MUHLENBERGIA TARAHUMARA (POACEAE: CHLORIDOIDEAE: CYNODONTEAE: MUHLENBERGIINAE), A NEW SPECIES FROM CHIHUAHUA, MEXICO

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ABSTRACT

Muhlenbergia tarahumara P.M. Peterson & Columbus, sp. nov., is described and illustrated. The new species occurs on rocky slopes, ridgetops, and white-tuff rock outcrops in the Sierra Madre Occidental and is known only from the municipality of Guachochi in Chihuahua, Mexico. Based on morphological and phylogenetic analysis of plastid and nuclear DNA sequence data, we conclude that the new species is sister to the *Aegopogon* clade that is nested within a clade of species in *Muhlenbergia* subgen. *Muhlenbergia*. *Muhlenbergia tarahumara* differs from *Aegopogon cenchroides* by having panicle branches 5–13 per culm, each with two terminal, one-flowered spikelets; glumes 3–5.8 mm long, shorter than the lemma and narrowly lanceolate; lemmas 3.6–7.3 mm long, lanceolate; paleas 3–4.6 mm long; and anthers 2.2–2.8 mm long, yellowish orange.

RESUMEN

Se describe e ilustra **Muhlenbergia tarahumara** P.M. Peterson & Columbus, sp. nov. La nueva especie habita en cuestas rocosas, en cimas de cerros y en afloramientos de tobas volcánicas blancas en la Sierra Madre Occidental y se conoce solamente en del municipio de Guachochi en Chihuahua, México. Basados en los análisis morfológicos y filogenéticos de las secuencias de ADN plastidial y nuclear, podemos concluir que la nueva especie es hermana del clado *Aegopogon,* el cual se encuentra anidado en el clado de especies de *Muhlenbergia* subgen. *Muhlenbergia*. *Muhlenbergia tarahumara* difiere de *Aegopogon cenchroides* por tener 5–13 ramas por culmo, cada una con dos espiguillas unifloras terminales; glumas de 3–5.8 mm de largo, más largas que el lema y estrechamente lanceoladas; lemas de 3.6–7.3 mm de largo, lanceoladas; páleas de 3–4.6 mm de largo; y anteras de 2.2–2.8 mm de largo, amarillento-anaranjadas.

On a 2003 collecting trip to the Sierra Madre Occidental in Chihuahua, Mexico, two unusual specimens were found and initially given fieldnames of *Aegopogon* (*Peterson & P. Catalán 17542*) and *Bouteloua* (*Peterson & Catalán 17621*). Later, when PMP was preparing treatments of *Bouteloua* and the tribe Muhlenbergiinae for northeastern Mexico (Peterson et al. 2007b; Herrera Arrieta et al. 2008), these specimens were reevaluated after seeing them in the United States National Herbarium (US) in separate unidentified folders of *Aegopogon* and *Bouteloua,* respectively. Upon closer inspection, these collections represented the same new species that could not be easily placed in *Aegopogon* or *Bouteloua,* nor any of the remaining genera currently placed in the Muhlenbergiinae (Peterson et al. 2001b, 2007a). Individuals of this new species are unique in having terminal, raceme-like panicles with only two spikelets at the end of each primary branch. A second opinion seemed warranted; PMP then sent a duplicate off to JTC for examination and incorporation into DNA sequence data sets that could possibly elucidate affinities of this enigmatic species. Subsequently, a third specimen was found (*Peterson et al. 8032*). As discussed below, analyses of DNA sequences from the new species placed it in subtribe Muhlenbergiinae.

Members of subtribe Muhlenbergiinae are grasses (Poaceae) in the subfamily Chloridoideae, tribe Cynodonteae (Peterson et al. 2001b, 2007a, in review). Muhlenbergiinae are highly variable morphologically, although the group can be generally characterized as follows: ligule a membrane (rarely a line of hairs); inflorescence a panicle, rebranched or composed only of primary branches; spikelets solitary, sometimes in pairs or triads, cleistogamous spikelets occasionally present in the leaf sheaths; floret 1 (rarely more), perfect, staminate, or sterile; glumes awned or unawned; lemmas 3-nerved, awned or unawned; base chromosome number $x = 8–10$ (Peterson 2000; Peterson & Herrera Arrieta 1995; Peterson et al. 1997, 2007a, b; Colum-

bus et al. 2007). Two subtypes of C_4 photosynthesis, NAD-ME (nicotinamide adenine dinucleotide cofactor malic enzyme) and PCK (phosphoenolpyruvate carboxykinase), have been found and verified by biochemical assays to occur in Muhlenbergiinae (Gutiérrez et al. 1974; Brown 1977; Hattersley & Watson 1992).

