

POA UNISPICULATA, A NEW GYNODIOECIOUS SPECIES OF CUSHION GRASS
FROM PERU WITH A SINGLE SPIKELET PER INFLORESCENCE
(POACEAE: POOIDEAE: POEAE: POINAE)

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ABSTRACT

A new Peruvian, high Andean, gynodioecious, cushion grass, *Poa unispiculata*, sp. nov. is described and illustrated. It is unique among all American species of *Poa* by having inflorescences composed of a single spikelet. It seems closely related to *P. perligulata* and differs by having a more compact habit, multiple equitantly distributed overlapping leaf sheaths with short distichous blades, presence of one spikelet per inflorescence, and gynodioecy with long anthers in bisexual plants.

RESUMEN

Se describe e ilustra una especie nueva para Perú altoandino, ginodioica *Poa unispiculata*, sp. nov., "pasto cojin," que forma densas matas en cojin. Es la única especie del género *Poa* en América, que presenta inflorescencias compuestas por una sola espiguilla. Parece estar estrechamente relacionada con *P. perligulata* de la cual difiere por el hábito más compacto con múltiples vainas foliares que se solapan y se hallan equitativamente dispuestas entre sí, con hojas dísticas, superpuestas, equidistantes, láminas cortas, por la presencia de una única espiguilla por inflorescencia, y por ser plantas ginodioicas, con anteras largas en las plantas perfectas.

A curious grass from Cerro de Pasco, Peru, has remained unidentified for many years. Renewed attempts to identify this little, puna cushion grass, have led us to the conclusion that it is a new species of *Poa* L. Two of the coauthors (RJS and PMP) traveled to Cerro de Pasco, Peru (the type locality) to obtain more material for study. It is unique among the American species of the genus because its inflorescences are reduced to a single spikelet.

Poa unispiculata Davidse, Soreng & P.M. Peterson, sp. nov. (**Figs. 1A–V; 2**). TYPE: PERU. PASCO: Cerro de Pasco, 4 km S on road to La Oroya, forming thick cushion on level ground, soil moist, elev. ca. 4400 m, 29 Jun 1977, J. Solomon 3334 (HOLOTYPE: MO (perfect plants); ISOTYPES: MO ♀ plants, SI, US ♀ plants, USM [not seen]).

A *Poa* L., species inflorescentiis unispiculis, apicis glumae retusis, apicis palearum profundis emarginis congeribus americanus diversa, recedit.

Plants herbaceous perennials, gynodioecious herbs forming low dense cushions to at least 19 cm in diameter and 1–1.5 cm thick; culms 1.5–4 cm long, decumbent, ascending, extensively branching intravaginally and rooting adventitiously from the lower nodes; prophylla prominent, about as long as adjacent sheaths, membranous, 2-keeled, glabrous but the keels densely covered with more or less erect prickle-hairs. **Leaves** strongly distichous, glabrous, 20–30 per culm (6–15 blades present at flowering, old blades disintegrating before the sheaths frequently with irregular fibers from their bases), crowded but more or less equitant along the culm, each at 1–2 mm above the next of the same rank; sheaths long persistent, smooth, glabrous, very pale, strongly 3-nerved at the base, 5-nerved near the apex but the marginal nerves notably less developed than the central and middle nerves; ligules to 1.5 mm long in lower leaves, graduated upwards to 3.1 mm long, prominent in the uppermost leaves, scarious-hyaline, smooth or sparsely scabrous below, glabrous, decurrent along the margins of upper sheaths, obtuse and prominent, and shallowly praemorse to acute with lateral dents flanking apex: blades, 3–8 mm long, 0.5–0.7 mm wide, divergent at nearly right angles at maturity, folded or open V-shaped in vivo, folded when dry, pale green, smooth, glabrous, 7–9-veined,

