



INCLUSION OF *DASYOCHLOA* IN THE AMPHITROPICAL GENUS *MUNROA* (POACEAE, CHLORIDOIDEAE) BASED ON MORPHOLOGICAL EVIDENCE

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Abstract. Amarilla, L. D.; J. O. Chiapella, N. Nagahama & A. M. Anton. 2013. Inclusion of *Dasyochloa* in the amphitropical genus *Munroa* (Poaceae, Chloridoideae) based on morphological evidence. *Darwiniana*, nueva serie 1(2): 241-252.

Munroa is a morphologically heterogeneous American genus of grasses, including five species with disjunct distribution in North and South America. *Dasyochloa* is a monotypic grass genus, common in western North America, with a controversial taxonomic position, because it has been alternatively included in *Erioneuron*, *Koeleria*, *Triodia*, and *Uralepis*. We evaluated the relationship of *Dasyochloa* with *Munroa* using a phylogenetic analysis of qualitative and quantitative morphological data. *Dasyochloa* was not supported as an independent genus from *Munroa*, as *Dasyochloa* and *Munroa* species formed a monophyletic group defined by seven synapomorphies. On this basis, we transfer *Dasyochloa* to *Munroa*, and propose the new combination *M. pulchella* together with the emended diagnosis of *Munroa*.

Keywords. America; amphitropical distribution; Chloridoideae; *Dasyochloa*; *Munroa*; phylogeny; taxonomy.

Resumen. Amarilla, L. D.; J. O. Chiapella, N. Nagahama & A. M. Anton. 2013. Inclusión de *Dasyochloa* en el género anfrotropical *Munroa* (Poaceae, Chloridoideae) sobre la base de evidencia morfológica. *Darwiniana*, nueva serie 1(2): 241-252.

Munroa es un género Americano morfológicamente heterogéneo, con cinco especies y distribución disyunta en América del Norte y del Sur. *Dasyochloa* es un género monotípico, común en el oeste de Norteamérica, con una historia taxonómica compleja porque ha sido incluido alternativamente en *Erioneuron*, *Koeleria*, *Triodia* y *Uralepis*. En este trabajo evaluamos las relaciones de *Dasyochloa* y *Munroa* con base en un análisis filogenético con caracteres morfológicos cualitativos y cuantitativos. *Dasyochloa* no resultó independiente de *Munroa*, ya que ambos géneros formaron un grupo monofilético definido por siete sinapomorfías. Sobre esta base, transferimos *Dasyochloa* a *Munroa* y proponemos la nueva combinación *M. pulchella*, junto con una enmienda en la diagnosis de *Munroa*.

Palabras clave. América; Chloridoideae; *Dasyochloa*; distribución anfrotropical; *Munroa*; filogenia; taxonomía.

INTRODUCTION

The monotypic genus *Dasyochloa* Willd. ex Rydb. was founded by Rydberg (1906) based on *Triodia pulchella* Kunth [= *D. pulchella* (Kunth) Willd. ex Rydb.]. This species occurs in North America, in arid and semiarid regions of the western USA and northern Mexico. The identity of

Dasyochloa as an independent genus has been questioned several times since its establishment, and the taxon has been placed under several genera, including *Triodia* R. Br. (Kunth, 1815), *Koeleria* Pers. (Sprengel, [1824] 1825), *Uralepis* Nutt. (Kunth, 1829) and *Erioneuron* Nash (Tateoka, 1961) (for a complete explanation of the complicated taxonomical history of *Dasyochloa*, see

Valdés-Reyna & Hatch, 1997). Sánchez (1983) and Valdés-Reyna & Hatch (1995), using anatomical data, considered *Dasyochloa* as an independent monotypic genus separated from *Erioneuron*. Valdés-Reyna & Hatch (1997), using morphological data and protein electrophoresis accepted a monotypic *Dasyochloa* with *D. pulchella* as its single species.

Munroa Torr. was described by Torrey (1857) based on *Crypsis squarrosa* Nutt. [= *M. squarrosa* (Nutt.) Torr.], and Philippi (1870) described the first South American taxon, *M. mendocina* Phil. Later, the addition of *M. decumbens* Phil., *M. andina* Phil. and *M. argentina* Griseb., raised the number of accepted taxa to five. Anton & Hunziker (1978) revised the genus and established three sections based on the articulation of the rhachilla: sect. *Munroa* (including only *M. squarrosa*), sect. *Hemimunroa* (Parodi) Anton & Hunz. (including *M. andina* and *M. decumbens*), and sect. *Apelytron* (Parodi) Anton & Hunz. (including *M. argentina* and *M. mendocina*).

Munroa occurs in two disjunct regions: in western North America (from Alberta and Saskatchewan to Sonora), and western South America, including mountain areas ranging from southern Peru through Bolivia and Chile and north-western Argentina (Anton & Hunziker, 1978). *Munroa squarrosa* occurs from southern Canada to northern Mexico and in its southern range has a nearly complete overlapping distribution with *D. pulchella* (Valdés-Reyna, 2003a); the other taxa, *M. andina*, *M. decumbens*, *M. mendocina* and *M. argentina*, inhabit arid and semi-arid regions above 1,200 m a. s. l. in South America (Anton & Hunziker, 1978).

