

FOUR NEW SPECIES OF *AXONOPUS* (POACEAE: PANICEAE) FROM TROPICAL AMERICA¹

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ABSTRACT

The following species of *Axonopus* sect. *Axonopus* are described: *A. rupestris*, from Goiás, Brazil, *A. casiquiarensis* from Guainía, Colombia, and Amazonas, Venezuela, *A. chimantensis* from Bolívar, Venezuela, and *A. jeanyae* from Coclé, Panama.

Axonopus is a predominantly tropical American grass genus with a few species extending into the American subtropics and the Old World tropics. Black (1963) monographed the genus and recognized 109 species. With continued exploration it has become apparent that new species remain to be described. On the other hand, it is also probable that some of the species recognized by Black must eventually be synonymized as intermediate populations become known.

Axonopus belongs to the tribe Paniceae and is distinguished by the absence of a lower glume, lower palea, and lower flower, and by its solitary, dorsally compressed spikelets borne inversely (i.e., with the back of the upper glume facing away from the rachis) in two rows on one or usually several to many racemes.

This paper reports on recent fieldwork in tropical America that has brought to light four undescribed species of *Axonopus* sect. *Axonopus*. These are published now so that the names will be available for two forthcoming floras, *Flora Mesoamericana* and *Flora of the Venezuelan Guayana*.

***Axonopus rupestris* Davidse, sp. nov.** TYPE: Brazil. Goiás: Mun. Presidente Kennedy, road from highway BR-153 to Itaporá, 12 km W of village of Presidente Kennedy, Fazenda Primavera along Ribeirão Feíno, ca. 3°25'S, 40°37'W, 400–500 m, 1 Feb. 1980, T. Plowman, G. Davidse, N. A. Rosa, C. S. Rosário & M. R. dos Santos 8216 (holotype, MG; isotypes, F, MO, NY). Figure 1.

Axonopus rupestris Davidse, sp. nov. *A. triglochoides* (Mez) Dedecca affinis sed spiculis brevioribus,

racemis paucispiculis, glumis minus valde nervis, et anthoeciis glabris differt.

Caespitose perennial; culms 10–35 cm tall, the internodes 1–2 mm wide, hollow, glabrous, the nodes 1–2, glabrous, the uppermost geniculate. Leaves erect; sheaths to 7.5 cm long, strongly distichous, conduplicate and keeled, apically winged, mostly glabrous, sparsely hirsute near the juncture with the blade; flag leaf sheath to 10 cm long; collar not differentiated, the sheath with a slight marginal constriction apically but otherwise merging imperceptibly with the blade; ligule a ciliate membrane 0.5–0.6 mm long, the membrane 0.1–0.2 mm long, the cilia 0.4–0.5 mm long; blades erect, mostly 5–10 cm long, folded, mostly 1–2 mm wide as folded, sparsely papillose-hirsute abaxially and adaxially along the midrib to glabrescent, the apex acute. Inflorescences 4.5–7 cm long; peduncles 1 or 2, the uppermost to 19 cm long; racemes usually 2, conjugate, sometimes 3 with the lowermost borne 5–10 mm below the upper pair, 4.5–6.5 cm long, widely spreading at maturity, the axil puberulent; rachis ca. 0.6 mm wide, glabrous, 14–16 spikelets per 25 mm; pedicels 0–0.1 mm long, glabrous; spikelets 2.9–3.5 mm long, 0.8–1 mm wide, elliptic-oblong, obtuse, the upper glume 0.2–0.3 mm longer than the lower lemma, 5-nerved, the lateral nerves marginal, the midnerve weakly developed, prominently pubescent marginally and between the nerves with hairs 0.5–1 mm long, the hairs longest apically, the upper ¼ glabrous; lower lemma marginally 4-nerved, the midnerve not developed, prominently pubescent marginally and between the nerves; anthoecium 0.5–0.9 mm shorter than the upper glume, stramineous,

¹ Fieldwork was conducted with the support of the Projecto Flora Amazônica in Brazil; NSF, CONICIT, MARNR, NGS, Fundación para el Desarrollo de las Ciencias Físicas, Matemáticas y Naturales in Venezuela; and NSF in Panama. I thank O. Huber, S. S. Tillett, B. Nelson, T. Plowman, N. A. Rosa, C. S. Rosário, M. R. dos Santos, C. W. Hamilton, J. S. Miller, and C. Brewer-Carías for help with my personal fieldwork, J. K. Myers for the illustrations, and O. Huber, J. D. Dwyer, and E. Kellogg for useful suggestions for improving the manuscript.