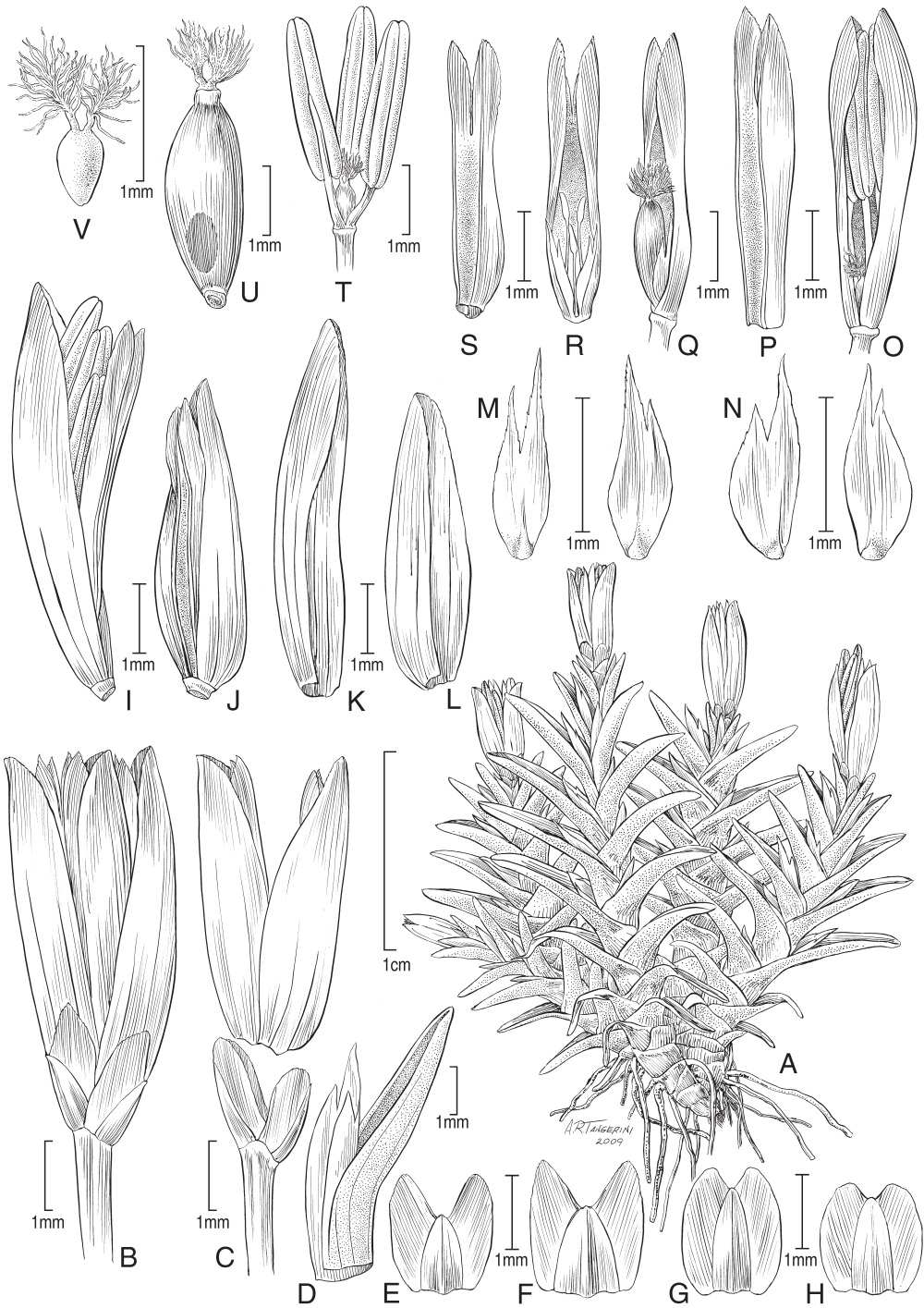


FIG. 1. Illustration of *Poa unispiculata* Davidse, Soreng & P.M. Peterson. A. Habit of bisexual plant (paratype, US). B. Bisexual inflorescence. C. Pistillate inflorescence (isotype, US). D. Ligule of paratype. E.–F. Lower and upper glumes of B. G.–H. Lower and upper glumes of C. I.–J. Florets of B & C. K. Lemma of B. L. Lemma of C. M.–N. Lodicules of B & C. O.–P. Pales dorsal and ventral views of B. Q.–S. Pales views of C. T. Flower of B. U. Caryopsis of C. V. Pistil of C.