The first hypothesis of a close relationship between *Dasyochloa* and *Munroa* was made by Parodi (1934), who noted similarities in several characters: spikelets in a short raceme not exceeding the blades of the fascicle, short leaves sheathed, ligules reduced to a fringe of short hairs, subsessile spikelets included in distal leaf sheaths, caryopses laterally compressed, papillate stigmas, and the special branching type, which consists of stems with the first internode well developed in length, and the successive internodes shorter and of variable length (see also Anton & Hunziker, 1978; Hunziker & Anton, 1979). Sánchez (1983, 1984) also found similarities in the leaf anatomy of *Dasy-*

ochloa and *Munroa*, and a recent molecular phylogenetic study of the Chloridoideae (Peterson et al., 2010a) showed *D. pulchella* as a sister taxon of *Munroa* in a well-supported clade.

Considering the sister relationship of *Dasyochloa* and *Munroa* in previous molecular phylogenies, their morphological affinities, and the overlapping distribution of *M. squarrosa* and *D. pulchella*, we hypothesize that *Dasyochloa* and *Munroa* form a single taxon. To test this hypothesis, we performed a cladistic analysis (parsimony) using morphological characters (discrete and continuous) to evaluate the phylogenetic relationship of *Dasyochloa* and *Munroa*.

MATERIAL AND METHODS

Plant material

Collections were made between 2010–2012, covering western Argentina and Bolivia, northern Chile and north western Mexico. Voucher specimens were deposited at CORD and XAL (Thiers, 2013). Field-collected specimens were identified using the keys and descriptions published by Anton & Hunziker (1978) and Valdés-Reyna & Hatch (1997). Plants used in the analysis were in full bloom, and were selected from different localities to cover the geographic range (Fig. 1) and represent the morphological variability of each species. Additional herbarium specimens were analysed from BAA, BAB, CORD, LIL, LPB, XAL, and UTC (Appendix 1).

Phylogenetic analysis

The data matrix was generated from direct observations of herbarium vouchers and from the literature (Parodi, 1934; Cáceres, 1950; Anton & Hunziker, 1978; Sánchez, 1983, 1984; Valdés-Reyna & Hatch, 1997; Allred, 2003; Peterson, 2003; Valdés-Reyna, 2003a, b, c; Stephenson & Saarela, 2007; Nicora & Rúgolo de Agrasar, 2009) and includes 11 taxa: all species of *Munroa* and *Dasyochloa pulchella* as ingroup, and *Erioneuron pilosum* (Buckley) Nash, *Blepharidachne bigelovii* (S. Watson) Hack., *Muhlenbergia montana* (Nutt.) Hitchc., and *Aristida adscensionis* L. as outgroups. The tree was rooted in *Brachyelytrum erectum* (Schreb.) P. Beauv. The outgroups and the root

