
A REVISION OF *RADDIELLA* (POACEAE: BAMBUISOIDEAE: OLYREAE)¹

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ABSTRACT

Raddiella is a genus of seven species of low- to mid-elevation, small herbaceous bamboos (Poaceae: Bambusoideae: Olyreae) that occurs from Panama and Trinidad to Bolivia and Brazil. *Raddiella esenbeckii* is widespread in savannas and cerrados, but its six congeners are rare, and many occur only on wet rocks in the spray zone below waterfalls. The new Brazilian species, *R. minima*, with the smallest leaves of any bambusoid grass, and *R. lunata*, with lunate female florets, are described. This first revision of *Raddiella* includes a key to the recognized species, descriptions, and distribution maps, as well as scanning electron micrographs of the female florets, which reveal taxonomically important interspecific differences.

Along with the Cuban genus *Mniochloa* Chase, members of *Raddiella* Swallen (Poaceae: Bambusoideae: Olyreae) are the smallest bambusoid grasses in the world. The genus was described (Swallen, 1948) on the basis of three species, *Raddiella nana* (Doell) Swallen (= *R. esenbeckii* (Steudel) Calderón & Soderstrom), the type species; *R. truncata* Swallen (= *Parodiolyra lateralis* (Nees) Soderstrom & Zuloaga); and *R. malmeana* (E. Ekman) Swallen. Swallen characterized the genus as monoecious with the male and female spikelets in different inflorescences; the pedicels of female spikelets not conspicuously thickened upwards; female spikelets with the glumes 3-nerved, and the floret indurate, white, and smooth.

Soderstrom (1965) described three new species of *Raddiella*, *R. kaieeteurana*, *R. maipuriensis*, and *R. potaroensis*, and included a key to the six species in the genus. Later, based on priority, Calderón & Soderstrom (1980) considered *R. esenbeckii* as the valid name for the type species of the genus and transferred *Panicum molliculmum* Swallen to *Raddiella* (as *R. molliculma*).

Examination of more herbarium material since Soderstrom's summary of the genus has revealed two distinctive new species of *Raddiella*, and a scanning electron microscope study of female florets has proven useful in clarifying species limits, warranting the following revision of the genus.

MATERIAL AND METHODS

Classical alpha taxonomic methods were used to study *Raddiella*. In addition, scanning electron micrographs were made of the female florets of a few populations of each of the species except *R. minima*, using the same procedures and equipment as described by Soderstrom & Zuloaga (1989). The vouchers for this study are marked with an asterisk (*) in the lists of specimens examined in the taxonomic treatment.

MORPHOLOGY

Species of *Raddiella* are remarkable in the Bambusoideae for their very small size. Most species appear to be annuals and represent the only annual bambusoids, excluding oryzoids. Many are obligate phreatophytes, growing only on wet rocks in the constantly moist spray zone of riversides below waterfalls; exceptions are the perennials *R. esenbeckii* and possibly *R. minima*, which often grow in dry savannas and cerrados. *Raddiella esenbeckii* and possibly *R. minima* are also unique in the genus in exhibiting nyctinasty, or sleep movements, the blades folding upwards at night or under water stress. The blades are firm and conspicuously asymmetrical in *R. esenbeckii* and *R. minima*, thinly membranous and only slightly asymmetrical in the other species.

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Species of *Raddiella* bear terminal and numerous axillary inflorescences; both types are contracted, few-flowered, and barely exerted from the leaf sheaths. The several inflorescences arising from the uppermost node each consist of several (rarely one as in *R. minima*) early-deciduous male spikelets on short, filiform pedicels. Several axillary inflorescences occur at each node, and the disposition of spikelets in these is more variable. Typically, the entire inflorescence is female, with spikelets borne on short, filiform pedicels. However, at a given node, inflorescences bearing 1–2 terminal female spikelets as well as 1–several short-pedicelled male spikelets positioned below them can be found. Exceptions to these patterns include *R. molliculma*, in which both terminal and axillary inflorescences are long-peduncled and each consists of 1–2 terminal male and 1–2 subterminal female spikelets; and *R. lunata*, with racemose-appearing inflorescences that may be up to 12-flowered, but in which the disposition of the sexes in the single, overly mature specimen is not entirely clear.

The spikelets of *Raddiella* are fairly typical of those of other olyroid genera. In the female spikelets, the glumes vary from persistent in *R. esenbeckii* and *R. minima*, to deciduous together with the floret in the other species. The glumes are 3–5-nerved, and there is a characteristic indurate, thickened, interglumal internode present. The female floret morphology is ellipsoidal in all species (Fig. 13) except for *R. lunata*, which has curious, lunate (crescent-shaped in profile) florets that taper to an acute point at both ends (Fig. 14). Floret epidermal texture, however, ranges from smooth to strongly papillose and is discussed in the section on anatomy below.

The male spikelets are hyaline and early deciduous, and their relative size with respect to the female spikelets is apparently of some taxonomic value.

The caryopses of most species are ovoid-ellipsoid, and the hilum is central punctiform or short-elliptical, a type not present in other bambusoid grasses (Calderón & Soderstrom, 1980). However, in *R. esenbeckii* (but not its putative sister species *R. minima*) the hilum is short-linear.

ANATOMY

A scanning electron microscope study of the mature female florets proved useful in clarifying species limits in *Raddiella*, just as in *Panicum* (Zuloaga, 1987) and *Olyra* (Soderstrom & Zuloaga, 1989). Most species of *Raddiella* had distinctive lemmatal epidermal features that are described

below. Common to all species was the presence near the base and/or apex of the palea of circular excavations, 10–15 μm diam., similar to those present on the female paleas of various species of *Olyra* L. and *Parodiolyra* Soderstrom & Zuloaga (Soderstrom & Zuloaga, 1989). These excavations are apparently caused by the deflation of certain cells when placed in the vacuum of the scanning electron microscope.

Raddiella esenbeckii (Figs. 1, 2). Female lemma completely smooth.

Raddiella kaieteurana (Figs. 3, 4). Both lemma and palea covered throughout with simple papillae 4–5 μm diam.

Raddiella lunata (Figs. 9, 10). Both lemma and palea with cells with a single large, central, compound papilla 9–11 μm diam., bearing on its raised margins 3–5 smaller papillae 3–4 μm diam.

Raddiella malmeana (not illustrated). Lemma completely smooth (but available floret slightly immature).

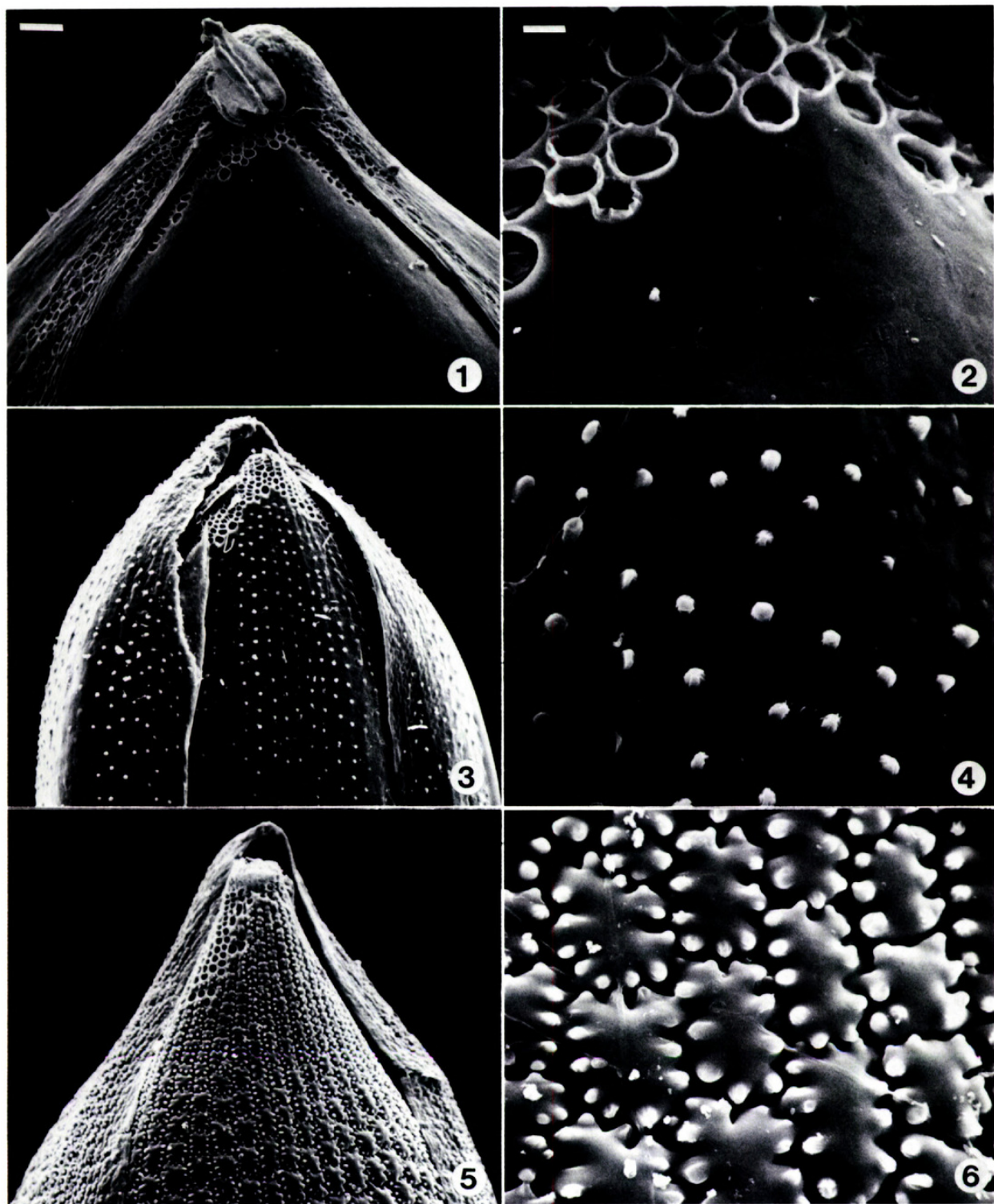
Raddiella minima. Not included in scanning electron microscope study; in an optical microscope, the lemma appears to be completely smooth, as in *R. esenbeckii*.