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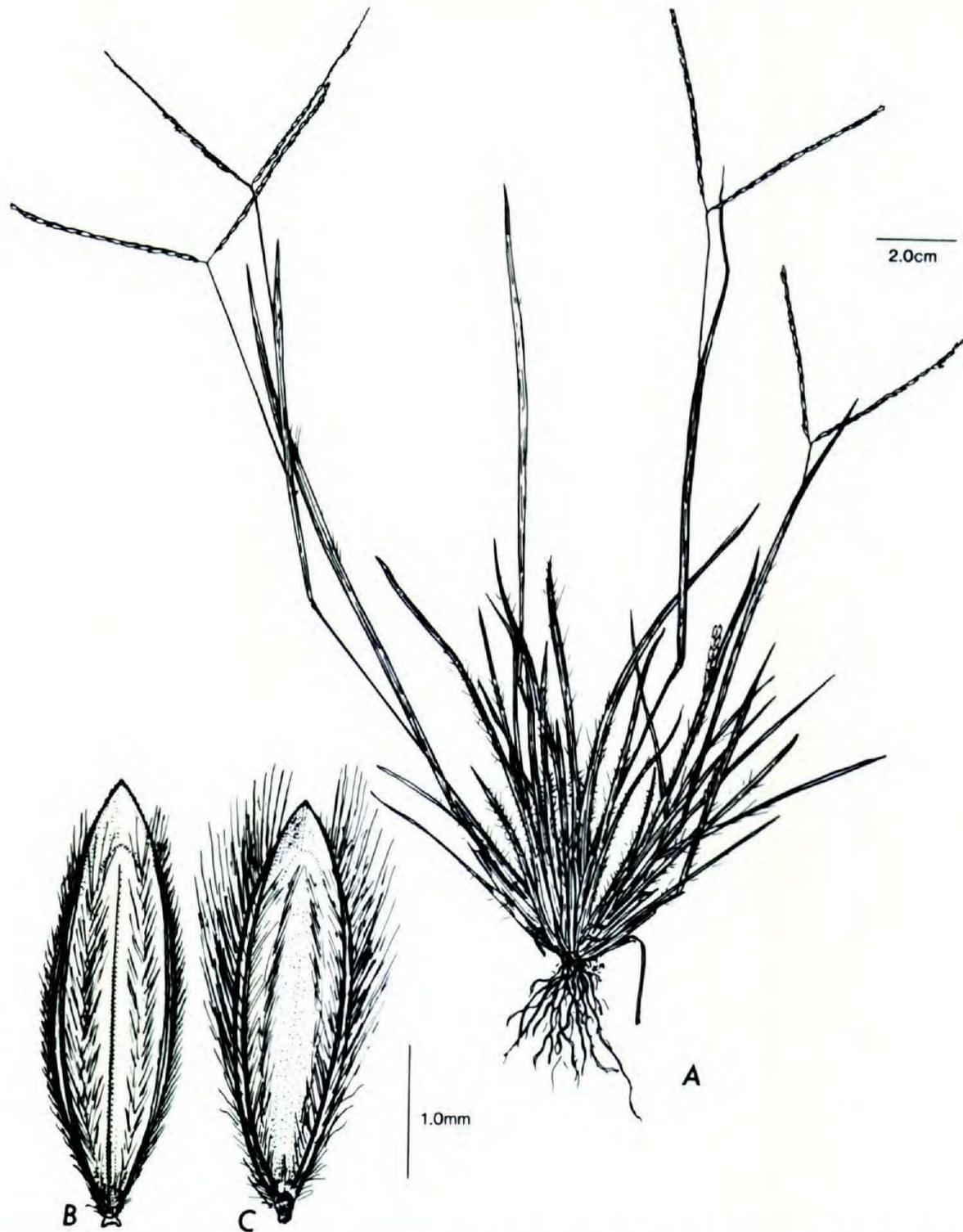


FIGURE 1. Isotype of *Axonopus rupestris*. — A. Habit. — B. Abaxial view of spikelet showing the upper glume. — C. Adaxial view of spikelet showing the lower lemma. [After Plowman et al. 8216 (MO).]

nearly glabrous at the tip, obtuse; lodicules 2, fleshy, truncate, glabrous; stamens 3, the anthers 1–1.2 mm long, dark yellow; styles 2, separate; stigmas plumose, white; caryopsis not seen.

This species is known only from the type collection, which was encountered in cracks and shallow, gravelly soil pockets of a black, granitic rock outcrop (Fig. 2). The epithet alludes to this rocky habitat.

This species, by virtue of its glabrous rachis, stramineous anthoecia, perennial habit, few racemes, and weakly developed midnerve of the glumes, belongs to sect. *Axonopus* ser. *Axonopus* of Black (1963). However, it does not seem closely related to any of the species grouped by Black in this series. Rather, *A. rupestris* seems most closely related to *A. triglochinoides*, a species of the Río Atabapo and upper Río Negro drainages, which

Black placed in sect. *Axonopus* ser. *Barbigeri* subser. *Barbigeri* because the midnerve of the glume is developed, although not as strongly as in typical members of this series.