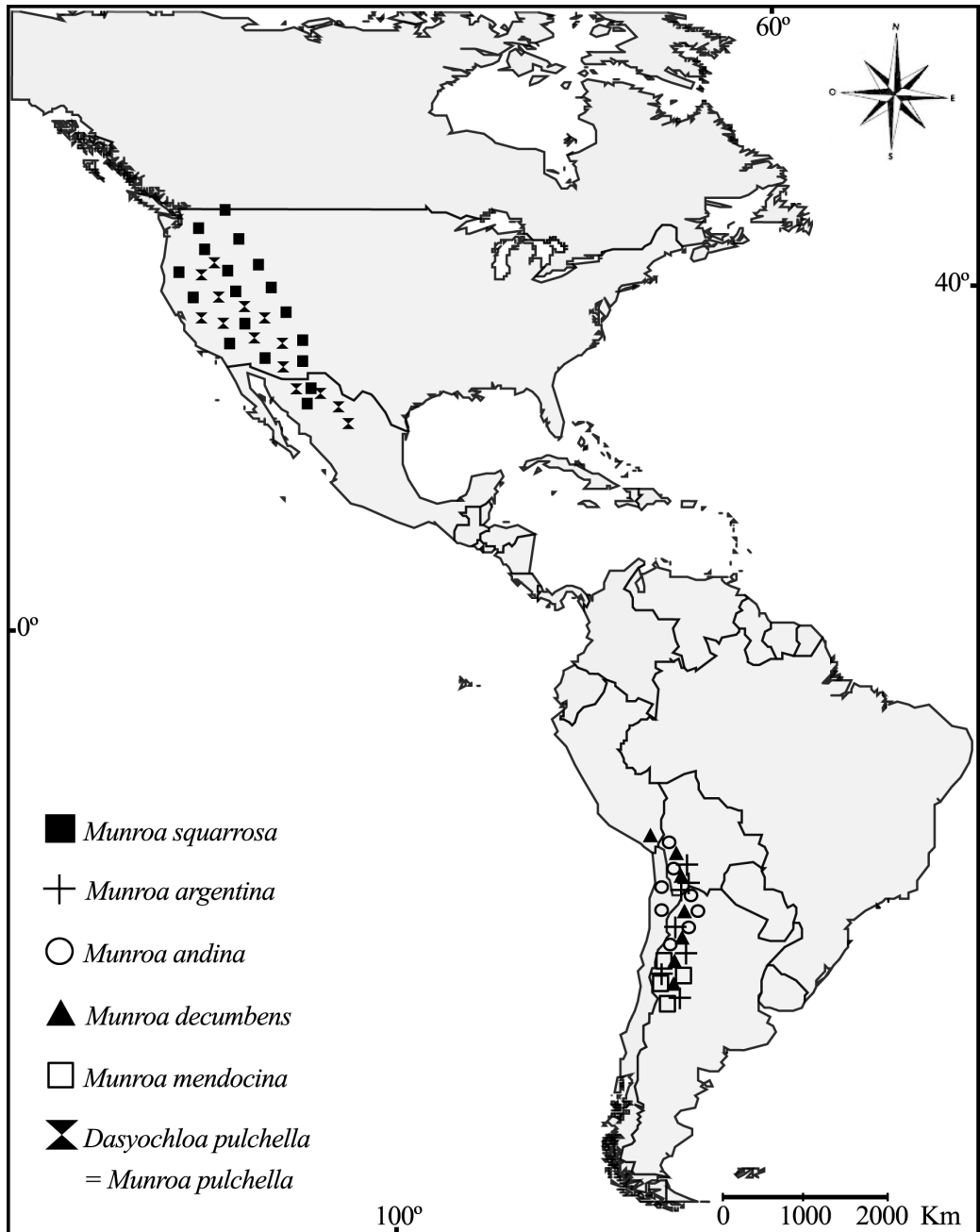


Fig. 1. Geographic localities of the collections of *Munroa* and *Dasyochloa* (= *M. pulchella*) species.

were selected according to the phylogeny of Peterson et al. (2010).

Phylogenetic analysis and character optimization were implemented on a data matrix of 63 vegetative and reproductive characters, 20 were quantitative and 43 were qualitative. The quantitative characters were expressed as intervals of minimum and maximum values, and qualitative characters were binary or multistate. Details of the character coding and the resulting data matrix are shown in Appendix 2 and Appendix 3.

Phylogenetic analysis under maximum parsimony criteria was carried out using TNT v. 1.1 (Goloboff et al., 2008), and characters were treated as non-additive and equal-weighted. This analysis was performed with 1,000 random addition sequences (RAS) and posterior exchange branches with tree bisection-reconnection (TBR) algorithm, saving 10 trees per replicate. Support and stability was estimated by Jackknife method (Farris et al., 1996), resampling 1,000 times and expressing support values as absolute frequencies (Jk) and GC values (present group/contradicted group) (Goloboff et al., 2003) following the methodology employed by De Gennaro & Scatagliani (2012). Synapomorphies were mapped only in *Dasyochloa* and *Munroa* clade. Retention index (RI) and consistency index (CI) were calculated according to Farris (1989) and Kluge & Farris (1969) respectively.

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RESULTS

Phylogenetic analysis generated one most parsimonious tree (72 steps, CI = 0.6; RI = 0.7). *Dasyochloa pulchella* and *Munroa* formed a monophyletic and supported clade (Jk = 92, GC = 90) and *D. pulchella* is sister to *Munroa* (Fig. 2). *Munroa*

species formed a clade (Jk = 88, GC = 86) which is divided into two clades and one subclade: *M. andina*-*M. decumbens* clade (Jk = 75, GC = 67), *M. squarrosa*-*M. mendocina*-*M. argentina* clade (Jk = 65, GC = 53), and *M. mendocina*-*M. argentina* subclade (Jk < 50, GC = 23).

Seven synapomorphies were detected for the *Dasyochloa*-*Munroa* clade and two synapomorphies for the *Munroa* clade (Fig. 2). Synapomorphies of the *Dasyochloa*-*Munroa* clade are: fertile branch length (4–15 cm), stolon length (3–9 cm), special branching type (present), raceme concealed in the sheath (present), bicellular microhairs with distal cell hemispherical (present), stigmas papillose (present), and caryopsis dorsiventrally compressed (present). Synapomorphies of the *Munroa* clade are: ligule length (0.4–2 mm) and strand of hairs on the lemma of terminal spikelet (present).

DISCUSSION

Our results confirm the phylogenetic affinity between *Dasyochloa* and *Munroa*, with a higher support and number of synapomorphies for the *Dasyochloa*-*Munroa* clade than those for the *Munroa* subclade. The synapomorphies of the *Dasyochloa*-*Munroa* clade: branching type, raceme concealed in the sheath, stigmas papillose and caryopses dorsiventrally compressed, had been already recognized by Parodi (1934) as diagnostic characters defining *Munroa*. The close relationship between *Dasyochloa* and *Munroa* is also supported by previous results obtained by Columbus et al. (2007), where *M. squarrosa* and *D. pulchella* formed a clade, and by Peterson et al. (2010: 590, Fig. 3; 2010b: 1544, Fig. 3) where *D. pulchella* was sister to *Munroa* (*M. argentina* and *M. andina*). Based on previous and present evidence, we synonymized *Dasyochloa* to *Munroa*.

TAXONOMIC TREATMENT

Munroa Torr., Pacif. Railr. Rep. 4 (5, no. 4) [Whipple]: 158. 1856 [Sep 1857], nom. et orth. cons., **emend.** Amarilla. TYPE SPECIES: *Munroa squarrosa* (Nutt.) Torr. (= *Crypsis squarrosa* Nutt.).