By far, the largest genus in the subtribe is *Muhlenbergia*, which has 154 species including the important North American range grass *M. montana* (Nutt.) Hitchc., amphitropical disjuncts *M. arenicola* Buckley and *M. torreyi* (Kunth) Hitchc. ex Bush, and seven species located in southeast Asia (Herrera Arrieta 1998; Peterson & Ortíz Diaz 1998; Peterson 2003; Wu & Peterson 2006; Herrera Arrieta & Peterson 2007; Peterson et al. 2007b). Species indigenous to North America number 127 (86%), and 125 of these occur in Mexico, where 56 species are endemic (Espejo Serna et al. 2000; Dávila-Aranda et al. 2004, 2006; Peterson & Herrera Arrieta 2005; Peterson et al. 2007a).

The remaining nine genera have four or fewer species, and four are monotypic. All are limited to the New World except for an occurrence of *Aegopogon cenchroides* Humb. & Bonpl. ex Willd. in Papua New Guinea (Veldkamp 1985). Five are endemic to North America. Apart from its presence in Papua New Guinea, *Aegopogon* (four species) is distributed in North and South America. *Bealia* (one species) is restricted to northern Mexico (Peterson 1989; Peterson et al. 1993). *Blepharoneuron* (two species) is found in North America and includes *B. tricholepis* (Torr.) Nash, an important range grass in the southwestern U.S.A. and northern Mexico (Peterson & Annable 1990, 2003). *Chaboissaea* (four species) has three species in central Mexico and *C. atacamensis* (Parodi) P.M. Peterson & Annable in Argentina and Bolivia (Peterson & Annable 1992; Peterson & Herrera Arrieta 1995; Sykes et al. 1997). *Lycurus* (three species) has one species limited to North America and two amphitropical disjuncts, including *L. setosus* (Nutt.) C. Reeder (Reeder 1985; Sánchez & Rúgolo de Agrasar 1986; Peterson & Morrone 1998). *Pereilema* (four species) is distributed in North, Central, and South America. *Redfieldia* (one species) is endemic to the U.S.A. (Reeder 1976). *Schaffnerella* (one species) is known only from San Luis Potosí, Mexico (Columbus et al. 2002). *Schedonnardus* (one species) is yet another genus with an amphitropical distribution.

Analyses of cpDNA *ndhA-intron, ndhF, rpl32–trnL$^{(UAG)}$, rps3, rps16-intron, rps16–trnK, trnL–F,* and nrDNA ITS sequences of species in the Muhlenbergiinae (Columbus et al. in press; Peterson et al. in prep.) indicate that the large genus *Muhlenbergia,* as delimited above, is not monophyletic because these nine, smaller genera are nested within it; therefore, expanding the circumscription of *Muhlenbergia* to include these nine genera seems warranted (Duvall et al. 1994; Peterson et al. 2001a, 2004; Peterson & Herrera Arrieta 2005; Peterson et al. 2007a). In this paper, in addition to describing a species new to science, we present a phylogenetic hypothesis and support for the generic placement of this unusual taxon.

Muhlenbergia tarahumara P.M. Peterson & Columbus, sp. nov. (**Figs. 1A–J; 2**). TYPE: MEXICO. CHIHUAHUA. Municipio Guachochi, Sierra Madre Occidental, 2 km W of Rio Coraréachi and E of Osichi (27°28'15.0"N, 107°31'5.0"W), 1960–2040 m, 30 Aug 2003, *P.M. Peterson & P. Catalán 17621* (HOLOTYPE: US-3470469!; ISOTYPES: CIIDIR!, K!, MO!, RSA!, US!).

Ab *Aegopogon cenchroides* Humb. & Bonpl. ex Willd. paniculis ramis 5–13 per culmo, omnibus cum duobus terminalibus unifloribusque spiculis; glumis 3–5.8 mm longis, brevioribus quam lemmatibus, anguste lanceolatis; lemmata 3.6–7.3 mm longis, lanceolatis; paleae 3–4.6 mm longis; antherae 2.2–2.8 mm longis, tangerinis, recedit.