FIG. 2. Habit of *Poa unispiculata* [P.M. Peterson, R.J. Soreng & K. Romaschenko 20382 (US)]. A bisexual individual in anthesis, *in vivo*, excavated and laying on top of the surrounding thatch. Photo by R.J. Soreng

the margins slightly involute and sparsely to regularly scaberulous, bases flattened and to 1.6 mm wide with age, abaxially smooth and shiny to slightly lustrous, with veins expressed, adaxially dull, smooth, with low narrow costae, apex blunt, the blade keel running in a nearly straight line (slightly upturned for ca 0.2 mm) into the apex, the margins being more downturned to meet the keel. **Inflorescence** composed of a single erect spikelet, barely exerted above the foliage; without nodal scars below the solitary spikelet; peduncles 5–6 mm long, smooth, glabrous, slightly thickened at the apex and laterally compressed. **Spikelets** slightly dimorphic, bisexual or functionally unisexual and pistillate, smooth, glabrous, 2(–3)-flowered (the 3rd, slightly reduced in all parts), often with a short rachilla extension to 0.4 mm long; glumes much shorter than the spikelets, keeled, about as broad as long, subequal, herbaceous in the central area, and broadly scarious-hyaline margins and lobes flanking the apex, edges smooth, apex obtuse to truncate or emarginate or retuse with a broad, U-shaped, 0.2–0.5 mm deep notch between the slightly flared, acute lobes; rachilla smooth, glabrous, terete, internode between 1st and 2nd floret mostly obsolete or up to 0.4 mm long, between the 2nd and 3rd florets ca. 1 mm long; callus of lemma not well-developed, blunt, glabrous, a narrow thickened rim at the base of the lemma; lemmas strongly laterally compressed and keeled, smooth, glabrous, thinly herbaceous in the lower 1/2–2/3, scarious-hyaline in the upper 1/3 and narrowly so along the margins to the base, apex and margins smooth, the lateral nerves extending ca. 1/2 way to the apex; palea slightly shorter to nearly as long as the lemma, smooth, glabrous, scarious-hyaline except for the thinly herbaceous keels and adjacent internerve and margins in the lower part, 2-nerved and 2-keeled, between the keels 0.5–0.7 mm wide in the sulcus, incised up to 1/3 the length, the 2 terminal lobes slightly flared in the distal ¼; lodicules 2, with or without a slender to 0.5 mm long lateral lobe nearly equaling the main lobe, smooth, glabrous; ovary glabrous, styles 2, ca. 1 mm long, terminal, bearing stigmatic hairs to

near the base, densely plumose, lateral branches simple; bisexual spikelets: lower glumes 1.3–1.6 mm long, 1–3-nerved; upper glumes 1.6–2.0 mm long, 1–3-nerved (both glumes 3-nerved in *Peterson, Soreng & Romaschenko 20382*); lemmas 4.9–5.5 mm long, 5(–7)-nerved, intermediate nerves faint, apex obtuse, slightly flared; lodicules 1.3–1.5 mm long, 0.3–0.5 mm wide, narrowly lanceolate, attenuate; stamens 3, filaments erect, apically exerted, anthers 2.3–2.6 mm long, glabrous; (pistil as in pistillate flowers but slightly smaller, and no caryopsis observed); pistillate spikelets: lower glumes 1.3–1.5 mm long; upper glumes 1.5–1.6 mm long; lemmas 3.3–4.6 mm long, 3-nerved, in the lower part becoming slightly thicker at caryopsis maturity, apex obtuse to truncate; lodicules 0.8–1.5 mm long, to 0.7 mm wide, asymmetrically elliptical; staminodes 3, 1.0–1.5 mm long including anthers, anther sacs 0.3–0.4 mm long, rudimentary, sterile; caryopses 1.3–1.5 × 0.4–0.5 mm, fusiform, brown, translucent, falling with the lemma and palea but not adherent to them, the adaxial (hilum) surface shallowly sulcate, the apex obtuse, the base acute; embryo ca. 1/3 as long as the caryopsis; hilum ca. 1/4 as long as the caryopsis, broadly elliptical.