Raddiella molliculma (Figs. 5, 6). Both lemma and palea with the central portion of each cell enlarged and protruding (ca. $30 \times 20 \mu\text{m}$), and with 10–12 papillae, 3–5 μm diam., present along the undulating margins.

Raddiella potaroensis (Figs. 7, 8). Both lemma and palea with cells with the central portion of each cell enlarged, 15–18 μm diam., surmounted by 7–10 smaller papillae 3–4 μm diam.

RELATIONSHIPS

The possible affinities of *Raddiella* with several other putatively related genera of the Olyreae are summarized in Table 1. It will be noted that the type species, *R. esenbeckii*, has several characters in common with *Parodiolyra lateralis* (Nees) Soderstrom & Zuloaga rather than with the phreatophytic species of *Raddiella* (with the possible exception of the poorly known *R. minima*): perennial habit; firmly membranous leaves; smooth female florets; and a short-linear rather than punctiform hilum. Arguing for the retention of the phreatophytic species within *Raddiella* is the presence of the following feature in common between them and *R. esenbeckii*: few-flowered panicles with the sexes usually separate, the males terminal and females axillary. Moreover, *R. esenbeckii* and *P. lateralis* have quite different chromosome numbers ($n = 10$ and 18 (Davidse & Pohl, 1978), respectively), and



FIGURES 1–6. Scanning electron micrographs of female florets of *Raddiella* species.—1, 2. *R. esenbeckii* (Pires 51123).—3. *R. kaieteurana* (Egler 1244).—4. *R. kaieteurana* (Maguire & Fanshawe 23089).—5, 6. *R. molliculma* (Gutiérrez & Schultes 616). Scale bar 50 μ m for 1, 3, 5; 10 μ m for 2, 4, 6.

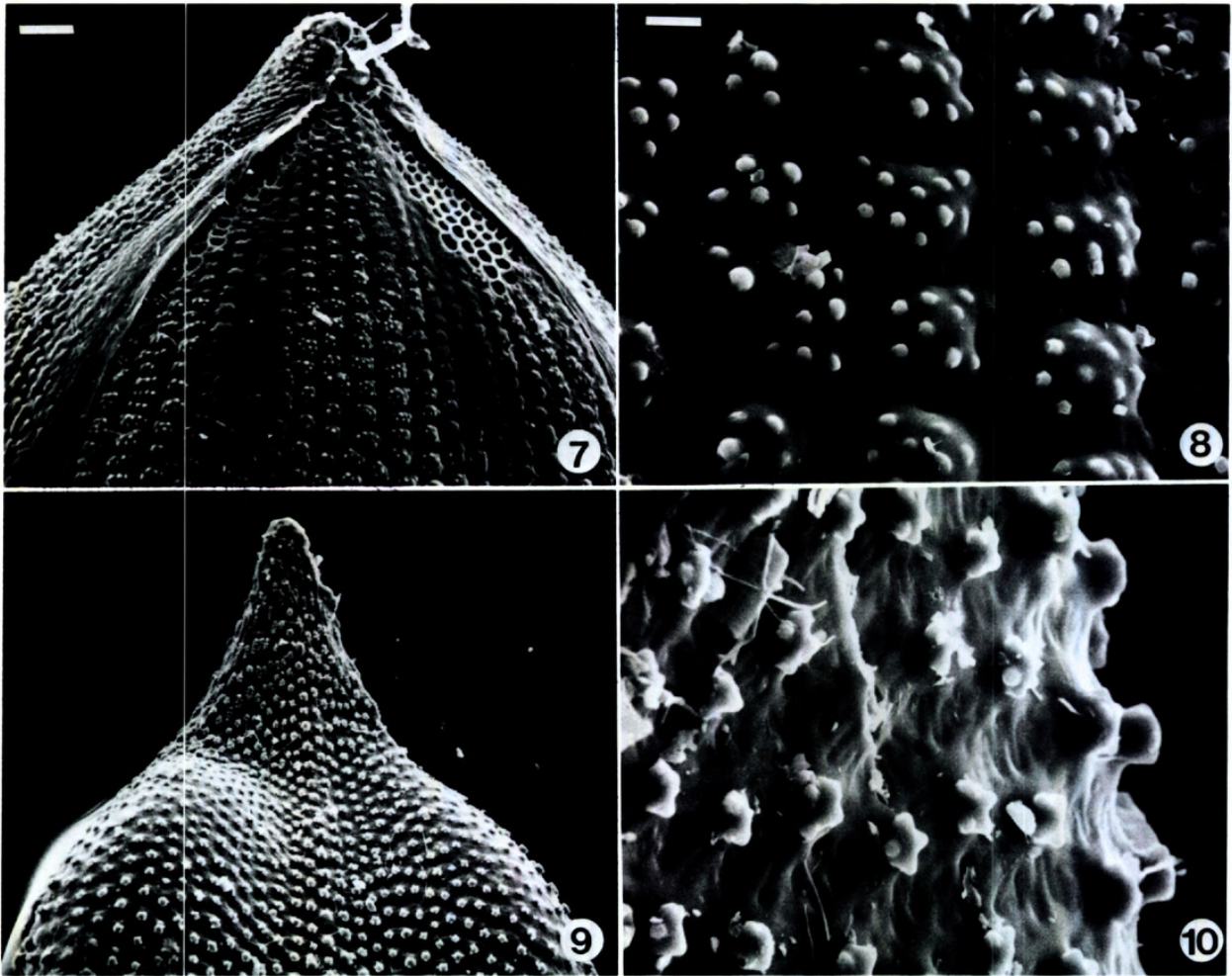
the latter has leaf blades that are not nyctinastic and female spikelets with indurate, strongly clasping glumes that become black at maturity.

TAXONOMIC TREATMENT

Asterisks (*) indicate vouchers used in this study.

Raddiella Swallen in Maguire et al., Bull. Torrey Bot. Club 75: 89. 1948. TYPE: *Raddiella nana* (Doell) Swallen [= *R. esenbeckii* (Steudel) Calderón & Soderstrom], Smithsonian Contr. Bot. 44: 21. 1980.

Plants small, monoecious, either tufted perennials or delicate annuals, often forming low mats.



FIGURES 7–10. Scanning electron micrographs of female florets of species of *Raddiella*.—7, 8. *R. potaroensis* (Maguire & Fanshawe 32277).—9, 10. *R. lunata* (Rondon s.n.). Scale bar 50 μm for 7, 9; 10 μm for 8, 10.