Caespitose perennials. Culms 18–35 cm tall, erect, terete near base, glabrous below the nodes, usually 3 nodes per culm; internodes glabrous and shiny. Leaf sheaths 0.8–8 cm long, shorter than the internodes above, pubescent above and mostly glabrous below; ligules 1–1.8 mm long, membranous, abaxially pubescent or glabrous, apex acute, often erose, minutely ciliolate; blades (2–)3.5–13 cm long, 0.2–1.3 mm wide, flat to tightly involute, apically acuminate, somewhat sinuous, antrorsely hirsute on both surfaces, the hairs 0.1–0.4 mm long. Panicles 3–6 cm long, 0.7–1.6 cm wide, narrow, terminal with 5–13 racemosely arranged primary branches, 1 per node; branches 0.5–1.4 cm long, with two terminal spikelets, deciduous, disarticulation near base, branches first ascending then spreading (bending sharply or curling near base) from the culm axis, usually secund, antrorsely hirsute, the hairs 0.2–0.4 mm long; inflorescence axis flattened, ending in terminal branch, margins hirsute; pedicels fused or 0.2–0.6 mm long, one slightly longer than the other, tightly appressed. Spikelets 4.5–7.8 mm long, appressed to one another, 1-flowered; glumes 3–5.8 mm long,

