slightly concave, light to brown, with convexly reflexed margins, narrowing toward the base. *Lodicules* similar to those of the lower floret but a little smaller. *Caryopsis* 1.5–2 mm long, 1.2 mm wide, ovoid, dark yellow; embryo manifest, ~ $\frac{1}{2}$ the length of caryopsis; hilum oblong, dark, subbasal.

DISTRIBUTION.—Trinidad, Venezuela, Colombia, Bolivia, Brazil, Paraguay, and Argentina.

ADDITIONAL SPECIMENS SEEN.—ARGENTINA. MISIONES: Posadas, inter Santa Ana et Loreto Municip., *Ekman 644?* (US); Posadas, Establecimiento Santa Ines, *Parodi 4188* (US). CORRIENTES: Dep. Santo-Tomé, Cuay Grande, *Ibarrola 1600* (NY); Dep. San Martín, San Martín, *Ibarrola 1675* (NY).

BOLIVIA. SANTA CRUZ: Buenavista, *Steinbach 6643* (US), *6656* (US).

BRAZIL. AMAZONAS: Mun. of Humaitá: Rio Madeira, road Humaitá to Labrea, km 20, *Prance et al. 3382* (US); 6 km pela estrada 319 para Pôrto Velho, *Gemtchujnicov & Janssen 35* (IBGE, SP); *Gemtchujnicov 1* (SP); 500 m ao sul da BR 230, km 4, *Janssen & Gemtchujnicov 511* (SP). DISTRITO FEDERAL: east of Lagoa Paranoá, *Irwin et al. 11212* (NY). GOIÁS: West of Rio Verde, near Rio Doce, *Chase 12074* (US); Chapada dos Veadeiros, ~40 km N of Alto do Paraíso, *Irwin et al. 33141* (NY). MATO GROSSO: between Bonito and Rondonópolis, *Chase 11907* (US). MINAS GERAIS: 1845, *Widgren 907, 1209* (US); Pouso Alegre, *Hoenhe s.n.* (SP, US); Diamantina, Serra

de São Antonio, *Chase 10386* (SP, US); 5–10 km west of Diamantina, Serra de São Antonio, *Chase 10435* (US); Poços de Caldas, *Chase 10676* (US); S.S. Paraíso; Bau, *Brade 17682 & Barbosa* (US); estrada Serro-Datas, 12 km depois de erro, *Burman 580* (SP); Soupa, na estrada Diamantina-São João da Chapada, *Burman 550*; estrada para Conselheiro Mata, perto de Guinda, *Burman 544 and 570* (SP); entre km 996-997.5 da antiga linha ferroviária Diamantina-Corinto, *Burman 761 & Sendulsky* (SP). PARA: Serra do Cachimbo, *Pires et al. 6105* (US). PARANA: without locality, *Dusen 3250* (US); Pinhaes, *Dusen 7778* (US); Curitiba, Banhado, Estação Experimental, *Swallen 8533* (US); Ponta Grossa, Faz. Cambijoan, *Brade 19637* (US); Mun. Senges, Rio do Funil, Fazenda Morungava, *Hatschbach & Lange 5332* (US); Mun. Tibagi, estrada Castro-Tibagi, Fazenda Palmito, *Hatschbach 5460* (US); Mun. Tibagi, Fazenda Ingrata, *Hatschbach 5464* (US); Mun. Jaguariaiva, Lageado 5 Reis, *Hatschbach 9076* (US); Mun. Castro, Carambei by Rio São João, *L.B. Smith et al. 14495* (US); Mun. Jaguariaiva, Barra do Rio das Mortes, Rio Jaguariaiva, *L.B. Smith et al. 14751* (US); Quatro Barras, *Clayton 4328* (SP, US); Mun. Imbituva, rodovia BR, km 277, *Hatschbach & Ravenna 23070* (US); Mun. de São José dos Pinhaes, Rio Pequeno, *Hatschbach 23465* (US); 6 km N of Mandirituba along Highway BR 116 to Curitiba, *Davidse & D'Arcy 11004* (SP). SANTA CATARINA: Lages, *Swallen 8112* (US); Mafra, *Reitz 5340* (US), Mun. Campo Alegre, Campo Alegre, lower fazenda of Ernest Scheide, *L.B. Smith & Klein 10540* (US); Mun. Mafra, 2–4 km south of Mafra by the Estrada de Rodagem Federal, *L.B. Smith & Klein 10674* (US); Mun. Pôrto União, between Matos Costa and Calmon (22 km), *L.B. Smith & Klein 10856* (US); Campo Alegre, Morro do Iquererim, *Reitz & Klein 6374* (US); São Francisco do Sul, Morro do Campo Alegre, *Reitz & Klein 10945* (US); Santa Cecilia, Banhado, *Reitz & Klein 11352* (US); Ireneopolis, Valões, *Reitz & Klein 11554* (US); Mafra, *Klein 3921* (US); Mun. Mafra, Campo Novo, 7 km from Mafra, *L.B. Smith & Klein 15759* (NY, US); Mun. Lages, Serra dos