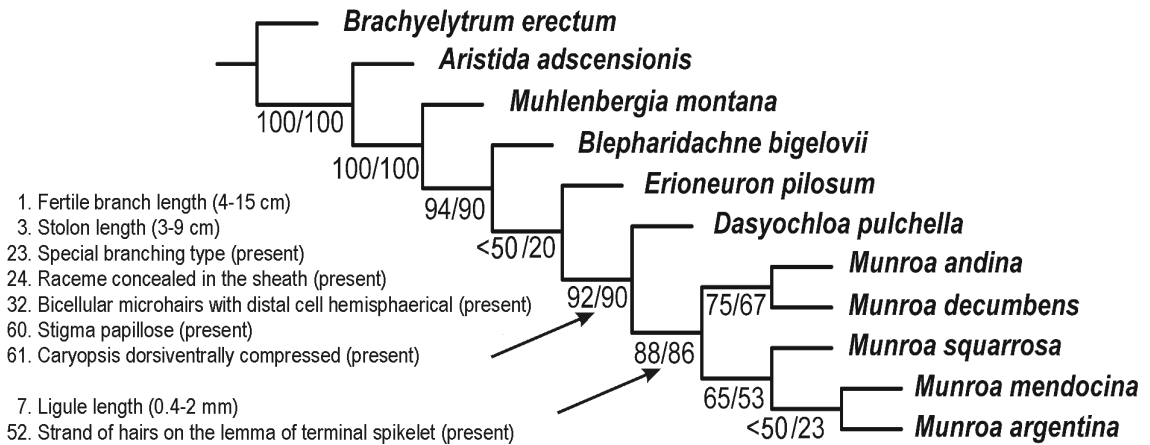


Fig. 2. Single most parsimonious tree based on cladistic analysis of 63 quantitative and qualitative morphological characters. Numbers below the branches indicate Jk and GC values respectively. Synapomorphies of *Dasyochloa*-*Munroa* clade and *Munroa* clade are shown on the left (character number, name, and state).

Dasyochloa Willd. ex Rydb., Agric. Exp. Sta. Agric. Coll. Colorado Bull. 100: 18, 37. 1906, **syn. nov.** TYPE SPECIES: *Dasyochloa pulchella* (Kunth) Willd. ex Rydb. (= *Triodia pulchella* Kunth).

Annual or perennial, gynomonoeious or monoecious; culms tufted, branched, often decumbent and stoloniferous, rooting at the lower nodes, forming short spur shoots at the end of long internodes. Basal sheaths shorter than the internodes, open, margins membranous. Ligules a fringe of hairs. Blades short, flat or conduplicate, usually covered with a cottony secretion. Prophylls developed, equal to or longer than the subtending sheath and with two nerves that end into awns. Inflorescences included in leafy fascicles with 1-4 or more sub-sessile spikelets, light green or purple tinged. Spikelets sessile or shortly pedicellate, dorsiventrally or laterally compressed, sometimes dimorphic in the same inflorescence in terms of the articulation of the rachilla, number, shape, texture and hairiness of glumes and sexuality. Glumes 1-2 or absent, equal or sub equal, 1-veined, membranous or, coriaceous, thick, often curved, shorter, equal or longer than the spikelet. Florets 2-10, rachilla disarticulating or not. Lemma 3-5-7-veined, membranous or coriaceous, 1-3 awned or mucronate, with awns 0.5-4.5 mm long, 2-4-lobate, lobes separated by awns or mucros, with tufts of hairs or

completely pilose on the base. Palea shorter than the lemma, 2-keeled, wrapping the flower, lanceolate, spatulate or lyre-shaped. Lodicules 2 or absent, membranous when present, free or fused to the margins of the palea. Stamens 2 or 3, exserted, sometimes reduced to staminodes. Ovaries with 2 long styles, and stigmas papillose. Caryopsis dorsiventrally compressed, with the scutellum ca. half of its length; hilum punctiform.

Distribution and habitat. American genus with disjunct distribution in North and South America: *Munroa squarrosa* and *M. pulchella* grow in North America while the remaining four species are from South America, distributed in Argentina, Bolivia, Chile and southern Peru. *Munroa* species inhabit arid and semi-arid regions, in open areas of plains and mountains at middle altitude with dry and sandy-stony modified soils.

Munroa pulchella* (Kunth) Amarilla, **comb. nov.*
Triodia pulchella Kunth, Nov. Gen. Sp.1: 155-156. 1815 [1816]. *Koeleria pulchella* (Kunth) Spreng., Syst. Veg. (ed. 16) [Sprengel] 1: 332. 1824 [dated 1825; publ. in late 1824]. *Uralep-is pulchella* (Kunth) Kunth, Révis. Gramin. 1: 108. 1829. *Tricuspis pulchella* (Kunth) Torr., Pacif. Railr. Rep. 4 (5, no. 4) [Whipple]: 156.

1857. *Dasyochloa pulchella* (Kunth) Willd. ex Rydb., Colorado Exp. Sta. Bull. 100: 18, 37. 1906. *Tridens pulchellus* (Kunth) Hitchc., Fl. Calif. [Jepson] 1: 141. 1912. *Erioneuron pulchellum* (Kunth) Tateoka, Amer. J. Bot. 48: 572. 1961. TYPE: Mexico. In subfrigidis, siccis, aprics reginii Mexicani inter Guanaxuati, Mina de Belgrado et Cubilete, *F. W. H. A. Humboldt & A. J. A. Bonpland s.n.* [holotype P cb 00669430; isotypes B-W 2046, US 91469! (fragment)].