Leaves small, pseudopetiolate; blades elliptical to ovate-triangular, often strongly asymmetrical and with an apiculate apex, exhibiting sleep movements or not. Inflorescences small, few-flowered, 1–several from both terminal and axillary nodes, barely exerted from the leaf sheaths, 2–6(–12) spikelets per inflorescence. Terminal inflorescences male and female or more commonly strictly male, rarely strictly female; axillary inflorescences either all female or with female and male spikelets; female spikelets minutely cupulate at apices. Spikelets 1-flowered, the broad female spikelets shorter than to as long as the narrow male spikelets. Female spikelets falling entire from pedicels or in one species the glumes persistent and the floret falling, ovate-lanceolate; glumes subequal, membranous, as long as the spikelet, acute, 3–5-nerved, the lateral nerves often obscure; floret elliptical to ovoid, acute, glabrous, thinly coriaceous, stramineous or becoming dark when mature, the margins of the lemma inrolled over the edges of the palea; style 1, stigmas 2. Caryopsis ovoid to globose, brownish tan; embryo small, basal; hilum punctiform or short-

linear. Male spikelets borne on filiform pedicels, hyaline, glabrous, early deciduous, linear to lanceolate; glumes absent; lemma 3-nerved; palea 2-nerved; stamens 3.

Distribution and ecology. Seven species ranging from Panama and Trinidad to Bolivia and Brazil (to São Paulo); savannas, forest margins, or among wet rocks near rivers and waterfalls, from near sea level to 1,500 m.

Raddiella has two centers of diversity: (1) the Guayana Highlands, with four species, two of them endemic (including the Colombian species *R. molliculma* at the far western edge of the Guayana Highlands formation); and (2) the western Brazilian Planalto from Rondônia to northern Mato Grosso and southern Pará, with five species including three endemics. More new species may be expected from both areas.

KEY TO THE SPECIES OF *RADDIELLA*

- 1a. Female florets smooth 2
- 2a. Leaf blades elliptical, \pm symmetrical, acute at both base and apex; female glumes de-

TABLE 1. Comparison of *Raddiella* with related genera.

	<i>Olyra</i>	<i>Parodiolyra</i> <i>lateralis</i>	<i>Parodiolyra</i> (2 species)	<i>Raddiella</i> <i>esenbeckii</i>	<i>Raddiella</i> (phreatophytic species)
Habit	Caespitose perennials	Caespitose to sprawling perennials	Sprawling perennials	Caespitose perennials	Sprawling annuals
Nyctinasty	—	—	—	+	—?
Leaf blade asymmetry	— (+)	+	—	+	—
Leaf blade texture	Firm	Firm	Firm	Firm	Delicate
Axillary inflorescences well developed	—	—, +	—, +	+	+
Inflorescence size	Large	Moderate	Moderate	Small	Small
Sexes in separate inflorescences	— (+)	—	—	+	+
Female spikelet pedicels clavate or filiform	c (f)	f	f	f	f
Female spikelet falling entire	— (+)	+	+	—	+
Female spikelet: thickened internode between glumes	—	+	+	+	+
Female floret texture	Variable	Smooth	Smooth, viscid	Smooth	Papillose or smooth
Hilum	Fully linear	Short-linear (1/2 to 3/4 length)	Short-linear (ca. 1/2 length)	Short-linear (ca. 1/2 length)	Punctiform
Chromosome <i>n</i> =	7, 10, 11, 20, 22	18	Unknown	10	Unknown

- ciduous along with the floret
..... 4. *R. malmeana*

2b. Leaf blades ovate-triangular, asymmetrical, the base truncate, the apex acute or apiculate; female glumes persistent, only the floret deciduous 3

3a. Female spikelets 1.9–2.7 mm long; male spikelets 3–5 mm long, (1–)2–4 per inflorescence; leaf blades 9–22 mm long, 4–11 mm wide; caryopsis with the hilum short-linear; wide-spread 1. *R. esenbeckii*

3b. Female spikelets 1–1.4 mm long; male spikelets ca. 1.3 mm long, 1 per inflorescence; leaf blades 4–6 mm long, 2.7–3.3 mm wide; caryopsis with the hilum punctiform; rare, Pará, Brazil 5. *R. minima*

1b. Female florets minutely papillose with simple or compound papillae all over surface 4

4a. Female florets lunate (crescent-shaped) in profile, dorsally compressed, abruptly beaked; female floret epidermis with a single compound papilla in the middle of each cell; rare, Rondônia, Brazil 3. *R. lunata*

4b. Female florets straight and lanceolate in profile, terete, not beaked; female floret
- epidermis without a compound papilla in the middle of each cell 5

5a. Inflorescences long-exserted, some peduncles at least 5 cm long; female florets with papillae along the cell margins; rare, Caquetá, Colombia 6. *R. molliculma*

5b. Inflorescences with bases included in leaf sheaths, or short-exserted on peduncles less than 1 cm long; female florets with 1–several papillae per cell; Venezuela, Guianas, Brazil 6

6a. Leaf blades with the lower surface hispid to strigose throughout; female spikelets 1.4–2 mm long; female floret epidermis with 1 simple papilla per cell; male spikelets 4–5.8 mm long 2. *R. kaieteurana*

6b. Leaf blades with the lower surface glabrous or with short, scabrid hairs only on the veins; female spikelets 1.3–2.3 mm long; female floret epidermis with 7–10 simple papillae per cell; male spikelets 2.7–4.2 mm long 7. *R. potaroensis*

1. ***Raddiella esenbeckii*** (Steudel) Calderón & Soderstrom, Smithsonian Contr. Bot. 44: 21. 1980. *Panicum esenbeckii* Steudel, Syn. Pl. Glumac. 1: 90. 1854; based on *Panicum laterale* var. β Nees, Agrost. Brasil. 213. 1829. Basis in part of *Olyra nana* Doell in C. Martius, Fl. Bras. 2(2): 329. 1877, nom. superfl. *Raddia nana* (Doell) Chase, Proc. Biol. Soc. Wash. 21: 185. 1908. *Raddiella nana* (Doell) Swallen, Bull. Torrey Bot. Club 75: 89. 1948. TYPE: Brazil. Amazonas: Rio Negro, Ega, *Martius s.n.* (holotype, M? not seen; the same specimen designated as a lectotype of *O. nana* M?, not seen). Figures 1, 2, 13A–D.

Densely tufted perennials, with up to 60 unbranched culms per clump. Culms sprawling, decumbent to geniculate, the erect portions 8–40 cm tall, wiry; internodes cylindrical, glabrous to sparsely pilose with short, retrorse hairs; nodes thickened, densely pilose with whitish retrorse hairs. Leaves in complements of 7–15, nyctinastic, the blades folding upwards at night or under water stress; sheaths striate, glabrous to short-pilose, densely so toward the summit, one margin membranous, the other short-ciliate, short-auricled, the auricle membranous on one side; ligules ca. 0.3 mm long, membranous, apically short-ciliate; pseudopetioles ca. 0.5 cm long, densely pilose; blades 9–22 mm long, 4–11 mm wide, ovate-triangular, asymmetrical, truncate at the base, acute and short-apiculate at the apex, flat, firmly membranous, either glabrous, or short-pilose near the base on the upper surface, to densely puberulent on both surfaces, the lower margins ciliate, the lower surface purplish in some specimens. Inflorescences terminal and axillary; terminal inflorescences 3–5, with male spikelets only, on cylindrical, glabrous peduncles 1–2 cm long, each inflorescence with (1–)2–4 male spikelets on short, glabrous pedicels; axillary inflorescences both female and male, the female inflorescences on short-pilose peduncles 5–8 mm long, each bearing 2 short-pedicelled female spikelets. Female spikelets 1.9–2.7 mm long, 0.7–0.9 mm wide, ovoid; glumes firmly membranous, greenish becoming blackish, sparsely to densely short-pilose with spreading hairs, 3-nerved, persistent, the internode between the glumes thickened, the lower glume acute, slightly shorter than the acuminate upper glume; floret 1.6–2 mm long, ellipsoid, coriaceous, smooth, shiny, glabrous, whitish becoming dark, deciduous. Caryopsis 1–1.2 mm long, 0.7–0.8 mm wide, long-ellipsoid, dorsally compressed; hilum short-linear, ca. $\frac{1}{3}$ the length of the caryopsis, extending from near the center to near the base; embryo ca. $\frac{1}{6}$ the length of the caryopsis.