Habitat.—Puna, 4380–4400 m, rare (ca. 10 clumps seen in 2007) in dense thatch, on low hummocks, and around the perimeters of shallow moist depressions in gentle, heavily and closely grazed, terrain, with *Aciachne* sp., *Alchemilla pinnata* Ruiz & Pav., *Calamagrostis minima* (Pilg.) Tovar, *Carex* sp., *Didymodon* sp., *Poa aequigluma* Tovar, and *P. humillima* Pilg. Other plants collected by J. Solomon at this location were: *Aloinella cucullifera* Steere, *Alternanthera lupulina* Kunth, *Astragalus* sp., *Baccharis caespitosa* (Ruiz & Pav.) Pers. var. *caespitosa*, *Barbula replicata* Taylor, *Bromus* sp., *Draba pickeringii* A. Gray, *Festuca rigescens* (J. Presl) Kunth, *Gentianella muscoides* (Gilg) T.N. Ho & S.W. Liu, *Senecio nutans* Sch. Bip., *Senecio spinosus* DC., *Senecio wernerioides* Wedd.

Comments.—*Poa unispiculata* is morphologically similar to *P. perligulata* Pilg., but differs by having a more compact habit with multiple equitantly overlapping leaf sheaths with short, tightly ranked, distichous blades, presence of one spikelet per inflorescence, and gynodioecy with long anthers in bisexual plants. We know of only one other species of *Poa* that consistently has a single spikelet per inflorescence (see discussion). Apical notching of spikelet bracts is rare in the genus, but also appears in *P. [sect. Anthochloa (Nees & Meyen) Soreng & L.G. Gillespie] lepidula* (Nees & Meyen) Soreng & L.J. Gillespie.

PARATYPE: PERU. Pasco: Cerro de Pasco, 4 km s, at junction of new and old roads to La Oroya (Hwy 3), 10°43'31.8"S, 76°15'08.4"W, 4382 m, 10 Mar 2007, perfect flowered plants only, P.M. Peterson, R.J. Soreng & K. Romaschenko 20382 (B, CONC, CORD, K, LPB, MO, US, USM).

DISCUSSION

Poa unispiculata is reasonably placed in the “punapoa” complex of *Poa* (Soreng et al. 2003) which is now considered to include dwarf alto-andinean species with reduced inflorescences that are frequently declinuous or pistillate only and apomictic (Negritto et al. 2008). *Poa unispiculata*, like *P. perligulata* and some other punapoa species, has smooth palea keels and is thus problematical for separation from members of the *Catabrosa* complex [*Catabrosa* P. Beauv., *Catabrosella* (Tzvelev) Tzvelev, *Paracolpodium* (Tzvelev) Tzvelev, *Hyalopoa* (Tzvelev) Tzvelev] with multiple flowered spikelets. However, *P. unispiculata* has strongly keeled lemmas with occasionally up to seven nerves, and lacks epidermal papillae; whereas in the *Catabrosa* complex there are usually three or rarely five nerves, papillae are usually present on blades and culms, and the prophylla (palea homologues) keels are smooth (versus densely covered with more or less erect prickle-hairs in *P. unispiculata*, and variously scabrous in other punapoa). In analyses of nuclear ribosomal and plastid DNA data punapoa species resolve among species of *P.* subgen. *Poa* supersect. *Homalopoa* (Dumort.) Soreng & L.G. Gillespie, whereas the *Catabrosa* complex stands well apart from *Poa* (Gillespie & Soreng 2005; Gillespie et al. 2008, 2009). Within a broad survey of *Poa* and allied genera, preliminary ETS and ITS nrDNA sequence data place the new species nearest to *P. aequigluma* or *P. perligulata* in a clade with *P. lepidula* and *P. gymnantha* Pilg. (L.J. Gillespie pers. comm. Feb. 2010).