Axonopus rupestris differs from *A. triglochinoides* in the smaller, much more conspicuously pubescent spikelets (2.9–3.5 vs. 3.9–4.8 mm), greater spikelet density on the inflorescence branches (14–16 vs. 6–7 spikelets per 25 mm), less prominently nerved glumes, and lack of a prominent tuft of hairs at the tip of the anthoecium. The two species are similar in the general facies of their inflorescences and leaves, especially in the prominently distichous, densely tufted sheaths. Both species are relatively uncommon, although local populations may consist of hundreds of individuals. *Axonopus triglochinoides* also grows in cracks of granite outcrops and shallow soil pockets.



FIGURE 2. *Axonopus rupestris* habit and habitat, type locality, Goiás, Brazil.

Axonopus chimantensis Davidse, sp. nov. TYPE: Venezuela. Bolívar: Distr. Piar, Macizo del Chimantá, sector centro-noreste del Chimantá-tepui, cabeceras orientales del Caño Chimantá, vegetación litófito y ribereña alrededor del comienzo E del Cañón recto del Río Chimantá superior, ca. 5°18'N, 62°09'W, ca. 2,000 m, 26–29 Jan. 1983, O. Huber & J. A. Steyermark 6931 (holotype, MO; isotypes, K, NY, US, VEN). Figure 3.

Axonopus chimantensis Davidse, sp. nov. *A. villosus* Swallen affinis sed foliis culmis ligulis et spiculis minoribus differt.

Caespitose perennial; culms 25–60 cm tall, the internodes 1–2 mm wide, hollow, somewhat flattened, glabrous or apically with two lines of pubescence along the margins, unbranched, the nodes 1, rarely 2, densely pilose; sheaths 3–9 cm long, very strongly distichous, conduplicate and keeled, apically winged, glabrous except for the upper $\frac{1}{3}$ of the margin and keel where ciliate, the margin membranous; flag leaf sheath 10–21 cm long; collar prominent, densely pilose; ligule a

ciliate membrane 0.3–0.5 mm long, the membrane 0.1–0.2 mm long, the cilia 0.2–0.4 mm long; blades folded, 6–18 cm long, 3.5–5 mm wide as folded, divergent, usually prominently ciliate on the margins, the keel sparsely ciliate to glabrescent, the tip obtuse, scabrous, adaxially very sparsely pilose to glabrous, abaxially glabrous. Inflorescence 3–10.5 cm long; axis 5–18 mm long; peduncles 1–2, usually well-exserted; racemes 2–4, 2.5–10 cm long, spreading at acute angles, the axils pubescent, the rachis 0.5–0.8 mm wide, scaberulous or pubescent marginally, 9–13 spikelets per 25 mm; pedicels 0.2–1.1 mm long. Spikelets 3–3.4 mm long, 0.9–1.1 mm wide, oblong-elliptic, obtuse; upper glume as long as the lower lemma or to 0.4 mm longer, 5-nerved, the midnerve developed, inconspicuously and sparsely short-pubescent between the nerves; lower lemma similar to the upper glume; antheridium 0.3–0.7 mm shorter than the upper glume, stramineous, apically with a distinct tuft of hairs, obtuse; lodicules 2, fleshy, minutely erose, glabrous; stamens 3, the anthers 1.2–1.5 mm long, purple; styles 2, separate; stigmas plumose, purple; caryopsis not seen.

Paratypes. VENEZUELA. BOLIVAR: Distr. Piar, Macizo del Chimantá, sector centro-noreste del Chimantá-tepui, cabeceras orientales del Caño Chimantá, ca. 5°18'N, 62°09'W, ca. 2,000 m, 26–29 Jan. 1983, Steyermark et al. 128195 (MG, MO, NY, US, VEN), 128007 (MO), Huber & Steyermark 6896 (MO, VEN); Dist. Piar, Macizo del Chimantá, altiplanicie en la base meridional de los farrallones superiores del Apacará-tepui, sector norte del Macizo, ca. 5°20'N, 62°12'W, ca. 2,200 m, 30 Jan.–1 Feb. 1983, Steyermark et al. 128405 (K, MO, VEN), Huber & Steyermark 7043 (MO, VEN), 7032 (MO, VEN); Chimantá Massif, central section, island in Río Tirica above Middle Falls below Summit Camp, 1,925 m, 5 Feb. 1955, Steyermark & Wurdack 463 (US, VEN); Chimantá Massif, central section, swampy savanna along tributary valley of E branch of headwaters of Río Tirica, 2,120 m, 13 Feb. 1955, Steyermark & Wurdack 836 (US, VEN).

Axonopus chimantensis belongs to Black's (1963) sect. *Axonopus* ser. *Barbigeri* subser. *Antipites* because of the perennial habit, non-pappillose-pilose rachis and spikelets, stramineous antheridia, developed midnerve of the glume, and broad, folded blades with obtuse apices. This group of species is best developed in northern South America, especially in the Guayana Region.