Male spikelets borne on minutely cupuliform pedicels, 3–5 mm long, ca. 1 mm wide, lanceolate, acuminate, greenish to purplish, hyaline, glabrous to sparsely hispid with short hairs; glumes occasionally present, to 3.7 mm long, linear-lanceolate, sparsely hispid; lemma as long as spikelet, lanceolate, acuminate, glabrous to sparsely hispid with short hairs; stamens with anthers 1.3–3 mm long.

Distribution and ecology. Panama and northern South America (including Trinidad) to Bolivia and central Brazil (Fig. 11); from 0 to 1,500 m in semishaded or more often dryish, open places: gallery forests, woodlands, savannas, and cerrados, often on rocky or sandy soil.

Chromosome number. $n = 10$ (Davidse & Pohl, 1972).

Representative specimens examined. PANAMA. PANAMA: 7 mi. N of Cerro Azul, 2,600 ft., 13 Nov. 1965, *Blum et al. 1789* (MO); Cerro Campana, 900 m, 21 Jan. 1984, *van der Werff & Herrera 6156* (MO); hills NE of Hacienda La Joya, 50–300 m, 9 Dec. 1934, *Dodge et al. 16882* (MO). HERRERA: N slope of Cerro Alto Higo, 2,400 ft., 5 Aug. 1978, *Hammel 4202* (MO). COLOMBIA. AMAZONAS: Bella Vista, Río Igará–Paraná, 8 Sep. 1973, *Sastre 2152* (US). META: La Macarena, Río Guayabero, Sabanas de Arenisca, Jan.–Mar. 1959, *García-Barriga & Jaramillo 17089* (US). VAUPÈS: Río Guainía, Caño del Caribe, between Isla del Venado and San José, 2°45'N, 67°50'W, 2 Nov. 1952, *Schultes et al. 18262* (US); Río Guainía basin, Río Naquieni, vicinity of Cerro Monachí, June 1948, *Schultes & López 10115* (US); Río Kananari, Cerro Isibukuri, 28 Oct. 1951, *Schultes & Cabrera 14452* (US). VENEZUELA. AMAZONAS: Piedra Araucaua, Río Yatua, 27 Sep. 1957, *Maguire et al. 41608* (US), 15 July 1959, *Wurdack & Adderley 43457* (US); Río Cunucunuma, occasional on moss-covered boulders, upriver from Playa Alto, 14 Nov. 1950, *Maguire et al. 29500* (US); banks of Río Cuao, above Cuao Creek, 25 Nov. 1948, *Maguire & Politi 27376* (US); Río Atacavi, ca. 1 km above the confluence with Río Atabapo, 6–19 July 1969, *Bunting et al. 3658* (US); Cerro Guida, Río Cunucunuma, Culebra Creek, 1,500–1,600 m, 21 Nov. 1950, *Maguire et al. 29629* (US). ANZOÁTEGUI: Fila El Purgatorio, S of El Zamuro, 10°02'N, 64°17'W, 1,100 m, 24 Nov. 1981, *Davidse & González 19335* (MO). BOLÍVAR: cercanías del campamento en el lado sur del Río Ichún, tributario del Río Paragua, debajo del Salto María Espuma, 4°46'N, 63°18'W, 30 Dec. 1961, *Steyermark 90470* (US); Dist. Heres, San Salvador de Paúl, 6°02'N, 62°53'W, 2 Dec. 1982, *Davidse & Huber 23128* (US). SUCRE: 8 km S de Santa Fé, 10°16'N, 64°24'W, 230 m, *Davidse & González 19069* (MO, US); carretera Guantá–Los Altos, *Tamayo 2146* (US). TÁCHIRA: Dist. Uribante, Siberia to Pregonero, 8°55'N, 71°40'W, 1,300 m, 11 July 1983, *van der Werff & González 5365* (MO). TRINIDAD. Aripo Savanna along the Cumuto road, 3 Nov. 1929, *Broadway 7685* (MO), 5 Aug. 1970, *Davidse 2550* (MO, US). GUYANA. Kaieteur savanna, 5 Sep. 1937, *Sandwith 1375* (US), 11 Feb. 1962, *Cowan & Soderstrom 1807* (US); Waranama ranch, *Harrison & Persaud 1069* (BRG, K); Lama Dam, *Jenman 5971* (BRG).



FIGURE 11. Distribution of *Raddiella esenbeckii*.

SURINAM. Brinckhill Nature Reserve, 14 Dec. 1967, *Wildschut & Teunissen 11346* (US); Moengo tapoe ad Grote Zwiebelzwamp, *Lanjouw & Lindeman 872* (NY, U); Sipaliwini savanna, *Oldenburger et al. 141* (U). FRENCH GUIANA. Passoura, 3 Apr. 1958, *Hook 942* (CAY); Savane des Singes, 5°05'N, 52°42'W, *Cremers & Hoff 10680* (CAY, US). BRAZIL. AMAPÁ: Matapi, *Pires & Silva 4797* (US); Igarapé do Paia, km 110 on road to Amapá, 20 July 1962, *Pires & Cavalcante 52233* (MO, NY, US). AMAZONAS: 3 km E of Borba near the Rio Madeira, 4°23'S, 59°35'W, 22 June 1983, *Hill 12753* (F, MO, US); Rio Jauri, affluent of Rio Aracá, 0°49'N, 63°20'W, July 1985, *Huber et al. 10710* (MO); Rio Urubú, Serra da Lua, 6 June 1968, *Prance et al. 5005* (MO); Manaus, Rio Cuieiras, Igarapé Cachoeira, 19 Dec. 1961, *Rodrigues & Wilson 3191* (US); km 38 on road from

Humaitá to Pôrto Velho, 6 May 1982, *Teixeira et al. 260* (MO). BAHIA: Serra do Sincorá, 16 km N of Barra da Estiva on the Paraguaçu road, 13°20'S, 41°20'W, 31 Jan. 1974, *Harley et al. 15746* (US); 2–5 km N of Lençóis, 11 June 1981, *Mori & Boom 14339* (MO). DISTRITO FEDERAL: Bacia do Rio Bartolomeu, 5 May 1980, *Heringer et al. 4626* (US); Chapada da Contagem, Parque Municipal do Gama, ca. 25 km W of Brasília, 1,100 m, 3 Feb. 1968, *Irwin et al. 19474* (US); 700–1,000 m, 31 Aug. 1964, *Irwin & Soderstrom 5801* (US). GOIÁS: ca. 10 km S of Alto do Paraíso, 22 Mar. 1969, *Irwin et al. 24921* (MO, US); S Serra Dourada, gallery forest 20 km E of Formosa, 13°45'S, 48°50'W, 18 May 1956, *Dawson 14956* (US); vicinity of Goiabeira, between Anápolis and Goiás, 23 Mar. 1930, *Chase 11510* (MO, US); ca. 3 km E of Alto Paraíso on road to Nova Roma, 7

Mar. 1973, *Anderson 6604* (MO, US). MARANHÃO: Pedra Caida, 35 km N of Carolina, 7°08'S, 47°25'W, 14 Apr. 1983, *Taylor et al. E-1240* (US). MATO GROSSO: ca. 5 km N of Barra do Garças, S face of mountain, 7 May 1973, *Anderson 9885* (US); km 762, Santarém-Cuiabá road, 9°35'S, 54°55'W, *Amaral et al. 806* (F, MO). MINAS GERAIS: Vaccaria, Serra do Cipó, Apr. 1925, *Chase 9257* (MO, US); Metallurgica, Serra de Ouro Branco, 23 Dec. 1929, *Chase 10290* (MO, US); Rio Jequití, ca. 25 km E of Diamantina, 790 m, 21 Mar. 1970, *Irwin et al. 27993* (MO, US); Serra do Espinhaço, 3.5 km by road SW of Rio Jequití and Mendanha, 14 Apr. 1973, *Anderson 8922* (US). PARÁ: 7 km SE of Vigia, 0°55'S, 48°04'W, 31 Mar. 1980, *Davidse et al. 17689* (MO); Rio Aruá, *Black 49-844* (US). RONDÔNIA: Abunã, Rio Madeira, 11 July 1968, *Prance et al. 5887* (MO); Pôrto Velho, caminho para o km 8, 26 May 1952, *Black & Cordeiro 52-14526* (US). SÃO PAULO: São José dos Campos, 16 Dec. 1909, *Löfgren 4680* (US). BOLÍVIA. BENI: Prov. Vaca Díez, 15 km W de Guayamerim, camino a Riberalta, en campos con rocas aflorantes, 17 Apr. 1979, *Krapovickas & Schinini 35062* (US).