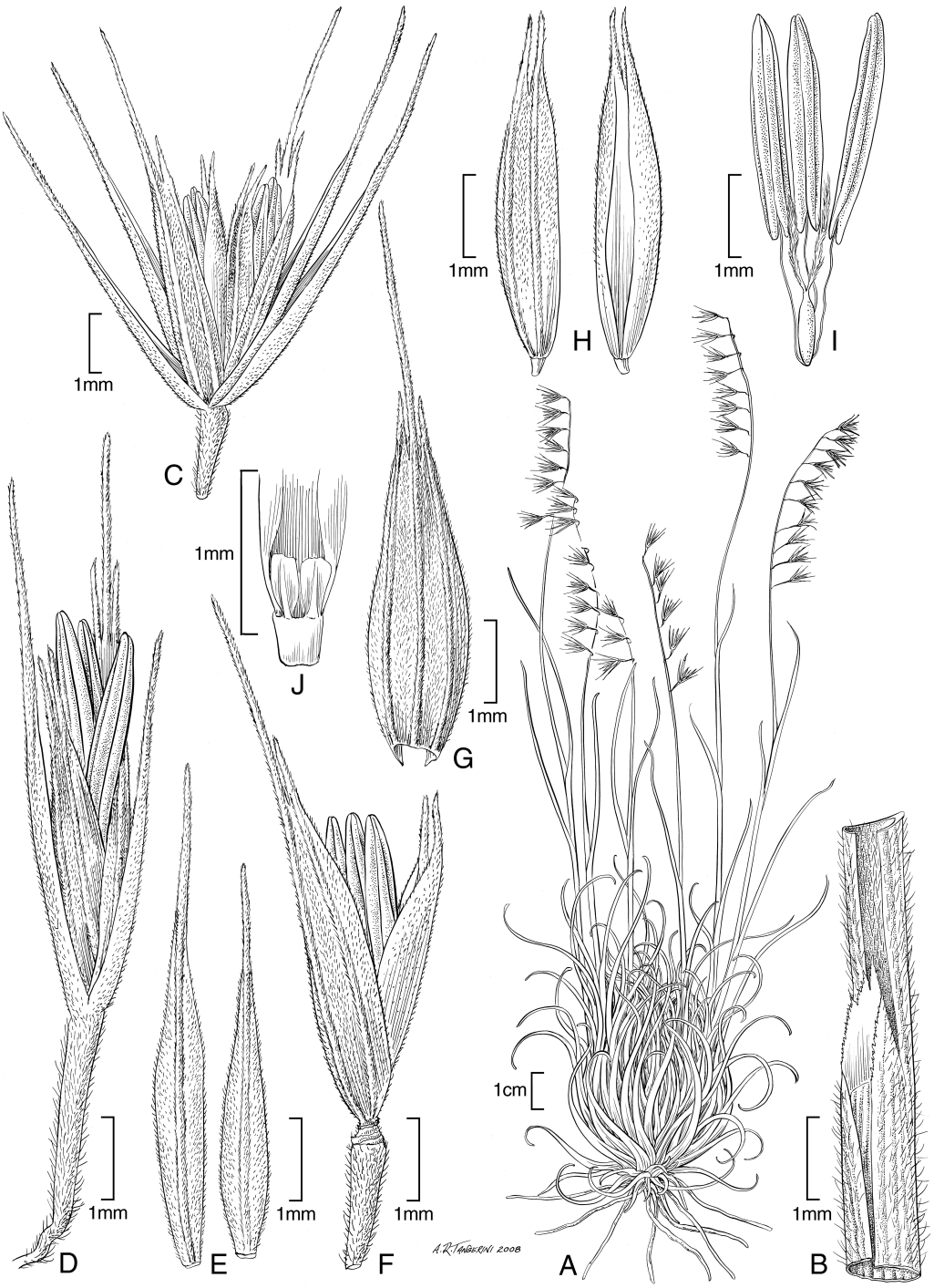

Fig. 1. *Muhlenbergia tarahumara* [*P.M. Peterson & P Catalán 17621* (US)]. **A.** Habit. **B.** Sheath, ligule, and blade. **C.** Two paired spikelets. **D.** Branch with two spikelets (only one seen from this perspective). **E.** Glumes. **F.** Floret on branch axis (glumes, other spikelet removed). **G.** Lemma. **H.** Paleas. **I.** Stamens and pistil. **J.** Lodicules.

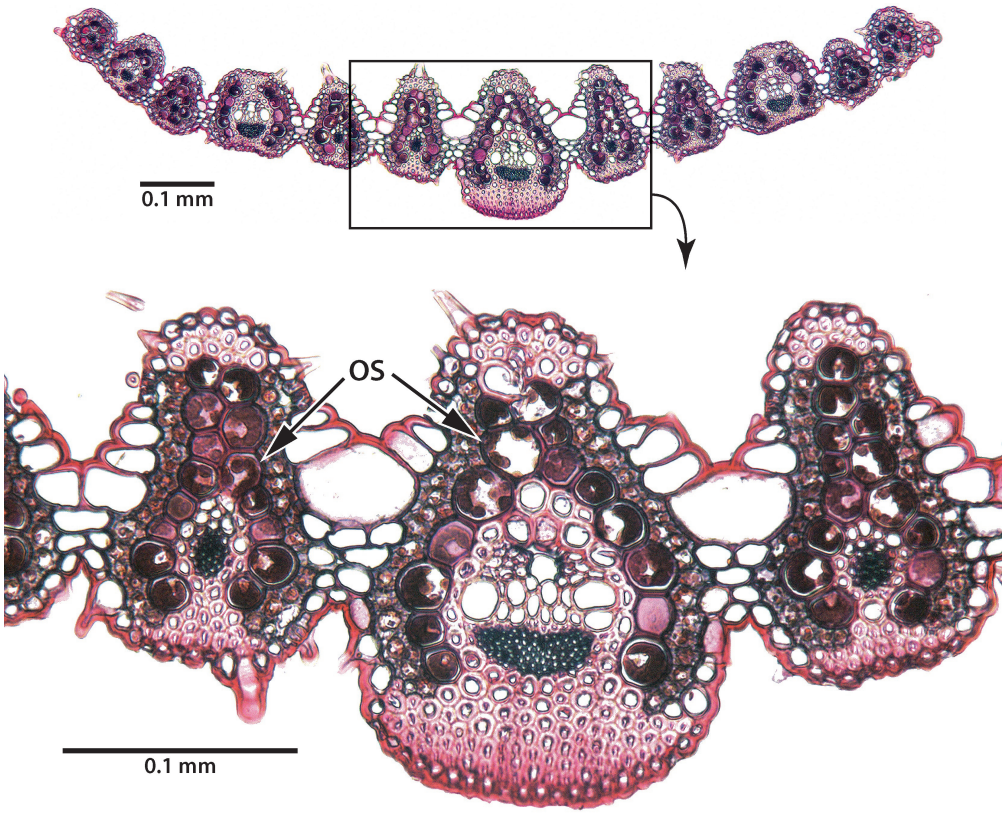

Fig. 2. Transverse section of the leaf blade of *Muhlenbergia tarahumara* [*P.M. Peterson & J.M. Saarela 22053* (US)]. Adaxial surface is at top. OS = outer sheath of vascular bundle.

narrowly lanceolate, usually equal in length, shorter than the lemma, membranous to chartaceous, 1-veined, pubescent, apex acuminate, awned, the awns 1.4–3.2 mm long; lemmas 3.6–7.3 mm long, lanceolate, awned, distinctly 3-veined, membranous to chartaceous, appressed pubescent, apex acute to acuminate, bifid, the central awn 2–3.7 mm long, straight or slightly recurved, the lateral veins extending into awns 0.6–1.3 mm long; paleas 3–4.6 mm long, shorter than the lemma, membranous, glabrous below and appressed pubescent near apex, 2-veined, apex acuminate, each vein extending as a mucro or awn 0.2–0.9 mm long; stamens 3, anthers 2.2–2.8 mm long, yellowish orange; lodicules 2, membranous; ovary glabrous with two styles and two stigmas. Caryopsis not seen.