Axonopus chimantensis seems most closely related to *A. villosus* and *A. steyermarkii* Swallen. Both of these are much larger than *A. chimantensis*. In addition *A. villosus* has slightly larger

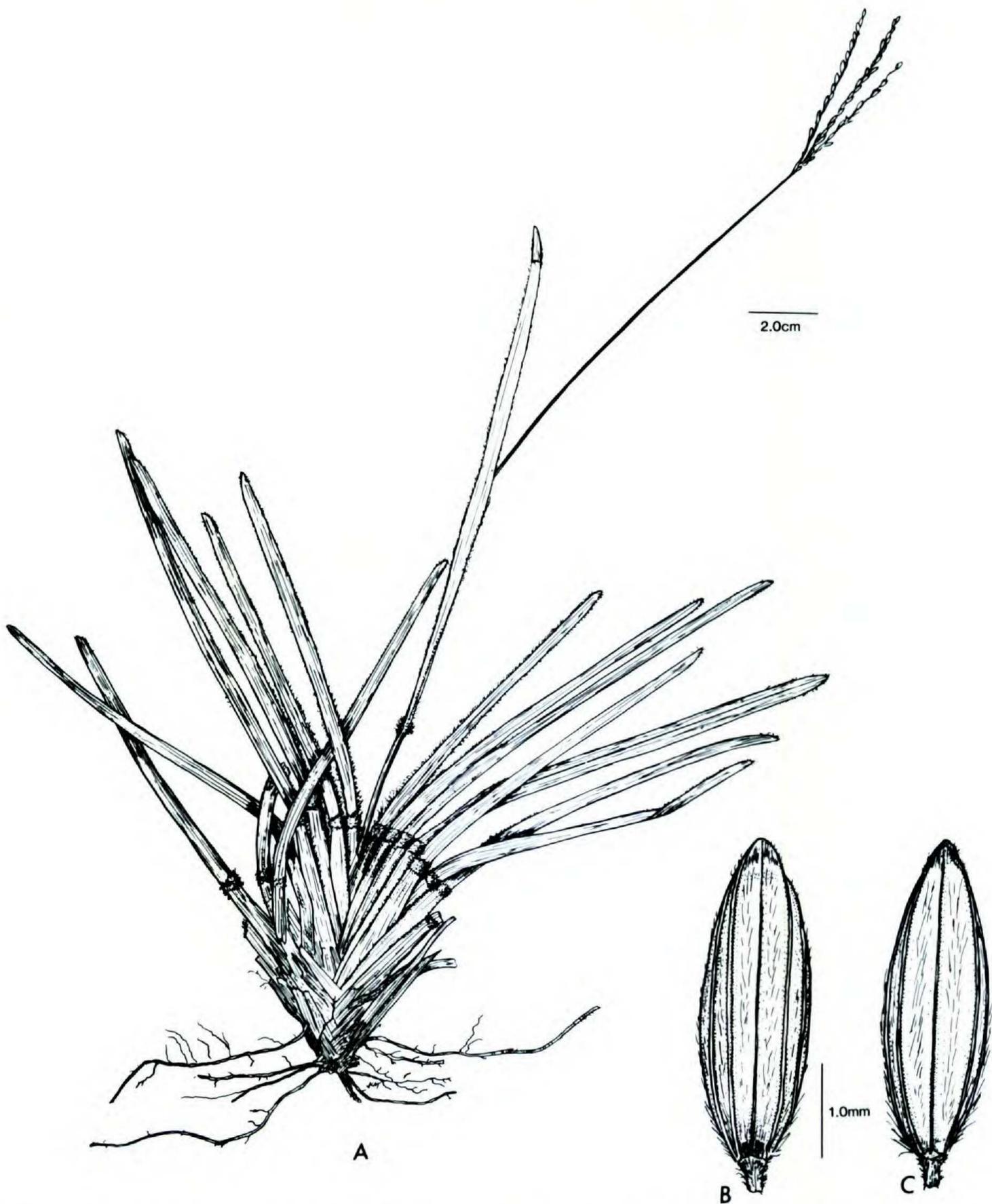


FIGURE 3. Holotype of *Axonopus chimantensis*.—A. Habit.—B. Abaxial view of spikelet showing the upper glume.—C. Adaxial view of spikelet showing the lower lemma. [After Huber & Steyermark 6931 (MO).]

and broader spikelets with more prominent nerves, larger ligules, relatively longer anthoecia, and a tendency toward densely pubescent blades and sheaths. *Axonopus steyermarkii* differs further in its nearly glabrous foliage, blades noticeably narrowed at their bases, and usually longer pedicels.

Many of the cited specimens of *A. chimantensis* have smut-infected spikelets.