Sieglingia pulchella (Kunth) Kuntze var. *parviflora* Vasey ex L. H. Dewey, Contr. U.S. Natl. Herb. 2(3): 538. 1894. TYPE: United States of America, Western Texas, *V. Havard* 7 (holotype probably US 908213 cb 00141433).

References. A detailed taxonomic description can be found in Valdés-Reyna & Hatch (1997).

Distribution and habitat. *Munroa pulchella* grows in western United States of America (Arizona, California, Nevada, Utah, Colorado, New Mexico, Texas) and north-western Mexico (Aguascalientes, north of Baja California, Chihuahua, Coahuila, Durango, Guanajuato, Hidalgo, Jalisco, Querétaro, México, Nuevo León, San Luis Potosí, Sonora, Tamaulipas and Zacatecas).

ACKNOWLEDGEMENTS

We are grateful to the “Consejo Nacional de Investigaciones Científicas y Técnicas” (CONICET), and the Myndel Botanica Foundation for financial support. We thank the curator and technical staff of BAA, BAB, CORD, LIL, LPB, XAL and UTC herbaria, and Dr. Joseph C. Kuhl (University of Idaho), R. Pozner (IBODA, CONICET-ANCEFN), F. Zuloaga (IBODA, CONICET-ANCEFN) and anonymous reviewers for useful suggestions to improve the manuscript.

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APPENDIX 1

Representative material examined

Munroa andina Phil.

ARGENTINA. **Catamarca**. Depto. Belén, “El Potrero” Laguna Blanca, 3500 m, 25-II-1934, *Peirano 299* (LIL 29802). **Jujuy**. Depto. Tilcara, Huacalera, Pampa Corral, 4000 m, 2-I-1955, *Cabrera 12108* (BAA); Abra Pampa, ruta 71 camino a Cochinoca, 19-II-2011, *Amarilla & Moreno 17* (CORD). **La Rioja**. Depto. Vinchina, Valle del Río Bonete cercanías de Las Cuevitas, 4-IV-1950, *Hunziker & Caso 4189* (BAB). **Salta**. Depto. San Antonio de los Cobres, *Cabrera 8699* (LP). **Tucumán**: Depto. Tañi del Valle, Lara, 3200 m, 16-II-1912, *Rodríguez 335* (LIL 11190).

CHILE. **I Región Tarapacá**. Prov. El Tamarugal, 6 km SW of Colchane on HWY towards Huara, 27-III-2001, *Peterson 15666* (CORD). **II Región Antofagasta**. Prov. Antofagasta, km 29,5 East from San Pedro de Atacama, 16-III-2001, *Peterson 15504* (CORD).

BOLIVIA. **Oruro**. Prov. Ladislao Cabrera, 11-III-2008, *Acho 53* (LPB). **Potosí**. Prov. Daniel Campos, 15-III-2008, *Acho 97* (LPB). **La Paz**. Prov. Gualberto Villarroel, 17-II-1992, *Beck 21006A* (LPB).

Munroa argentina Griseb.

ARGENTINA. **Catamarca**. Depto. Andalgalá, Las Minas, 6-III-1916, *Jørgensen 1696 p.p.* (BAA, LIL 45082). Depto. Tinogasta, Vallecito a Agua Negra, 2400 m, 7-II-1930, *Schreiter 6308* (LIL 1992). **Jujuy**. Depto. Humahuaca, Humahuaca, 3050 m, 16-II-1931, *Parodi 9703* (BAA). **La Rioja**. Depto. Famatina, Las Gredas, 1700 m, II-1907, *Kurtz 14387* (CORD). **Mendoza**. Depto. Las Heras, entre Uspallata y Ciénagas de Yalguaraz, 16-XII-1956, *Ruiz Leal & Roig 18372* (BAA). **Salta**. Depto. Ca-

fayate, Cafayate, Ruta 40, lecho del río Chuscha, 28-III-2010, *Chiapella & Amarilla 2712* (CORD). Depto. Rosario de Lerma, Puerta Tastil, 24-II-1972, *Cabrera et al. 22421* (BAA). **San Juan**. Depto. Jáchal, al norte de la escuela Entre Ríos, 22-III-2010, *Chiapella & Amarilla 2596* (CORD). **Tucumán**. Depto. Tañi del Valle, río Tañi del Valle entre el Molle y Carapunco, 28-III-2010, *Chiapella & Amarilla 2728* (CORD); Amaicha del Valle, Colalao del Valle, ruta 307 alrededores del museo Pachamama, 16-III-2011, *Amarilla 11* (CORD).

BOLIVIA. **Chuquisaca**. Prov. Nor Sinti, 1 km al sur de Camargo, 26-II-1995, *Wood 9498* (LPB). **Potosí**. Prov. Nor Chichas, 2-IV-1999, *López 522* (LPB).

Munroa decumbens Phil.