Poa is the largest genus of grasses (Gillespie & Soreng 2005) and is well known for its diverse breeding systems (Anton 1978; Anton & Connor 1995; Negritto & Anton 2000; Soreng 1991; Soreng & Keil 2003). Although bisexual species are the most common, species exhibiting dioecism, gynodioecism, and gynomo-

noecism are well known in both North and South America (Soreng 1991, 2007). A few andinean species are known only from populations composed of plants with pistillate spikelets, e.g., *P. perligulata* Anton & Connor 1995; Negritto & Anton 2000; Negritto et al. 2008).

Our judgment of breeding system of the new species is based on only three separate plants available to us for study from the type collection, and the one new collection of 10 plants (which we collected parts of). *Poa unispiculata* is judged to be a gynodioecious species because two of the cushions collected in the original gathering produced only pistillate spikelets and the third only bisexual spikelets. All individuals plants of the newer gathering had bisexual spikelets with anthers well exerted (Fig. 2), and no pistillate plants were found. No fruit were found in the bisexual spikelets from either gathering. Apparently all these individuals were collected from a single population from an area possibly less than 30m². The breeding system obviously needs confirmation and additional field studies are necessary. It could be that plants have bisexual flowers early in the season, and that a proportion of individuals shift to pistillate flowering later in the season (Soreng & Keil 2003). It is assumed that each cushion as collected is an individual plant that has attained its present dimensions through continual branching and rooting at the nodes, but because of the very dense, compact growth, it is impossible to be sure that no additional individuals were mixed within the cushions. To compensate for reduction in reproductive capacity of each culm harboring a single spikelet, a single mat of *P. unispiculata* can potentially produce several hundred flowering shoots per flowering season (e.g., the US isotype has approximately 200 flowering culms in one mat of 14 cm diam.).

Anton and Connor (1995) listed 14 other gynodioecious species then known from the Americas. The breeding system of four of the North American “partially gynodioecious” species was reclassified as sequentially gynomonocious (Soreng & Keil 2003) and another as subdioecious (Soreng 2007), which is considered intermediate between gynodioecism and dioecism. Of the South American species listed, four belonging to *Poa* subgen. *Andinae* were transferred to a new genus, *Nicoraepoa* Soreng & Gillespie (Soreng & Gillespie 2007) [quite likely *P. stepparia* Nicora belongs here also], and one was reclassified as gynomonocious, while yet another species was recharacterized as gynodioecious (Negritto & Anton 2000). Therefore, only four cases of gynodioecism exist in North America [*P. leibergii* Vasey, *P. stebbinsii* Soreng (which can also produce staminate inflorescences), *P. cusickii* Vasey subsp. *cusickii* and *P. chambersii* Soreng (both of which are gynodioecious in part of their ranges and dioecious over the rest), and two exist in South America (*P. cabreriana* Anton & Ariza and *P. lilloi* Hack.; Negritto & Anton 2000)]. So, actually gynodioecism is quite rare in *Poa*.

It is well known that dioecious species of *Poa* sect. *Dioicopoa* E. Desv. differ noticeably in the size of the spikelets, glumes, and florets (Giussani 2000; Soreng 2007; Soreng and Peterson 2008); pistillate spikelets have fewer and larger florets, and, if pubescent, have substantially more and longer hair. Differences among pistillate and perfect-flowered individuals of gynodioecious species of *Poa* have not been noted before, but are apparent in *P. unispiculata*. In this species the two spikelet types are slightly sexually dimorphic. The pistillate spikelets tend to have smaller and fewer florets, and the lemmas are 3-nerved, whereas the lemmas of the bisexual florets typically have an additional 1 (or 2) faint intermediate nerves. Besides the very obvious differences in the stamens, the pistils of the pistillate spikelets are slightly larger. Fruit set was abundant in the pistillate plant, but no fruit were observed in the bisexual plants, presumably because most of its spikelets were pre-anthesis or at anthesis. Possibly the pistils are infertile in the plants with fertile anthers (our bisexual plants), in which case the species is dioecious, but this would be an exceptional pattern in *Poa*, as pistils are rudimentary or at least more obviously reduced in species known to be dioecious. Solanaceae have minimally reduced sex organs in some dioecious species, but pollinator attraction and reward factors are in play there (Martineab et al. 2006) that do not apply to wind-pollination. In the bisexual plants the florets are longer and broader, and thus appear more prone to wind dispersal than those in the pistillate plants, which seems contrary to expectation unless they actually do produce seed.