The rachis of the racemes in *A. chimantensis* varies from pubescent to scabrous, a characteristic also attributed to *A. villosus* by Black (1963). Black cited Steyermark & Wurdack 463 and 863

as *A. villosus*, but I refer them to *A. chimantensis*. As far as presently known, *A. chimantensis* is endemic to the large Chimantá-tepui system in Bolívar and derives its epithet from this.

Axonopus steyermarkii is endemic to Cerro Marahuaca and nearby Cerro Duida in Amazonas, Venezuela. *Axonopus villosus* occurs in the same area as *A. steyermarkii* and may reach as far north as the Río Manapiare.

***Axonopus casiquiarensis* Davidse, sp. nov. TYPE.** Venezuela. Amazonas: Dpt. Atabapo, Cucurital de Caname, S bank of the middle part

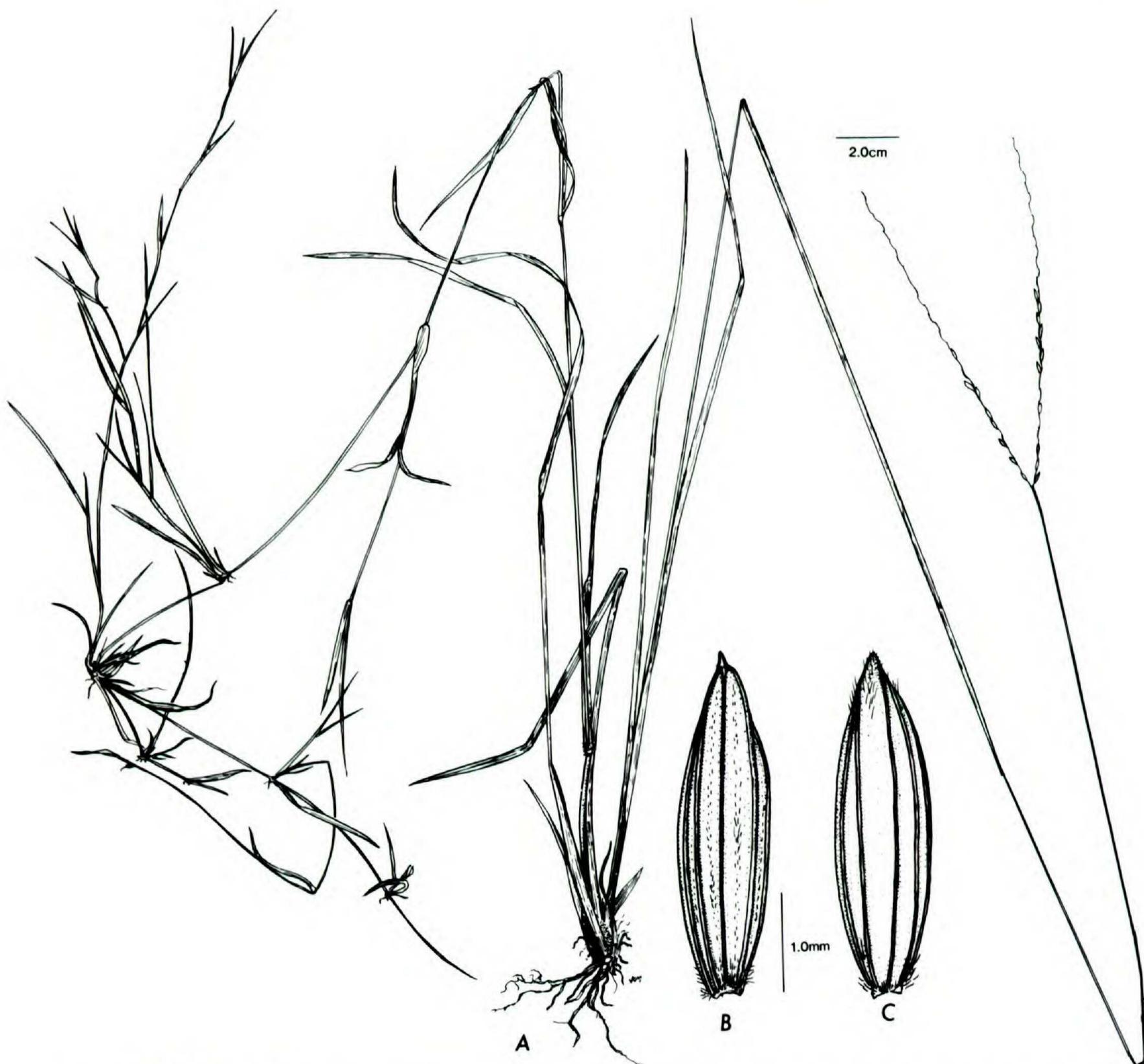


FIGURE 4. Holotype of *Axonopus casiquiarensis*. —A. Habit. —B. Abaxial view of spikelet showing the upper glume. —C. Adaxial view of spikelets showing the lower lemma. [After Davidse et al. 16907A (MO).]

of Caño Caname, 67°22'W, 3°40'N, ca. 100 m, 30 Apr.–1 May 1979, G. Davidse, O. Huber & S. S. Tillett 16907A (holotype, MO, mounted as 2 sheets; isotypes, K, US, VEN). Figure 4.