ARGENTINA. **Catamarca**. Depto. Tinogasta, Entre Cazadero Grande y El Quemado, 3550 m, 21-III-1951, *Vervoort 3188* (BAA, LIL 364811). **Jujuy**. Depto. Rinconada, Mina Pirquitas, 4300 m, 1-III-1964, *Schwabe 816* (BAA). **La Rioja**. Depto. Vinchina, Las Cortaderas, entre El Peñón y El Jagüel, 27-II-1879, *Hieronymus & Niederlein 237* (CORD); Rosario Vera Peñalosa, Chepes, frente al cementerio, 20-III-2010, *Chiapella & Amarilla 2576b* (CORD). **Salta**. Depto. Los Andes, entre San Antonio y Cangrejillos, 3850 m, 25-II-1972, *Cabrera et al. 22432* (BAA). **San Juan**. Depto. Iglesia, Punta del Cerro de Los Médanos, 3040 m, 4-III-1962, *Ruiz Leal 22154* (BAA). **Tucumán**. Depto. Tañi del Valle, El Molle, 3000 m, 3-II-1933, *Parodi 10998* (BAA).

BOLIVIA. **Oruro**. Prov. Avaroa. S. Pagador, 8-III-1993, *Peterson 12764* (LPB). **Potosí**. Prov. Quijarro, 26-III-1992, *Peterson 13092* (LPB).

PERU. **Arequipa**. Prov. Arequipa, 28-III-1949, *Vargas 1981* (LIL). *Munroa mendocina* Phil.

ARGENTINA. **Catamarca**. Depto. Belén, Belén, lecho del río Belén, 25-III-2010, *Chiapella & Amarilla 2656* (CORD). Depto. Tinogasta, Tinogasta, ruta provincial 3, a 1 km del límite con La Rioja, 24-III-2010, *Chiapella & Amarilla 2618*

(CORD). **La Rioja**. Depto. Chilecito, ruta 40 entre Soñogasta y Villa Unión, 11-IV-2012, *Nagahama 128* (CORD); General Lavalle, ruta 40 entre Soñogasta y Villa Unión, 11-IV-2012, *Nagahama 129* (CORD). **Mendoza**. Depto. San Rafael, Los Pocitos, desde escuela Parlamentos hacia Sosneado (ruta 144), 9-III-2011, *Fortunato 10001* (BAB). **San Juan**. Depto. Jáchal, Ruta 40 entre Jáchal y Tucunuco, 8-III-2011, *Fortunato 9960* (BAB).

Munroa pulchella (Kunth) Amarilla

MEXICO. **Coahuila**. Munic. Sacramento, Ruta 30 entre Sacramento y Cuatro Ciénegas, 7-IX-2011, *Angulo & Amarilla 380* (XAL). **Chihuahua**. Munic. Ciudad Jiménez, Ruta 80D a 10 km de ruta 16, 10-IX-2011, *Angulo & Amarilla 391* (XAL); Munic. Ciudad Jiménez, Ruta 45, llegando a Ciudad Jiménez, 10-IX-2011, *Angulo & Amarilla 389* (XAL). **Durango**. Munic. Gómez Palacio, Ruta 45 hacia el norte, 40 km antes de Torreón, 6-IX-2011, *Angulo & Amarilla 369* (XAL). **Tamaulipas**. Munic. Ciudad de Maíz, Ruta 101 llegando a la frontera con San Luis Potosí, 13-IX-2011, *Angulo & Amarilla 400* (XAL).

Munroa squarrosa (Nutt.) Torr.

MEXICO. **Chihuahua**. Munic. Juan Aldama, Ruta 16 pasando Juan Aldama camino a Ojinaga, 10-IX-2011, *Angulo & Amarilla 392* (XAL).

UNITED STATES OF AMERICA. **Colorado**. Nathrop co., Chaffe Country, 30-VIII-1913, *Hitchcock s.n.* (LIL 412388). **New Mexico**. Quay, 10 millas SE Logan, 13-VIII-1939, *E. Williams s.n.* (LIL 140306). **Texas**. Sine locus, 10-VII-1950, *Thornton s.n.* (LIL 388355). **Utah**. Kane co., Colorado plateau, 27-VIII-2008, *Fertig 24313* (UTC); White Cliffs, 2-IX-2005, *Fertig 22317* (UTC). **Wyoming**. Johnson co., Fork Powder River, 1901, *Leslie 256* (CORD); Thernopolis co., 28-VII-1937, *Weatherwax 2212* (LIL).

APPENDIX 2

Morphological quantitative (1—20) and qualitative (21—64) characters. Quantitative characters

were measured in centimetre (cm) and millimetre (mm). See matrix in Appendix 3.