This species is variable in stature. Alone among members of the genus, the leaf blades exhibit sleep movements, folding upwards at night or under water stress.

The superficially similar *Parodiolyra lateralis* differs in its sprawling habit, larger, more rigid blades lacking sleep movements, and larger, more open mixed panicles with mature female spikelets with blackish, indurate, 3–7-nerved glumes that strongly invest the floret.

2. *Raddiella kaieteurana* Soderstrom, Mem. New York Bot. Gard. 12(3): 6. 1965. TYPE. Guyana: Kaieteur Plateau, on moist cliff faces along trail from Kaieteur Plateau to Tukeit, 1,100 ft., 4 Feb. 1962, *R.S. Cowan & T.R. Soderstrom 1742*. (holotype, US*; isotypes, GH, K, NY, P). Figures 3, 4, 13E–G.

Delicate mat-forming herbs of indefinite duration. Culms weak, decumbent, rooting and branching at the lower nodes, the flowering portion 5(–20) cm long, many-noded; internodes compressed, glabrous. Leaves with the sheaths striate, longer than the internodes, greenish to purplish, with long hairs near the apex, otherwise sparsely pilose to glabrescent; ligules membranous, 0.3–0.5 mm long; pseudopetioles 0.5 mm long, hirtellous; blades 8–17 mm long, 3–8 mm wide, flat, delicately membranous, densely hispid to strigose on both surfaces with long and short hairs, the base slightly asymmetrical, obtuse, and subcordate, the apex acute and slightly apiculate, the margins ciliate throughout or only toward the base of the blade. Inflorescences terminal and axillary from the upper nodes, with bases included in leaf sheaths or short-exserted on peduncles less than 1 cm long; terminal inflo-

rescences 2–6, mostly male, each bearing 1–2 spikelets, or occasionally female spikelets present; axillary inflorescences female, exserted up to 3 mm on filiform peduncles and bearing 1–3 female spikelets on divergent pedicels 1.5–5 mm long. Female spikelets 1.4–2 mm long, 0.6–0.8 mm wide, ellipsoid, falling entire; glumes ovate-elliptical, acuminate, subequal, prominently nerved, sparsely short-pilose with spreading hairs to uncommonly glabrous, greenish, the lower glume 3-nerved, separated from the 3–5-nerved upper glume by a short internode; floret 0.8–1.7 mm long, 0.5–0.6 mm wide, narrowly ellipsoid, dorsally compressed, minutely papillose, whitish becoming brownish at maturity; lemma evidently 3–5-nerved. Caryopsis 0.6–0.8 mm long, 0.4–0.7 mm wide, broadly ellipsoid; hilum oblong, placed in the middle of the caryopsis and extending slightly toward the base; embryo $\frac{1}{4}$ or less the length of the caryopsis. Male spikelets borne on pedicels 0.5–2.3 mm long, 4–5.8 mm long, 0.6–0.8 mm wide, fusiform, hyaline, sparsely short-pilose toward the apex; glumes occasionally present, to 4 mm long, linear-lanceolate; lemma 3–5-nerved; stamens with anthers 2–2.8 mm long.

Distribution and ecology. Venezuela (Bolívar), Guyana, Surinam, and northern Brazil (Pará); on damp cliff faces or in the spray of waterfalls, from 100 to 810 m (Fig. 12).

Additional specimens examined. VENEZUELA. BOLÍVAR: Dist. Piar, Amaruay-tepui, S side about 1 km from SW corner of tepui, 5°54'N, 62°15'W, 550–810 m, 26 Apr. 1986, *Liesner & Holst 20369* (MO). GUYANA: semishaded rock face in forest along trail from Kaieteur Falls to Tukeit, about 1 km E of the airstrip, 300 m, *Cowan & Soderstrom 2027* (K, NY, US); 29 Apr. 1944, *Maguire & Fanshawe 23087* (MO, NA, NY, US*); 24 Feb. 1962, *Cowan & Soderstrom 1918* (US); Apr. 1988, *Hahn et al. 4163* (BRG, US); anno 1881, *Jenman 1277* (US). SURINAM: Tafelberg, base of N escarpment, under drips, 390 m, 11 Aug. 1944, *Maguire 24327* (MO, NA, NY, U); NW side, *Geyskes 998* (U). BRAZIL. PARÁ: Rio Cururú (affluent of Rio Tapajos), Cachoeira Kereputiá, in a hole on sandstone rocks, 3 Mar. 1960, *Egler 1244* (US*).

As presently conceived, this species is variable. In *Egler 1244* the female spikelets are only 0.9–1 mm long and the glumes are covered with short hairs, but scanning electron micrographs revealed that female floret texture is similar to that of typical *R. kaieteurana*. An unusual feature of *Cowan & Soderstrom 1918* is the presence of terminal female inflorescences with two spikelets. *Liesner & Holst 20369* differs from typical *R. kaieteurana* in its short-pilose to glabrous leaf blades and completely glabrous female glumes.

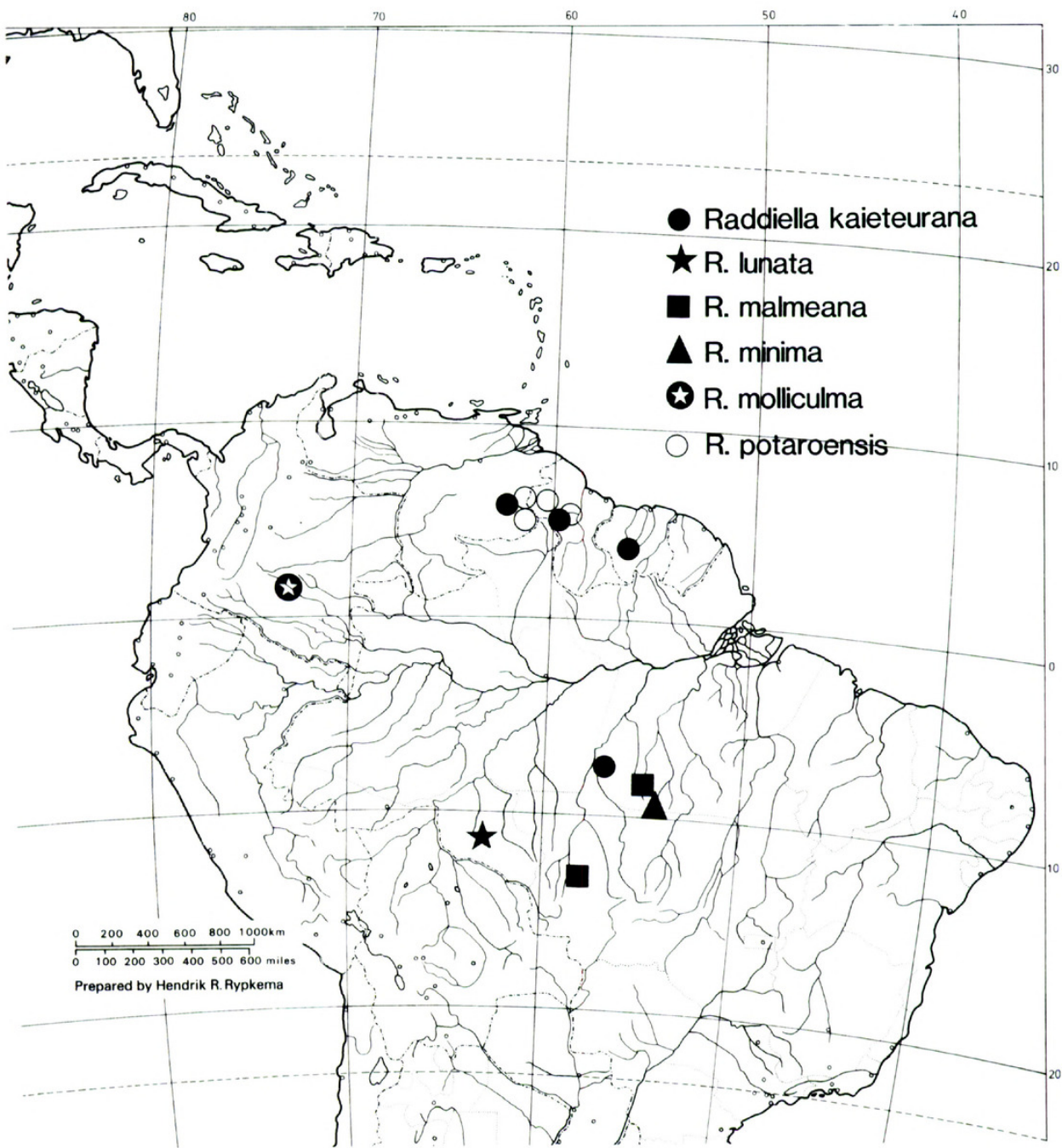


FIGURE 12. Distribution of *Raddiella kaieteurana*, *R. lunata*, *R. malmeana*, *R. minima*, *R. molliculma*, and *R. potaroensis*.