Axonopus casiquiarensis Davidse, sp. nov. *A. comans* (Trin.) Kuhl. et *A. camargoanus* Black affinis sed stolonibus, basibus culmi gracilioribus et foliis latioribus differt.

Stoloniferous perennial; stolons infrequent, when present well-developed, to 70 cm long, leafy, frequently rebranching and producing tufts of leaves at the nodes, the internodes to 20 cm long; culms 24–90 cm tall, the internodes ca. 1 mm wide, hollow, slightly flattened, glabrous, the nodes 1–2, usually appressed-pubescent, rarely

glabrous. Sheaths mostly 3–12 cm long, rounded on the back, not strongly distichous, not winged, usually glabrous, sometimes pilose at the base, auricular hairs 1–3 mm long usually present; flag leaf sheath to 29 cm long; collar not differentiated; ligule a ciliate membrane 0.1–0.2 mm long, the membrane nearly obsolete to 0.1 mm long, the cilia ca. 0.1 mm long; blades mostly 7–60 cm long, 1–3 mm wide, flat to convolute, commonly ciliate in the lower $\frac{1}{3}$, otherwise glabrous, the apex acute. Inflorescence 4–15 cm long; axis 2–30 mm long; peduncles 1 or 2, usually well-exserted; racemes 2–3(–5), 4–14.5 cm long, nearly appressed to spreading at acute angles, the axils puberulent; rachis 0.3–0.5 mm wide, scaberulous, 10–15 spikelets per 25 mm; pedicels 0.1–0.7 mm long. Spikelets (2.5–)2.7–3.7(–4.1)

mm long, 0.8–1.3 mm wide, oblong-elliptic to lanceolate-elliptic, obtuse; lower glume as long as to 0.3 mm shorter than the lower lemma, 5–7-nerved, the midnerve developed, slightly sulcate between the nerves, usually sparsely pubescent between the nerves, sometimes nearly glabrous or strongly pubescent; lower lemma similar to the upper glume; anthoecium 0.1–0.7 mm shorter than the upper glume, stramineous, apically with a distinct tuft of hairs, obtuse; lodicules 2, fleshy, inconspicuously 3-lobed, glabrous, vasculated; stamens 3, the anthers 1.5–2.2 mm long, purple; styles 2, separate; stigmas plumose, purple; caryopsis ca. 1.5 mm long and 0.7 mm wide, elliptic-obovate, the hilum elliptic-punctate, the embryo ca. $\frac{1}{2}$ the length of the caryopsis.

Paratypes. COLOMBIA. GUIANÍA: Río Atabapo, ca. 7 km S of San Fernando de Atabapo, 67°43'W, 3°55'N, 28 Apr. 1979, *Davidse 16825* (MO, VEN). VENEZUELA. AMAZONAS: DPT. ATABAPO: Caño Caname, 67°22'W, 3°40'N, 29 Apr.–4 May 1979, *Huber et al. 3643* (MO, VEN), 30 Apr. 1979, *Huber et al. 3651* (MO, VEN), 2 May 1979, *Davidse et al. 17049* (COL, K, MO, TFAV, VEN), 67°13'W, 3°40'N, 3 May 1979, *Davidse et al. 17126* (MO, VEN), 67°23'W, 3°41'N, 2 May 1979, *Davidse et al. 17084* (MO, VEN); Caño Yagua, 66°34'W, 3°36'N, *Davidse et al. 17421* (MO, VEN), 66°41'W, 3°29'N, 7 May 1979, *Davidse et al. 17314* (MO, VEN); 5 km al S de la Laguna Yagua, 66°38'W, 3°43'N, 22 Jul. 1980, *Huber & Tillett 5476* (MO, VEN); Río Atabapo, 20 km S of San Fernando de Atabapo, 67°39'W, 3°50'N, 29 Apr. 1979, *Davidse et al. 16856* (INPA, MG, MO, VEN); Caño Cotuá, cerca Cerro Yapacana, 66°50'O, 3°40'N, 14–28 Feb. 1978, *Huber 1605, 1679* (MO, VEN), 66°52'W, 3°38'N, 6 May 1979, *Davidse et al. 17262* (MO, NY, VEN), 17229, 17239 (MO, VEN). DPT. CASIQUIARE: medio Río Temi, 67°29'O, 2°57'N, 24 Feb. 1979, *Huber 3410* (K, MO, TFAV, VEN). DPT. RIO NEGRO: lower Río Baria, 66°32'–66°25'W, 1°27'–1°10'N, 22–23 Jul. 1984, *Davidse 27688* (F, MEXU, MO, NY, TFAV, VEN); Río Pasimoni, 66°35'–66°32'W, 1°53'–1°27'N, 23–25 Jul. 1984, *Davidse 27757* (MO, NY, VEN), 66°32'W, 1°38'N, 9 Feb. 1981, *Huber & Medina 5888* (MO, VEN), 66°33'W, 1°35'N, 8 Feb. 1981, *Huber & Medina 5858* (VEN); Río Siapa, 66°25'W, 2°05'N, 7 Feb. 1981, *Huber & Medina 5807* (VEN).