Fertile branch length (1): cm. First internode length (2): cm. Stolon length (3): cm. Sheath length (4): cm. Blade length (5): cm. Blade width (6): cm. Ligule length (7): mm. Inflorescence length (8): cm. Inflorescence width (9): mm. Spikelet length (10): mm. First glume length (11): mm. Second glume length (12): mm. Lemma length (13): mm. Palea length (14): mm. Lemma central awn length (15): mm. Anther length (16): mm. Caryopsis length (17): mm. Caryopsis width (18): mm. Scutellum length (19): mm. Lodicule length (20): mm. Habit (21): perennial 0, annual 1. Rhizomes (22): absent 0, present 1. Special branching type (23): absent 0, present 1. Raceme concealed in the sheath (24): absent 0, present 1. Prophyll (25): absent 0, present 1. Sheaths with adaxial surface pilose (26): absent 0, present 1. Sheaths with hairs at the throat (27): absent 0, present 1. Blades with the adaxial surface pilose (28): absent 0, present 1. Ligules (29): absent 0, present 1. Ligule hairy (30): absent 0, present 1. Bicellular micro hairs in the abaxial epidermis of leaves (31): absent 0, present 1. Bicellular micro hairs with hemispherical distal cell in the abaxial epidermis of leaves (32): absent 0, present 1. Morphological dimorphism in spikelets (33): absent 0, present 1. Number of spikelets (34): less than four 1, more than four 0. Spikelets pedicellate or sub sessile (35): pedicellate 0, sub sessile 1. Number of florets per spikelets (36) one 0, more than one 1. Rhachilla disarticulating above the glumes (37): yes 0, no 1. Rhachilla disarticulating between the florets (38): yes 0, no 1. Number of glumes on lateral spikelets (39) zero 0, two 1. Glumes awns (40) without awn 0, with awn 1.

Glume relative length (41): equal to sub-equal 0, different 1. Number of glumes on terminal spikelets (42): two 0, one 1. Glumes fused or non-fused (43): non-fused 0, fused 1. Consistency of lemma on lateral spikelets (44): coriaceous 0, membranous 1, papyraceous 2. Consistency of lemma on terminal spikelets (45) coriaceous 0, membranous 1, papyraceous 2. Central awn of lemma (46): absent 0, present 1. Lateral awn of lemma (47): absent 0, present 1. Insertion of awns on the lemma (48): terminal 0, dorsal 1. Lemma veined (49): 5-veined 0, 3-veined 1, 7-veined 2. Lemma lobes (50): without lobes 0, 2-lobes 1, 3-lobes 2, 4-lobes 3. Strands of hairs on the lemma of lateral spikelets (51): absent 0, present 1. Strands of hairs on the lemma of terminal spikelets (52): absent 0, present 1. Lemma with adaxial surface pilose (53): absent 0, present 1. Lodicules (54): absent 0, present 1. Lodicules vascularization (55): absent 0, present 1. Lodicules fused or non-fused (56): non-fused 0, fused 1. Sex expression (57): monoclinal 0, gynomonocious 1, andromonocious 2. Number of stamens (58): three 0, two 1. Staminodes (59): absent 0, present 1. Stigma papillose (60): absent 0, present 1. Caryopsis dorsiventrally compressed (61): absent 0, present 1. Hilum form (62): punctuate 0, linear 1. Transversal cut of leaf (63): "U" form 0, "V" form 1.

APPENDIX 3

Data matrix used in the phylogenetic analysis. Numbers indicate the morphological characters listed in Appendix 2; ?, indicates missing data; "--", indicates non-applicable data.

	1	2	3	4	5	6	7	8	9	10
<i>M. squarrosa</i>	7.0-15	7.0-13	5.5-9.0	3-6	0.8-1.0	1.5-2	0.5-1	1-2.5	10-15	6-10
<i>M. argentina</i>	8.0-13	5.5-8.0	5.0-9.0	3-5	0.8-1.1	1-1.5	0.5-2	1-1.4	5-10	5-8
<i>M. mendocina</i>	6.5-18	4.0-8.0	4.0-9.0	3-7	0.7-1.1	1.5-2	0.5-0.8	1-1.5	10-13	8-10
<i>M. decumbens</i>	4.0-15	3.5-5.0	3.0-8.8	3-5	0.3-0.4	1.5-2	0.5-1	0.9-1.2	9-11	5.5-8
<i>M. andina</i>	4.0-9.5	2.5-5.0	3.5-7.0	4-7	0.4-0.8	1-1.7	0.4-0.8	0.9-1.2	8-11	6-7
<i>D. pulchella</i>	4.5-9.5	3.5-8.5	3.0-8.0	3-5	1.0-5.0	0.5-1	3-5	1.2-2.4	11-15	6-9.2
<i>E. pilosum</i>	10-30	4.0-9.0	-	3-5.5	1.5-5.0	1-1.5	2-3.5	1-2.0	10-15	6-12
<i>B. bigelovii</i>	9-20	5.5-8.5	-	3-5	1.0-4.5	1-1.5	0.5-0.9	1.5-3.0	10-15	5-7
<i>M. montana</i>	10-62	8.0-60	-	20-25	5.0-12	1-2.5	4-14	4-24	20-60	3-7
<i>A. adscensionis</i>	10-60	4.0-6.0	-	6-36	1.0-12	1-2.5	0.4-1	5-15	5-30	10-40
<i>B. erectum</i>	34-65	3.0-5.0	-	30-65	7.0-16	11-17	2-3.5	9-14	?	29-36