3. *Raddiella lunata* Zuloaga & Judziewicz, sp. nov. TYPE. Brazil. Rondônia: Serra dos Pacáas Novos, Cab. do Cautário, planta umbrophila, na entrada das lapas, firmas, predas, etc., Mar. 1917, *C. Rondón s.n.* [as *J.G. Kuhlmann 1863*] (holotype, RB; isotypes, K, MO, NY, SI, SP, US*). Figures 9, 10, 14.

Ab omnibus conspecificis differt: spicula, flosculo et caryopside lunatis abrupte rostratis, necnon flosculo papilla composita in medio cuiusque cellulae praedito.

Delicate, sprawling, mat-forming annuals. Culms decumbent, rooting and branching at the lower nodes, the erect portions 7–15 cm tall, many-noded, unbranched; internodes cylindrical, hollow, glabrous; nodes thickened, with short, retrorse, whitish hairs. Leaves with the sheaths striate, glabrous, slightly inflated, the margins membranous, the auricles membranous, glabrous, the summit truncate; ligules not noted; pseudopetioles ca. 0.1 mm long, brownish, short-pilose; blades 10–15 mm long, 2.5–3.5 mm wide, lanceolate, delicately

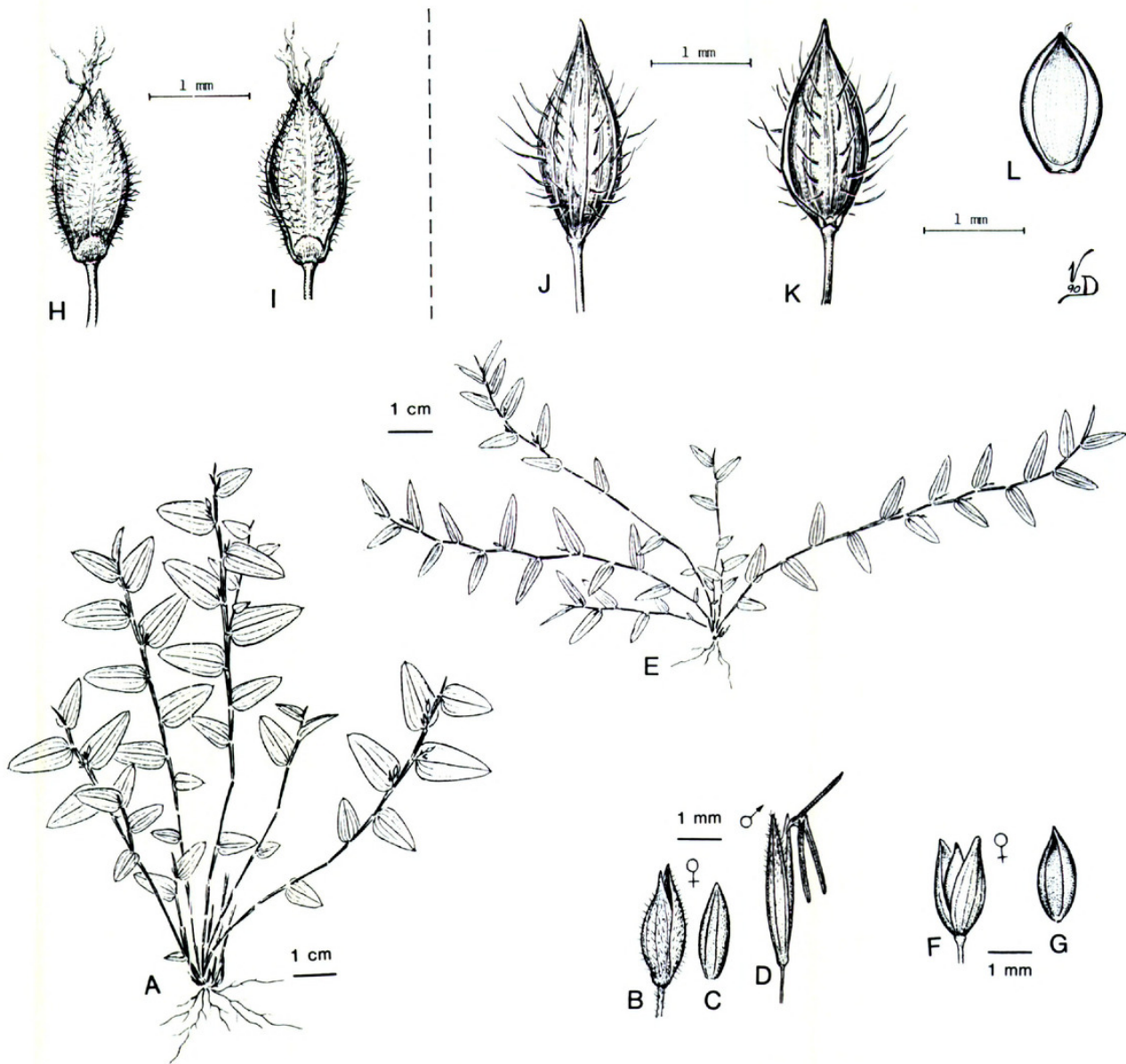


FIGURE 13. A–D. *Raddiella esenbeckii* (Huber 2126).—A. Habit.—B. Female spikelet.—C. Female floret.—D. Male spikelet. E–G. *Raddiella kaieteurana* (Liesner 20414).—E. Habit.—F. Female spikelet.—G. Female floret. H, I. *Raddiella molliculma* (Grassl 10024).—H. Female spikelet, dorsal view.—I. Female spikelet, ventral view. J–L. *Raddiella potaroensis* (Cowan & Soderstrom 2162).—J. Female spikelet, dorsal view.—K. Female spikelet, ventral view.—L. Female floret.

membranous, glabrous to sparingly short-pilose on both surfaces (especially on the veins below), the base slightly asymmetrical, acute at the apex, the margins scabrous. Inflorescences both terminal and axillary, with 1–several inflorescences produced at each node, short-exserted on glabrous, filiform peduncles up to 10 mm long; individual inflorescence a contracted, racemelike panicle 5–10 mm long, the rachis slightly sinuous, glabrous, alternately bearing 2–12 spikelets on short pedicels 0.5–1.5 mm long, or occasionally with a lower branch up to 3 mm long bearing 2 spikelets; terminal spikelet female, the lateral ones male or occasionally a few females. Female spikelets ca. 1 mm long, obovoid,

lunate in profile, falling entire; glumes delicately membranous, short-hispid, 3-nerved, the lower glume not covering the apex of the floret, the upper glume as long as the floret, flat; floret 0.8–1 mm long, 0.5–0.6 mm wide, obovoid, dorsally compressed, concave on the ventral side, convex on the dorsal side, acute at the base, rather abruptly beaked at the apex, coriaceous, whitish becoming brown at maturity, strongly papillate; lemma conspicuously grooved on the dorsal surface, slightly winged, the margins covering the edges of the palea with wide margins. Caryopsis 0.6–0.8 mm long, 0.5–0.6 mm wide, ovoid, lunate, of the same general morphology as the floret, slightly winged; hilum