Comments.—The new species can be distinguished from all other species of *Muhlenbergia* by having a terminal, raceme-like panicle with only two spikelets at the end of the branch. It closely resembles species of *Aegopogon*, which have the same kind of inflorescence, including the deciduous branches, but with three spikelets per branch, and some species of *Bouteloua*. The species is named after the Tarahumara people who are indigenous to the northern Sierra Madre Occidental.

Distribution and Habitat.—*Muhlenbergia tarahumara* is known only from three locations in the Sierra Madre Occidental in Chihuahua, Mexico, where it occurs on rocky slopes, ridgetops, and white-tuff rock outcrops with species of *Pinus, Quercus, Cupressus, Arctostaphylos, Vaccinium, Comarostaphylis, Aristida, Aegopogon tenellus* (DC.) Trin., *A. cenchroides, Muhlenbergia lucida* Swallen, *M. montana, M. pauciflora* Buckley, *M. polycaulis* Scribn., and *M. rigida* (Kunth) Kunth; 1880–2075 m.

Additional specimens examined. **MEXICO. Chihuahua:** Municipio Guachochi, Sierra Madre Occidental, 41.3 km S of Creel on road to Batopilas, 2075 m, 10 Sep 1989, *P.M. Peterson, C.R. Annable & Y. Herrera Arrieta 8032* (RSA, US-3513942); Sierra Madre Occidental, Yamuco, 1 mi E of hwy N of Río Urique crossing towards Basihuare and Creel, 27°23'59.4"N, 107°29'20.4"W, 1880–1900 m, 26 Aug 2003, *P.M. Peterson & P. Catalán 17542* (CIIDIR, RSA, US-3468887); 5 Sep 2008, *P.M. Peterson & J.M. Saarela 22053* (RSA, US); 6 Sep 2008, *P.M. Peterson & J.M. Saarela 22079* (US).

Leaf anatomy.—Cross-sections of the leaf blade were done with a rotary microtome on fresh-field fixed material (*Peterson & Saarela 22053*), stained, and mounted prior to observation (Sharman 1943; Columbus 1999; Peterson & Herrera Arrieta 2001). Permanent slides are deposited at RSA and US. The following description employs much of the standardized terminology proposed by Ellis (1976).

The leaf blade in transverse section displays Kranz anatomy, which is associated with C_4 photosynthesis (Fig. 2). It is nearly flat (becoming involute on drying) and both surfaces have rounded or flat-topped, longitudinal costal (above/below the vascular bundles) ribs alternating with V-shaped intercostal furrows; a conspicuous rounded midrib projects abaxially. The furrows are up to 1/2 the thickness of the blade; those on the abaxial surface are more shallow. The vascular bundles (VBs) have two sheaths, an inner (mestome, XyMS+; Hattersley & Watson 1976) continuous sheath of sclerenchyma and an outer (parenchymatous, PCR tissue; Hattersley et al. 1977) sheath of chlorenchyma. The outer sheath is uneven in outline and its cells contain round chloroplasts that are distributed centrifugally/peripherally within the cell (Prendergast et al. 1987). The VBs differ in size, development of metaxylem, whether or not the outer sheath is continuous, and the amount of sclerenchyma present on the adaxial and abaxial sides. There are four primary VBs (with large metaxylem vessels; includes the midvein), four secondary VBs, and four tertiary VBs arranged as follows: iii-i-iii-i-ii-ii-i-ii-ii-i-iii-iii. The phloem is not sclerosed. In the innermost five VBs, the outer sheath is extended adaxially into the rib. The outer sheath is interrupted by sclerenchyma on the abaxial side of all VBs except three of the four tertiary VBs, and on the adaxial side of the two lateral primary VBs nearest the midvein. A narrow layer of smaller, isodiametric, indistinctly radiate chlorenchymatous cells surrounds the outer sheath (PCA tissue; Hattersley et al. 1977). Sclerenchyma girders (in contact with the outer sheath) are present on the adaxial and abaxial sides of all VBs. The largest girder (many cells in five series/rows) forms the midrib, whereas those of the tertiary VBs are smallest (< 10 cells in one or two series). Abaxial girders associated with primary and secondary VBs, as well as those on the adaxial side of the two lateral primary VBs nearest the midvein, are broadest near the epidermis. The blade margin has two or three subepidermal fibers. Bulliform cells are largest adaxially adjacent to the midvein and become progressively smaller towards the margin; those on the abaxial side are smaller than their adaxial counterparts. Colorless cells one or two columns wide extend between bulliform cells on both sides of the blade, dividing the chlorenchyma associated with adjacent VBs.