	11	12	13	14	15	16	17	18	19	20
<i>M. squarrosa</i>	3-4.2	2.5-4	2.5-3	3-4.5	0.8-1.2	1-1.5	1.2-1.5	1-1.1	0.3-0.5	0.2-0.3
<i>M. argentina</i>	4.8-5.2	4.7-5.2	2.5-5	3-4.5	0.8-1.3	1-1.5	1-1.6	0.9-1.3	0.6-1	0.2-0.3
<i>M. mendocina</i>	-	-	3.2-6	2.5-3.5	0.4-0.9	1-1.5	1.1-1.5	1-1.2	0.6-0.8	-
<i>M. decumbens</i>	4.5-6.5	8-10	2.9-3.8	2.5-3	0.8-1	0.7-0.9	1.4-1.7	0.8-1	0.6-0.8	-
<i>M. andina</i>	4-5.2	4.5-5.6	3-5	2-2.8	3-4.5	0.4-0.7	1-1.3	0.5-1	0.7-0.8	0.2-0.2
<i>D. pulchella</i>	6-8.5	6.8-9	3-5.5	2.3-3.5	2-4	0.2-0.4	1-1.5	0.9-1	0.5-0.7	0.2-0.3
<i>E. pilosum</i>	4-7	4-7	3-6	3-6	0.5-2.5	0.3-1	1-1.5	0.8-1.1	0.5-0.7	0.2-0.3
<i>B. bigelovii</i>	5.0-6	5.5-6.0	5-6	5-6	2.5-3	0.5-2.3	1.5-2.0	1-1.5	0.9-1.3	-
<i>M. montana</i>	1-3.2	1.5-4	2.8-3.5	2.8-3.5	6-25	1.5-2.3	1.8-2	?	0.5-1.3	0.1-0.2
<i>A. adscensionis</i>	4-8	3-11	6-9	6-9	7-15	0.3-0.7	4-7	1.2-1.8	?	?
<i>B. erectum</i>	0.3-1.1	0.9-7	9-13	7-12	13-17	3.5-6	5.5-7.5	1.5-2	?	?

APPENDIX 3. Continued.

	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35
<i>M. squarrosa</i>	1	0	1	1	1	1	1	0	1	1	1	1	1	0	1
<i>M. argentina</i>	1	0	1	1	1	1	1	1	1	1	1	1	1	0	1
<i>M. mendocina</i>	1	0	1	1	1	1	1	0	1	1	1	1	0	0	1
<i>M. decumbens</i>	1	0	1	1	1	1	0	0	1	1	1	1	0	0	0
<i>M. andina</i>	1	0	1	1	1	1	0	0	1	1	1	1	1	0	0
<i>D. pulchella</i>	0	0	1	1	1	1	1	1	1	1	1	1	0	0	1
<i>E. pilosum</i>	0	1	0	0	1	1	1	1	1	1	1	0	0	1	0
<i>B. bigelovii</i>	0	0	0	0	1	0	1	1	0	-	1	0	0	0	[0,1]
<i>M. montana</i>	0	0	0	0	0	0	0	1	1	0	1	0	0	0	0
<i>A. adscensionis</i>	1	0	0	0	0	1	0	0	1	0	0	0	0	1	1
<i>B. erectum</i>	0	1	0	0	0	0	0	1	1	0	0	0	0	0	0

	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50
<i>M. squarrosa</i>	1	[0,1]	1	1	0	0	1	0	0	1	0	0	0	1	1
<i>M. argentina</i>	1	1	0	1	0	0	0	1	0	0	0	0	1	1	1
<i>M. mendocina</i>	1	1	0	0	-	-	-	-	0	0	0	0	1	1	1
<i>M. decumbens</i>	1	0	1	1	0	1	0	0	1	1	1	0	0	0	1
<i>M. andina</i>	1	0	1	1	0	1	1	0	1	1	1	1	1	2	3
<i>D. pulchella</i>	1	0	0	1	0	0	0	0	1	1	1	0	0	1	1
<i>E. pilosum</i>	1	0	1	1	0	0	0	0	1	1	0	0	0	1	1
<i>B. bigelovii</i>	1	0	0	1	1	0	0	0	2	2	1	1	0	1	2
<i>M. montana</i>	1	0	0	1	0	0	0	0	1	1	1	0	0	1	0
<i>A. adscensionis</i>	0	0	0	1	0	1	0	0	0	0	1	1	0	1	0
<i>B. erectum</i>	0	0	0	1	1	1	0	0	0	0	1	0	0	0	0

APPENDIX 3. Continued.

	51	52	53	54	55	56	57	58	59	60	61	62	63
<i>M. squarrosa</i>	0	1	[0,1]	0	1	1	[1,2]	0	0	1	1	0	0
<i>M. argentina</i>	1	1	0	0	1	1	1	1	0	1	1	0	1
<i>M. mendocina</i>	1	1	0	1	-	-	2	1	1	1	1	0	1
<i>M. decumbens</i>	1	1	0	1	-	-	2	1	1	1	1	0	1
<i>M. andina</i>	1	1	0	0	1	0	2	1	1	1	1	0	1
<i>D. pulchella</i>	0	0	1	0	1	0	0	0	0	1	1	0	0
<i>E. pilosum</i>	0	0	1	0	1	1	1	0	0	0	0	0	1
<i>B. bigelovii</i>	0	0	1	1	-	-	1	1	1	0	0	1	1
<i>M. montana</i>	0	0	1	0	1	0	0	0	0	0	0	0	1
<i>A. adscensionis</i>	0	0	1	0	0	0	0	0	0	0	0	1	?
<i>B. erectum</i>	0	0	1	0	0	0	0	0	0	0	0	1	?