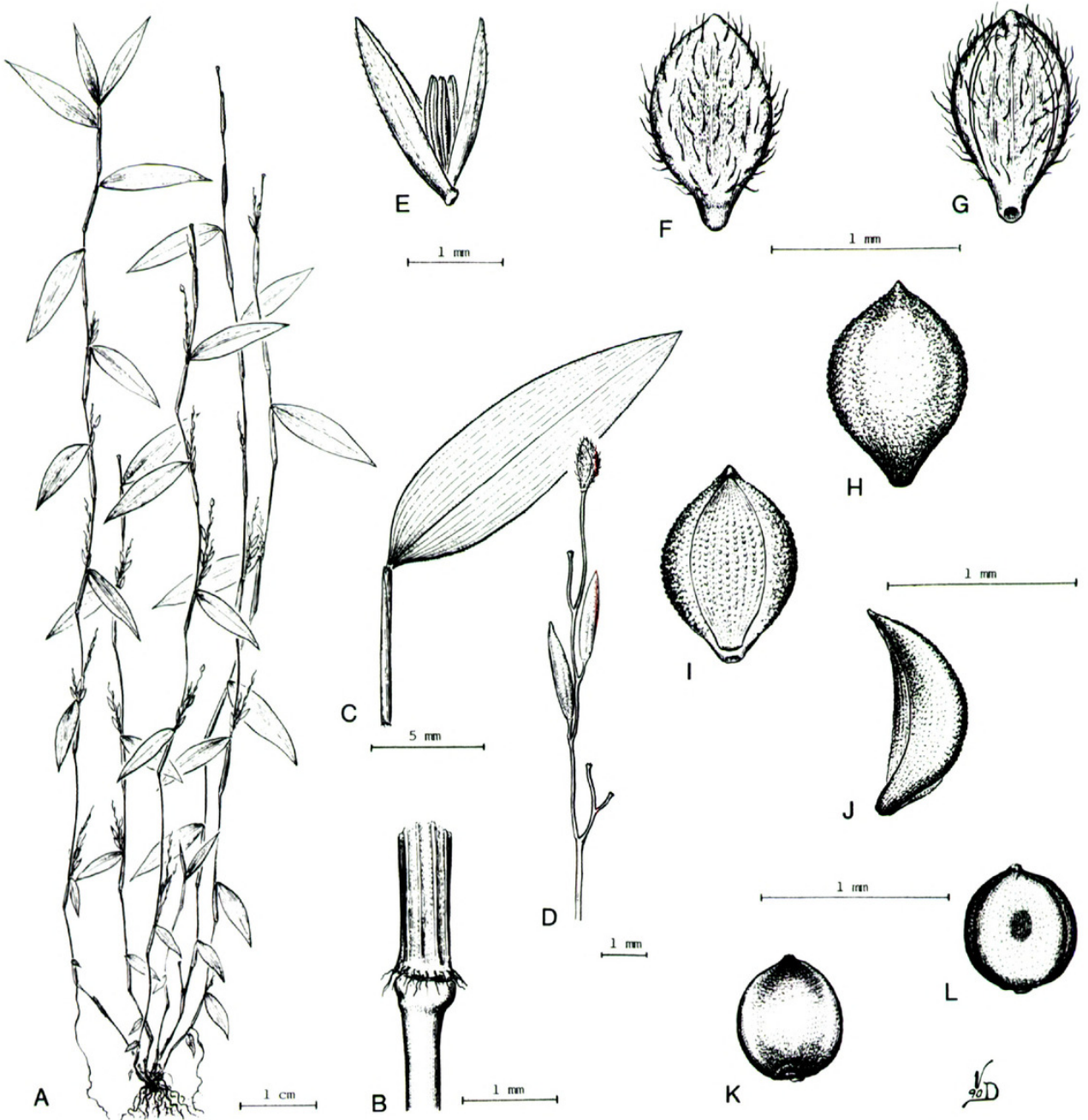


FIGURE 14. *Raddiella lunata* (Rondon s.n.).—A. Habit.—B. Detail of a node.—C. Leaf.—D. Inflorescence.—E. Male spikelet. F–J. Female spikelet.—F. Lower glume.—G. Upper glume. H–J. Floret.—H. Dorsal view.—I. Ventral view.—J. Lateral view. K, L. Caryopsis.—K. Dorsal view.—L. Ventral view.

rounded at the middle portion of the caryopsis; embryo $\frac{1}{2}$ the length of the caryopsis. Male spikelets 1.7–2.7 mm long, lanceolate-elliptical, acute, hyaline, glabrous; lemma 3-nerved; stamen with anthers 1–1.5 mm long.

Distribution and ecology. Known only from the type collection made in the Serra dos Pacáas Novos in Rondônia, Brazil (Fig. 12).

This species differs from all other congeners in its lunate (crescent-shaped, hence the specific epithet) female floret that tapers rather abruptly to both ends, and the surface of the floret, which has

a single compound papilla on each cell. The form of the female spikelets could be associated with dispersion by water.

In the mature plants at hand, the culms disarticulate readily at the nodes. Whether this represents an adaptation for dispersal or is merely indicative of senescence is unclear.

4. *Raddiella malmeana* (E. Ekman) Swallen, Bull. Torrey Bot. Club 75: 89. 1948. *Olyra malmeana* E. Ekman, Ark. Bot. 10(17): 21. 1911. *Raddia malmeana* (E. Ekman) A.

Hitchc., Contr. U.S. Natl. Herb. 22: 505. 1922. TYPE. Brazil. Mato Grosso: Santa Ana da Chapada, Buriti, in pruruptis rupis ad cataractam junta cum Sphagni, 16 June 1894, Malme (*Regnell Expedition I*) 1684 (holotype, S n.v.; isotype, US*).

Annuals. Culms decumbent and rooting at the lower nodes, the erect portions to 20 cm tall (according to original description), many-noded, unbranched; internodes glabrous. Leaves with the sheaths longer than the internodes, striate, glabrous, the margins membranous, the auricles membranous; ligules ca. 0.3 mm long, membranous; pseudopetioles ca. 0.5 mm long, narrow, brownish, glabrous; blades 5–10 mm long, 2–4 mm wide, elliptical, delicately membranous, flat, sparingly short-pilose on both surfaces or with scabrid hairs on the veins only on the lower surface, \pm symmetrical, acute at both base and apex, the margins scaberulous. Inflorescences terminal and axillary from the uppermost nodes, partially included in the sheaths; terminal inflorescences bearing male spikelets only; axillary inflorescences bearing female spikelets, congested, few-flowered, the axis and pedicels smooth, glabrous, to 2 mm long. Female spikelets 1.8–2.1 mm long, 0.5–0.6 mm wide, narrowly ovoid, falling entire; glumes acuminate, short-hispid with long, thickened hairs mainly on the nerves, the lower glume 3-nerved, the upper glume 3–5-nerved; floret ca. 1.5 mm long, narrowly ovoid (but none fully mature), whitish, smooth, shiny. Caryopsis not seen. Male spikelets 1.7–2 mm long, ca. 0.4 mm wide, lanceolate, hyaline, glabrous, shiny; lemma 3-nerved; stamens with anthers ca. 1 mm long.

Distribution and ecology. Endemic to wet rocks near streams at low elevations in Mato Grosso and Pará, Brazil (Fig. 12).

Additional specimens examined. BRAZIL. MATO GROSSO: Utiarity, Rio Papagaio, margin of waterfall, May 1918, Kuhlmann 1866 (US). PARÁ: estrada Santarém–Cuiabá, 877 km de Cuiabá, vale de solo pedregoso, embaixo da Cachoeira da Luz do Rio Curuá, 8°45'S, 54°57'W, 350 m, 2 May 1983, Silva 196 (MO).

This species is related to *R. potaroensis* and *R. kaieteurana*, but differs in its smooth female florets, and in female and male spikelets of similar size.

5. *Raddiella minima* Judziewicz & Zuloaga, sp. nov. TYPE. Brazil. Pará: Município de Itaituba, km 771 estrada Santarém–Cuiabá,

próximo a divisão Pará–Mato Grosso, mata de cerrado solo pedregoso, vegetação rupestre, 9°35'S, 54°35'W, 22 Apr. 1983, I.L. Amaral, N. Silva, O.P. Monteiro, J. Lima, L. Brako, W.D. Reese & M. Dibben 883 (holotype, INPA; isotypes, MO, NY).

A *Raddiella esenbeckii* differt lamina minore (4–6 \times 2.7–3.3 mm) et spiculis mascula et femina minoribus (1–1.3 mm longis), caryopside hilo punctiformi centrali praedita.