Ilhéus, *L.B. Smith & Klein 16053* (US). SÃO PAULO: Cantareira, Horto Botânico, *Usteri s.n.* (SP); São José dos Campos, *Löfgren 3848* (US); São Paulo, *Pickel 5215* (US); São Paulo, Alto da Boa Vista, *Pickel 5813* (US); Jeriguara, Fazenda da Estiva, *Mattos 11679 & Bicalho* (SP); Estação Florestal de Paraguaçu Paulista, 6 km N of city, *Clayton 4636* (SP, US); São Paulo, Agua Funda, *Bordo 17* (SP).

COLOMBIA: CUNDINAMARCA: Bogotá, between Río Guejar & Río Ariari, *Uribe s.n.* (US sheet no. 888782); San Martín, ½ km NE, *Hermann 11170* (US sheet numbers 1879784 and 2487601); Savanna of San Martín, 100 miles (161 km) southeast of Bogotá, *Shaw s.n.* (US); META: Meta, Cabuyano, *García Barriga 5191* (US); ~20 km southeast of Villavicencio, *Killip 34310* (US); 20 km southeast of Villavicencio, *Alston 7567* (US); Río Meta, María, *Cuatrecasas 3750* (US). LOS LLANOS: Río Casanare, Esmeralda, *Cuatrecasas 3888* (US sheet numbers 1773359 and 2780374).

PARAGUAY: locality unknown, *Balansa 25* (fragment, US); cursus superioris fluminis Apa, *Hassler 11446* (US). ALTO PARANA: Nacunday, *Montes 10919* (US sheet numbers 2183621, 2594564), *11016* (US sheet numbers 2183641, 2594589). CORDILLERA: Valenzuela, *Rojas 9501* (US); San Bernardino, *Rojas 10365* (US). GUAIRA: Cordillera de Villa-Rica, *Hassler 8690, 8690a* (fragments, US). MISIONES: Santiago, Estancia La Soledad, *Pedersen 3182* (US). PARAGUARI: Yaguaron, *Balansa 4364* (US). PARAGUARIA CENTRALIS: Regio lacus Ypacaray, *Hassler 12430*; prope Sapucay, *Hassler 13017* (US), *12902* (US); Caapucu, Barrerito, Jaguar, *Rosengurt B-5386* (US); Caapucu, Estancia Barrerito, Potero de Paiva, *Ramírez 164* (US). SAN PEDRO: Alto Paraguay, Primavera, *Woolston G-97* (SP).

TRINIDAD: Piarco Savanna, *Soderstrom, Bhorai & Goodland 994* (US).

VENEZUELA. AMAZONAS: Esmeralda, Alto Orinoco, *Williams 15474* (US); Guapuchana, Río Orinoco, orilla izquierda, ~20 km por arriba de su confluencia con el Ventuari, *Foldats 214-A* (US). ANZOATEGUI: Vicinity of San Tomé (San-

tame), Río Guara Guara, *Chase 12509* (US); margen del morichal, cabeceras del [Río] Guanipa, *Pittier 14877* (US); cabecera del Río Guanipa, *Pittier 14639* (US); orillas del morichal del Río Laisme, *Pittier 15013* (US). APURE: Alto-Apure, *Jahn 199a* (US). BOLIVAR: Cuayapo, *Williams 12004* (US); El Tigre, cerca del Río Cuchivero, *Williams 13334* (US); Parguara, *Velez 2366* (US). MONAGAS: 7.5 km SW of Santa Barbara, *Pursell 9305*, *Curry & Kramer* (US); Río Purgatorio, *Chase 12597* (US).

DISCUSSION.—*O. versicolor* is extremely variable in its height as well as in the size of its leaves, inflorescences, and spikelets. The smallest specimens found are no more than about 20 cm tall, with inflorescences ~4–6 cm long and spikelets ~2 mm long. The largest plants reach 2 m in height and have panicles up to 30 cm long. In the larger plants, the spikelets also may be twice

as long and twice as wide as in the smaller plants. In between are plants that present the entire range of diversity in size in both vegetative and spikelet features. Plants at either extreme are strikingly different and could easily be judged as two distinct species, but apart from the difference in size, no basic morphological difference can be found to separate them.

The smallest plants occur only in the northern part of Brazil, Venezuela, Bolivia, and Colombia. In the central part of Brazil the plants become larger and reach medium size; further south, in the states of Santa Catarina and in Paraná, they become larger, attaining maximum size in Paraguay.

Brown (1977:17) reported this species to have a non-Krantz anatomy with a $^{13}\text{C}/^{12}\text{C}$ ratio of -25.3. This was based on a study of *Chase 10435*.

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