By virtue of its few, scaberulous racemes, stramineous anthoecia, perennial habit, well-developed midnerve of the glume, and narrow leaves *A. casiquiarensis* belongs to sect. *Axonopus* ser. *Barbigeri* subser. *Barbigeri* of Black (1963).

It is related to *A. comans* and *A. camargoanus* of central to southern Brazil both of which lack stolons, and have consistently convolute blades and thickened, usually deeply buried culm bases.

Both *A. comans* and *A. camargoanus* inhabit wet savannas, whereas *A. casiquiarensis* grows in

white-sand savannas and river banks, including sandy pockets on granite rock outcrops.

This species is distributed in Colombia and Venezuela in the lowland area (elev. 80–125 m) centering around the Departamento Casiquiare from whence it derives its epithet. So far it has been collected from the Río Baria and the Río Siapa in the south to Cerro Yapacana and the Río Atabapo in the north.

Approximately one-fifth of the cited collections have some specimens with conspicuous, long stolons. Apparently in this species, as in many of its congeners capable of producing stolons, stolon production is negatively correlated with density of plants and in general is highly dependent upon local growing conditions. Those plants (e.g., *Davidse et al. 17421*, *Huber & Medina 5858*) from completely open exposures in herbaceous, white-sand savannas have very short, erect, stiff leaves, whereas those from more favorable sites, such as sabanetas (e.g., *Davidse et al. 16856*) and the margins of savannas (e.g., *Davidse et al. 16907A*), have a more luxurious, lax growth habit.

***Axonopus jeanyae* Davidse, sp. nov.** TYPE: Panama. Coclé: area between Caño Blanco del Norte, Caño Sucio and Chorro del Río Tife, 80°36'30"–80°38'W, 8°42'19"–8°43'06"N, spray basin of waterfall, 3 Feb. 1983, *G. Davidse & C. W. Hamilton 23570* (holotype, MO; isotypes, ISC, PMA, US). Figure 5.

Axonopus jeanyae Davidse, sp. nov. *A. ciliatifolius* Swallen affinis sed nodis et spiculis pubescentibus et gluma et lemmate anthoecio longiore differt.

Densely tufted, caespitose perennial; culms 50–75 cm tall, the internodes 1–2 mm wide, solid or nearly so, glabrous, flattened, especially toward the base, the nodes mostly 2, blackish, often noticeably elongated, appressed pubescent with hairs to 1.5 mm long. Sheaths mostly less than 10 cm long, keeled, not strongly distichous, glabrous, the overlapping margin ciliate at least when young; flag leaf sheath to 16 cm long; collar not differentiated; ligule a ciliolate membrane 0.5 mm long, the membrane 0.2 mm long, the cilia 0.3 mm long; blades to 25 cm long, 2–3 mm wide, folded at the base, flat to folded above, papillose-ciliate towards the base, otherwise glabrous, the apex obtuse, scabrous. Inflorescence 6–12 cm long; axis 2–24 mm long; peduncles usually 2, well-exserted; racemes 2–5, 4–11 cm long, spreading at acute angles, the axils puberulent to