Tiny, straggling herbs of indefinite duration. Culms to 6 cm long, filiform, geniculate, multi-branched, internodes purple, glabrous; nodes with a few very short retrorse hairs. Leaves in loose complements of 3–5; sheaths shorter than the internodes, usually shorter than the blades, glabrous to short-pilose, 5-nerved, slightly inflated, the upper margins ciliate, abruptly truncate at the short-ciliate summit; ligule membranous, ca. 0.2 mm long; pseudopetiole 0.1–0.2 mm long, glabrous to short-pilose; blades 4–6 mm long, 2.7–3.3 mm wide, ovate-triangular, asymmetrical, glabrous, the base truncate, the apex acute and apiculate, the margins scaberulous, the abaxial surface occasionally purplish. Inflorescences terminal and axillary, terminal inflorescences 2–6, ca. 10 mm long, filiform, each terminated by a single male spikelet; axillary inflorescences 1 per each axil, ca. 3 mm long, partly included in the leaf sheath, each of 2(–3) female spikelets on short, filiform pedicels. Female spikelets 1–1.4 mm long; glumes lanceolate-ovate, acuminate, 3-nerved, glabrous to short-hispid, persistent; floret 0.9–1.2 mm long, ovoid, acute, dorsally compressed, smooth, shiny, white becoming dark, deciduous; lemma 3-nerved. Caryopsis 0.7 mm long, 0.6 mm wide, ovoid-globose; hilum punctiform, central; embryo small, basal. Male spikelets ca. 1.3 mm long, the lemma soon deciduous, elliptical, hyaline, glabrous; anthers ca. 0.6 mm long.

Distribution and ecology. Known only from the type collection, made in campo rupestre near the borders of the states of Mato Grosso and Pará, Brazil (Fig. 12).

Raddiella minima is related to *R. esenbeckii*, but differs in its conspicuously smaller leaf blades and male and female spikelets; caryopsis with punctiform, central hilum; and solitary male spikelet per inflorescence. It is not certain whether the leaves exhibit sleep movements as in *R. esenbeckii*.

Along with the Cuban endemic *Mniochloa pulchella* (Griseb.) Chase, this species is one of the world's smallest bambusoid grasses, hence its specific epithet.

6. **Raddiella molliculma** (Swallen) Calderón & Soderstrom, Smithsonian Contr. Bot. 44: 22. 1980. *Panicum molliculmum* Swallen in R. Schultes, Bot. Mus. Leaflet 16: 57. 1953. TYPE: Colombia. Caquetá (as "Vaupés"): Cerro de El Castillo, Río Apaporis, moist, shaded sandstone ledge with mosses and *Selaginella* spp., 16 Jan. 1942, *Gutiérrez & Schultes 616* (holotype, US*; isotype, COL). Figures 5, 6, 13H, I.

Delicate annuals. Culms decumbent, sprawling, geniculate, the erect portions 5–10 cm tall, many-noded, unbranched; internodes glabrous; nodes compressed, short-pilose with retrorse hairs. Leaves puberulent throughout with spreading, short-pilose hairs; sheaths striate, shorter than the internodes, the upper margins short-ciliate, the summit pilose; ligules membranous-ciliate; pseudopetioles ca. 0.6 mm long, brownish, short-pilose; blades 7–12 mm long, 3–4.5 mm wide, ovate-lanceolate, flat, delicately membranous, slightly asymmetrical, the base truncate, the apex acuminate, the margins scaberrulous. Inflorescences terminal and axillary, abundantly produced from the uppermost nodes (6–15 from the terminal node), long-exserted on glabrous, filiform peduncles 5 cm long; individual inflorescences 2–5 mm long, few-flowered, with 1–2 terminal, short-pedicelled male spikelets and 1–2 subterminal female spikelets or occasionally with 1 or more male spikelets below; pedicels up to 1 mm long, glabrous. Female spikelets 1.3–1.5 mm long, 0.6–0.7 mm wide, narrowly ellipsoid, falling entire at maturity; glumes lanceolate-ovate, acuminate, subequal, greenish, short-hirsute, 3-nerved, the lateral nerves inconspicuous; floret ca. 1.3 mm long, 0.6–0.7 mm wide, ellipsoid, whitish, shiny, papillose. Caryopsis 0.8 mm long, 0.6 mm wide, ellipsoid, brownish; hilum oblong in the middle portion of the caryopsis; embryo small, basal. Male spikelets 1.3–2.2 mm long, 0.5–0.6 mm wide, narrowly elliptical, acuminate, hyaline, short-hispid; lemma 3-nerved; stamens with anthers 0.9–1.3 mm long, purple.

Distribution and ecology. Restricted to the Cerro de El Castillo in Caquetá, Colombia (Fig. 12), at elevations of 240–300 m on moist, shaded, sandstone cliffs.

Additional specimens examined. COLOMBIA. CAQUETÁ: Upper Río Apaporis basin, Cerro de El Castillo, 27 July 1943, *Schultes 5668a* (US), *Grassl 10024* (US).

7. **Raddiella potaroensis** Soderstrom, Mem. New York Bot. Gard. 12(3): 6. 1965. TYPE.

Guyana. Kaieteur Plateau, bottom of Potaro Gorge near Kaieteur Falls to W rim of splash-basin of Falls, 700 ft., 13 Mar. 1962, *R. S. Cowan & T. R. Soderstrom 2162* (holotype, US*; isotypes, K, NY). Figures 7, 8, 13J–L.

Raddiella maipuriensis Soderstrom, Mem. New York Bot. Gard. 12(3): 7. 1965. TYPE: Guyana. Imbaimadai Savannas, Upper Mazaruni River, abundant in spray of Maipuri Falls, Karaurieng River, 1,250 m, 25 Oct. 1951, *B. Maguire & D. B. Fanshawe 32277* (holotype, US*; isotypes, NY, U).

Annuals. Culms weak, decumbent, branching and rooting at the lower nodes, the flowering portions 5–20 cm tall; internodes cylindrical, glabrous; nodes thickened. Leaves with the sheaths longer than the internodes, striate, glabrous, the margins membranous, the apex somewhat truncate, one side of the summit forming an auricle; ligules 0.2–0.4 mm long, membranous; pseudopetioles ca. 0.5 mm long, glabrous; blades 9–17 mm long, 3–7 mm wide, elliptical, flat, glabrous or with short, scabrid hairs only on the veins, slightly acute and asymmetrical at both ends. Inflorescences mainly axillary (one terminal inflorescence in the type of *R. maipuriensis*), 2–4 produced from each node, with the bases included in the leaf sheaths or short-exserted on peduncles less than 1 cm long, 2–3 spikelets per inflorescence, either all female or the terminal female and 1–2 male spikelets below; pedicels of male and female spikelets 1–3 mm long, filiform, glabrous. Female spikelets 1.3–2.3 mm long, ellipsoid to ovoid; glumes subequal, acute to acuminate, sparsely hispid with spreading, straggling hairs, weakly to strongly 3–5(–7)-nerved; floret 1–1.3 mm long, 0.7–0.8 mm wide, ellipsoid, acute, firmly coriaceous, shiny, whitish becoming olivaceous at maturity, papillose; lemma 3-nerved. Caryopsis ca. 0.9 mm long, 0.7 mm wide, slightly obovoid; hilum punctiform in the middle portion of the caryopsis; embryo ca. ¼ the length of the caryopsis. Male spikelets 2.7–4.2 mm long, 0.6–0.7 mm wide, lanceolate, glabrous; lemma 3-nerved; stamens with anthers 1.7–2 mm long.

Distribution and ecology. Apparently endemic to the Pakaraima Plateau of western Guyana and adjacent Bolívar, Venezuela (two sterile collections); on wet rocks near and in the spray zone of waterfalls, from 200–1,250 m (Fig. 12).

Additional specimens examined. VENEZUELA. BOLÍVAR: Sierra de Lema, in tufts at base of uppermost waterfall of headwaters of Río Chicanán at base of high sandstone NE-facing bluffs, headwaters of Río Chicanán, 80 km SW of El Dorado, *Steyermark 89568* (US); La

Gran Sabana, S of El Dorado along road to Santa Elena, ca. km 202, Salto Camá, 1,000 m, *Davidse* 4872 (MO). GUYANA. Kaieteur Falls, spray zone below falls, Apr. 1988, *Hahn et al.* 4635 (BRG, US).

Judziewicz (1991) did not find enough differences between *R. maipuriensis* and *R. potaroensis* to separate them as species and therefore placed the first name in the synonymy of the latter. It may be noted that the surfaces of the female florets of both taxa are identical under the scanning electron microscope. The type specimen of *R. maipuriensis* is larger than the rest of the material studied of this species, with culms ca. 20 cm tall, leaf blades 2 cm long and 0.7 cm wide, and female spikelets 1.8–2.3 mm long with acuminate, strongly nerved glumes. Two sterile Venezuelan collections, *Davidse et al.* 4872 and *Steyermark* 89568, are tentatively referred to this species based on their nearly glabrous leaf blades.

EXCLUDED SPECIES

Raddiella truncata Swallen, Bull. Torrey Bot. Club 75: 89. 1948 [= *Parodiolyra lateralis* (Nees) Soderstrom & Zuloaga].

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