Molecular analyses.—DNA was obtained from field-collected leaf material (*Peterson & Saarela 22053*) and was sequenced for *ndhA-intron, ndhF, rpl32–trnL$^{(UAG)}$, rps3, rps16-intron, rps16–trnK, trnL–F,* and ITS. To determine the phylogenetic position of the new species within Chloridoideae, the sequences were aligned with the Columbus et al. (2007) data set, representing 66 chloridoid genera and the Peterson et al. (in review) data set representing 96 chloridoid genera. Upon analysis, the new species resolved in the Muhlenbergiinae clade. To determine its position within Muhlenbergiinae, the sequences were aligned with the two separate data sets that included all ten genera in the subtribe and 80–90% of the species in *Muhlenbergia* (Columbus et al. in prep.; Peterson et al. in prep). Analyses of the Muhlenbergiinae data sets revealed that the new species is a member of a subclade that includes *Aegopogon*, *M.* subgen. *Muhlenbergia*, and *Pereilema*. Its position within the subclade was not resolved in the *trnL–F* phylogeny (Columbus et al. in prep.), although in the combined *ndhA-intron, ndhF, rpl32–trnL$^{(UAG)}$, rps3, rps16-intron, rps16–trnK* phylogeny (Peterson et al. in prep.) the new species was supported as sister to *Aegopogon cenchroides* and *A. tenellus*. However, in the ITS phylogeny the new species is supported as the sister of *Aegopogon* (Columbus et al. in prep; Peterson et al. in prep.).

DISCUSSION

The new species is unique among members of the Muhlenbergiinae in having only two spikelets per branch, these racemosely arranged along the panicle axis. Reduction of the number of spikelets per branch is also seen in *Muhlenbergia diversiglumis* Trin. (a member of *M.* subgen. *Muhlenbergia*) where there are 2–5 spikelets per branch (Peterson & Annable 1991). However, *M. tarahumara* resembles most closely *Aegopogon* in morphology, which supports the phylogenetic hypothesis that these taxa are sister (Columbus et al. in prep.; Peterson et al. in prep.). *Aegopogon* differs from *M. tarahumara* in having three spikelets per branch. The three spikelets are dimorphic—one is larger and hermaphrodite and two are smaller (sometimes rudimentary; one often not developed in *A. bryophilus* Döll) and staminate or neuter. In *M. tarahumara*, no spikelet dimorphism is evident.

Leaf anatomy suggests *M. tarahumara* undergoes the PCK subtype of C_4 photosynthesis. The presence of two bundle sheaths, uneven outline of the outer sheath, round shape of the chloroplasts in the outer sheath, and the centrifugal/peripheral position of these chloroplasts within each cell are together predictive of PCK (Fig. 2; Prendergast et al. 1987). *Aegopogon* likewise has PCK anatomy (Columbus 1996). Peterson and Herrera Arrieta (2001) reported that the species in *M.* subgen. *Muhlenbergia* possess PCK-like anatomy, whereas the remaining species have NAD-ME anatomy. However, *M. tarahumara* differs from species of *Aegopogon* and *M.* subgen. *Muhlenbergia* by having mesophyll chlorenchyma that forms a narrow layer around the outer sheath and is not continuous between adjacent vascular bundles, being separated by columns of colorless cells. This pattern is partially seen in *M. pauciflora* and *M. polycaulis* (Peterson & Herrera Arrieta 2001), where the vascular bundles near the middle of the blade have columns of colorless cells that separate adjacent vascular bundles. However, near the leaf blade margins the tertiary vascular bundles of *M. pauciflora* and *M. polycaulis* have chlorenchyma cells that are continuous between each adjacent vascular bundle. In addition, *Muhlenbergia pauciflora*, like *M. tarahumara*, has well developed abaxial sclerenchyma girders that are broadest near the epidermis (Peterson & Herrera Arrieta 2001).

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