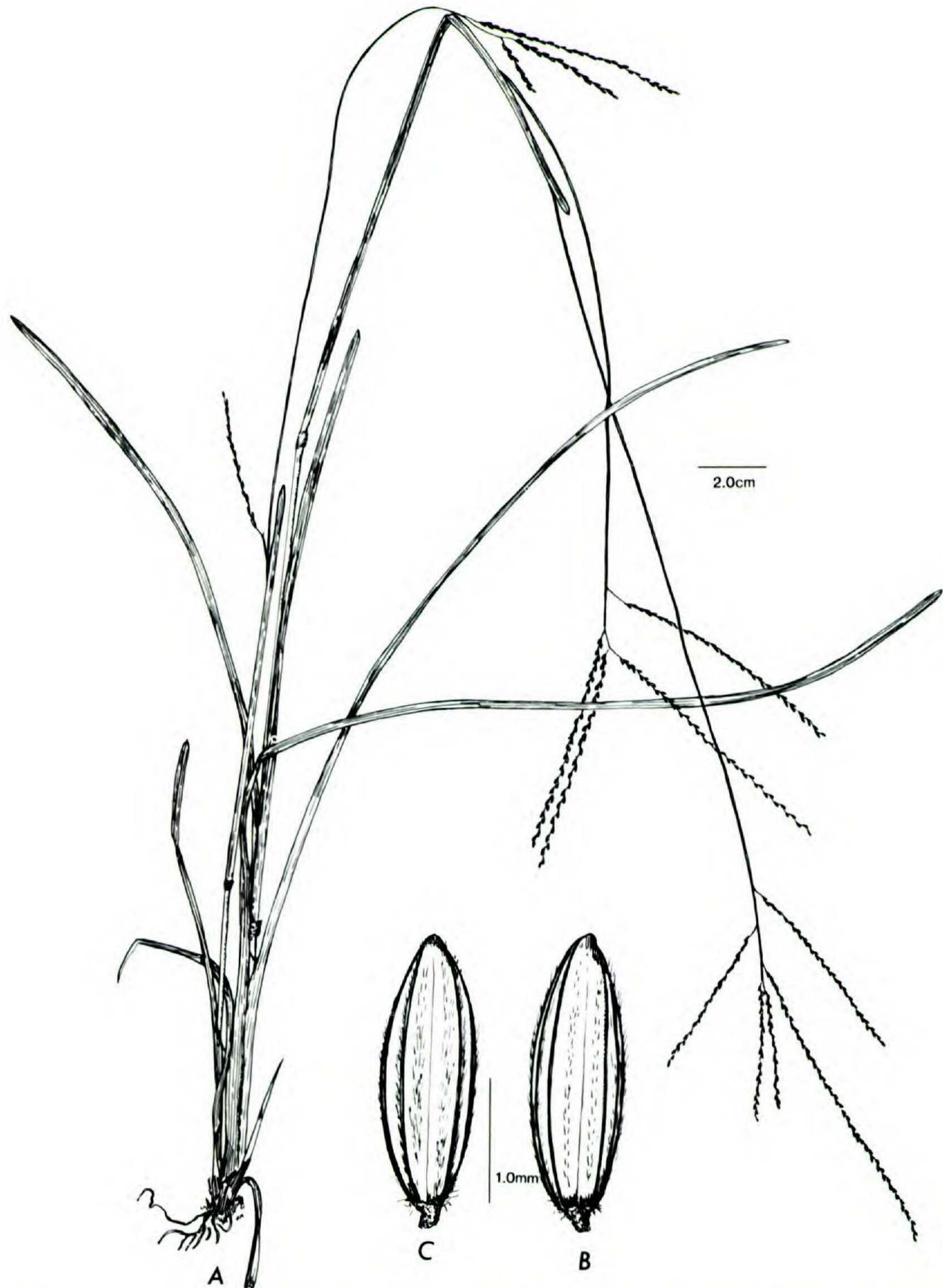


FIGURE 5. Holotype of *Axonopus jeanyae*.—A. Habit.—B. Abaxial view of spikelet showing the upper glume.—C. Adaxial view of spikelet showing the lower lemma. [After *Davidse & Hamilton 23570 (MO)*.]

pubescent, the rachis 0.4–0.6 mm wide, glabrous, 10–13 spikelets per 25 mm; pedicels 0.2–0.5 mm long, glabrous. Spikelets 1.9–2.5 mm long, 0.7–0.8 mm wide, elliptic-oblong, obtuse; upper glume about as long as the lower lemma, 4.5-nerved, the midnerve not or only weakly developed, with appressed lines of pubescence between the nerves; lower lemma similar to the upper glume; anthoecium 0.1–0.4 mm shorter than the upper glume, brown, apically minutely papillate, obtuse; lodicules 2, minutely 3-lobed, fleshy, vasculated, glabrous; stamens 3, the anthers 1.0–1.1

mm long, purple; styles 2, separate; stigmas plumose, purple; caryopsis 1.3 mm long, 0.7 mm wide, oblong, broadly obtuse, the hilum elliptic-punctate, the embryo ca. $\frac{1}{2}$ the length of the caryopsis.

The perennial habit, glabrous racemes, and brown anthoecia place *A. jeanyae* in sect. *Axonopus* ser. *Suffulti* of Black (1963). This new species appears to be most closely related to *A. ciliatifolius* Swallen, a species so far known only from Belize. *Axonopus ciliatifolius* differs in its

glabrous nodes and more fragile, glabrous, less strongly nerved glume and lower lemma, both of which are as long as the anthoecium.

The epithet recognizes the contributions of my wife, Jeany Vander Neut Davidse, to the *Flora Mesoamericana* project. She is largely responsible for processing the thousands of collections

generated by Missouri Botanical Garden collectors in Mesoamerica.

LITERATURE CITED

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