As far as we are aware, 3-nerved lemmas are not known elsewhere in the genus (except in some species from New Guinea; Veldkamp 1994), but in *Poa unispiculata* this seems to be a clear specialization in an

otherwise faintly 5(–7)-nerved species, as judged from the lemmas of the bisexual spikelets. This character state (often used to characterize genera and tribes) is clearly secondarily derived.

Another curious characteristic of *Poa unispiculata* is the flared scarious-hyaline margins of the glumes which extend upward as lobes beyond the herbaceous keel and back, leaving a U-shaped notch (Fig. 1. B, E–H), and the deep narrow notch between the somewhat flared and scarious-hyaline distal lobes of the palea. These are reminiscent of the flared scarious-hyaline margins of glumes, lemmas, and paleas, and notches of various depth in those, in *Poa lepidula*. The latter species was formerly treated as the sole species of the genus *Anthochloa*, but is now accepted as *Poa* sect. *Anthochloa*, and closely related to the punapoa group (Gillespie et al. 2007, 2008). The flared scarious-hyaline margins are an obvious adaptation for wind dispersal.

In *Poa*, inflorescence size varies widely from highly branched panicles with hundreds of spikelets as in large plants of *P. occidentalis* Vasey or *P. palustris* L. to highly compact inflorescences with very few spikelets primarily in species from high elevations on all continents except Antarctica. *Poa unispiculata* is thus an example of the ultimate extreme in panicle size reduction. It appears most closely related to a group of diminutive, alto-andinean species from the Andes of Peru, Bolivia, and northern Argentina and Chile (*Poa* group punapoa; in particular, *P. humillima*, *P. aequigluma*, *P. chamaeclinis* Pilg., and *P. perligulata*, the later three of which are generally recognized as strictly pistillate; Soreng et al. 2003). *Poa humillima* is gynomonoeious (Anton 1978) and differs in its more clearly naviculate leaf blades apices, abaxially smooth leaf blades, short branched, compact, ovate panicles 0.5–1(–1.5) cm long with less than 10 spikelets; single bisexual proximal florets with (1–)2 pistillate distal florets; broader, subflabellate upper glumes; shorter lemmas (2–2.8 mm long); scaberulous glume and lemma apical margins ($\times 50$); all spikelets (2–)3-flowered; and fertile anthers ca. 1 mm long. *Poa aequigluma*, *P. chamaeclinis*, *P. perligulata* all have relatively longer glumes (subequal to the floret pair in *P. aequigluma* and *P. perligulata*), pistillate spikelets only (as do a few other South American species, and a several North American species at least in part), and only two florets per spikelet. Recently discovered populations of *P. aequigluma* from Ancash, Peru, at the northernmost end of the species range, have bisexual spikelets with normal looking anthers about 3 mm long (Peterson, Soreng, LaTorre & Rojas Fox 21550, 21593, 21684). These latter three species also share the obsolete or nearly obsolete rachilla internode between the proximal two florets with *P. unispiculata*. The leaf arrangement differs in these three species from that in *P. unispiculata*. All vegetative branching is intravaginal as in *P. unispiculata*, but leaves of the other species are fewer in number, the sheaths more elongated, and the leaf blades, which are mostly longer, diverge at approximately the same level (versus equitantly).

Inflorescences reduced to one or a few spikelets are relatively rare in Poaceae, but according to a search on the *World Grass Species* website (Clayton et al. 2002) are known in at least 73 other species in more than 30 genera, of which eight are annuals and 66 are perennials. However, among those species that produce inflorescences with single spikelets, the solitary condition is usually facultative. Individuals of most of these species also produce inflorescences with more than one spikelet.

We know of only a ten grass species that always have an inflorescence consisting of a single true spikelet (*Anomochloa* Brongn. and *Streptochaeta* Schrad. ex Nees can be excluded from our sample by not having fully evolved “grass spikelets”). This extremely rare condition is known in one other species of *Poa*, an alpine, cushion grass, *P. inconspicua* Veldkamp, from the Cartestenz Mountains of New Guinea (Veldkamp 1979, 1994). This species belongs to the remotely related *P.* sect. *Pauciflorae* Pilg. ex Potztl (L.J. Gillespie, unpublished DNA data), nine species of which have a single floret per spikelet, and seven others have 1–2 florets per spikelet (Veldkamp 1994). *Poa pygmaea* Buchanan, another unrelated, alpine cushion grass, from ca. 45° S in New Zealand, comes close in having inflorescences with 1–3 spikelets (Edgar & Connor 2000; Gillespie et al. 2009). One spikelet per inflorescence occurs rarely in depauperate specimens of *P. leibergii* Scribn [(1–)6–17(–22) spikelets] from the Pacific Northwest in North America. Obligate unispiculate inflorescences are additionally known in two of the three species of the genus *Aciachne* Benth. (Pooideae, Stipeae; *A. flagellifera* Laegaard and *A. pulvinata* Benth.) cushion plants of the high Andes and Costa Rica (páramo del Cerro Chirripó). In these two species the fully developed spikelet is subtended by one or two scars which

may represent minute, vestigial spikelets. In the third species, *A. acicularis* Laegaard, inflorescences with two or rarely three spikelets may occur on the same plant with predominantly single-flowered inflorescences (Laegaard, 1987). Obligate unispiculate inflorescences have also been reported in one species of *Rytidosperma* Steud. (Danthonioideae, Danthoniae), *R. oreoboloides* (F. Muell.) H.P. Linder, a cushion species from also from the Cartestenz Mountains of New Guinea where it grows intermixed with *Poa inconspicua* among other alpine plants (Veldkamp 1979). All of the above taxa with strictly one spikelet per inflorescence are from high elevation grasslands. *Lygeum* Loebl. ex L. (Pooideae, Lygeae) with only the single species of low, arid Mediterranean hills, *L. sparteum* L., has a large single-flowered compound spikelet per inflorescence that is derived from the fusion of two spikelets that is subtended by a somewhat larger, loose spathe. The above genera have non-Kranz anatomy and presumably C₃ metabolism. A few other species with single spikelet inflorescences are known or presumed to have C₄ metabolism (Zuloaga 1987; Aliscioni et al. 2003). Within *Distichlis* Raf. (Chloridoideae, Cynodonteae) both of the species formerly treated as *Monanthochloe* Pilg. ex Potztl, *D. littoralis* (Engelm.) H.L. Bell & Columbus, coastlines of the southern United States and Mexico, and *D. acerosa* (Griseb.) H.L. Bell & Columbus, saline flats of northern Argentina (Bell & Columbus 2008), occur at sea level or in low plains up to ca. 350 m. The dwarf alto-andinean species *Distichlis humilis* Phil. has 1–4 spikelets, but can be distinguished from our species by the 7–11 veined lemmas. *Panicum cupressifolium* A. Camus (Panicoideae, Paniceae), which has single spikelets per inflorescence, occurs at moderately high elevations in the mountains of Madagascar (massif de L'Andringitra, 2000–2500 m) in a rocky/scrubby zone. Evidently, obligately single-spikelet inflorescences have evolved in grasses most commonly open habitats, in plants with C₃ metabolism, in alpine-like situations of tropical to subtropical latitudes.

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