Phenetic patterns in *Poa* section *Dioicopoa*: a new species from the Puneña and Altoandina phytogeographical provinces of Argentina

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Based on multivariate analyses, a new dioecious species of *Poa* from the Puneña and Altoandina phytogeographical provinces of Argentina is described. This species is most similar to *Poa calchaquiensis* of *Poa* section *Dioicopoa*. The ligule length, plant size, and glabrous pistillate anthocia distinguish *Poa nubensis*. A key for identification and illustrations are also included. © 2008 The Linnean Society of London, *Botanical Journal of the Linnean Society*, 2008, 157, 239–248.

ADDITIONAL KEYWORDS: dioecism – numerical analyses – *Poa calchaquiensis* – Poaceae – *Poa nubensis* – Puna.

INTRODUCTION

*Poa* L. includes 575 species distributed worldwide (Gilliespi & Soreng, 2005) divided into three subgenera: *Andineae*, *Arctopoa*, and *Poa*. *Poa* section *Dioicopoa* E. Desv. of subgenus *Poa* comprises 29 species in America and five infraspecific taxa (Soreng, Giussani & Negritto, 2003). Excluding the North American species *Poa arachnifera* Torr., all other species of *Poa* section *Dioicopoa* inhabit temperate and austral regions of South America. Giussani (2000) revised the South American dioecious species of *Poa*, and arranged the species into complexes of phenetic similarity and placed many species into synonymy.

Five Andean species of *Poa* section *Dioicopoa* are found above 3000 m, mostly within the Puneña and Altoandina phytogeographical provinces (Cabrera & Willink, 1973; Cabrera, 1976). The phytogeographical province Puneña extends to the high Andean plateau, or ‘Altiplano’, between 15° and 27° latitude, and between 3400 and 4400 m altitude from northern Peru to 2000 m in north-western Argentina. At the highest altitudes, the Puneña province joins with the Altoandina province (Cabrera & Willink, 1973), which ranges from 4400 m in Venezuela to 500 m in the southern island of Tierra del Fuego (Cabrera & Willink, 1973). Both the Altoandina and Puneña provinces are exposed to low precipitation, low temperatures, high solar radiation, and great thermal amplitude. According to Cabrera (1957, 1976) and Cabrera & Willink (1973), grasses are frequent in both areas, *Poa* being an important representative in grass and shrub steppes.

Negritto & Anton (2000) revised the genus *Poa* for north-western Argentina and found only three dioecious species in the area: *P. calchaquiensis*, *P. dolichophylla* Hack., and *P. pilcomayensis* var. *calamagrostidea* Hack., the latter considered as a synonym of *P. dolichophylla* (Soreng et al., 2003). These two species exhibit a disjunct area of distribution: *P. dolichophylla* inhabits moist and shady slopes in the ‘Yungas’, whereas *P. calchaquiensis* grows in open grasslands of the Puneña and Altoandina provinces of Bolivia and Argentina. *Poa buchtienii* Hack.,

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a species previously cited for Bolivia, is now a synonym of *P. calchaquiensis* (Soreng et al., 2003).

Several dioecious specimens of *Poa* section *Dioicopoa* collected above 4000 m in north-western Argentina cannot be assigned to any of the known dioecious species of this section based on the most recent available treatments (Giussani, 2000; Negritto & Anton, 2000). The objectives of the present study were to relate the morphological variability of the unidentified specimens to the South American *Poa* section *Dioicopoa*, and to test, based on diagnostic features, whether or not they belong to a new species.

**MATERIAL AND METHODS**

**SPECIES AND SPECIMENS ANALYSED**

A matrix with 455 operational taxonomic units (OTUs) and 40 morphological characters was used to explore the similitude of 15 specimens with species of *Poa* section *Dioicopoa*. All the unknown specimens are dioecious specimens with rhizomes and pistillate glabrous anthocodia that inhabit grass steppes at high altitudes of the Puneña and Altoandina provinces in north-western Argentina. The matrix included 415 specimens of 25 taxa of *Poa* section *Dioicopoa*, as published in Giussani (2000) and Giussani, Nicora & Roig (2000). Fifteen dioecious specimens that were unidentified or misidentified as *P. calchaquiensis* and 25 new individuals of *P. calchaquiensis* were added (Appendix 1). Considering the specimens of *P. calchaquiensis* included in Giussani (2000), 47 individuals of *P. calchaquiensis* were available for this study. An increase in the number of OTUs was made to cover the full range of morphological variation of the most similar taxa according to previous taxonomic treatments (Giussani, 2000; Negritto & Anton, 2000), and to reflect the distribution range of the species considered. Voucher specimens are deposited in the following herbaria: BAA, BAB, CORD, LIL, LP, LPB, SI, and US (Holmgren, Holmgren & Barnett, 1990).

A list of species included in the analyses is presented in Appendix 2. The complete matrix used for numerical analyses is available on request from the senior author.

**MORPHOLOGICAL CHARACTERS**

Forty morphological characters, including anatomical and epidermal leaf characters, were measured for the numerical analyses (Appendix 3) (see Giussani, 2000 for a complete description of the characters). Only four characters of the complete list used in previous analyses were excluded as too trivial to describe the variability amongst the species: lodicule length and width (these characters were correlated with the length and width of all other structures of the spikelets), number of culm nodes, and thickness of the long cells. Measurements were standardized following Giussani (2000).

**MULTIVARIATE ANALYSES**

Phenetic similarities were examined by principal component analysis (PCA). This ordination technique represents distances between major groups more accurately than any clustering method (Sneath & Sokal, 1973). Numerical analysis was performed on a standardized character matrix. Invariant characters were removed before PCA was performed. Data were transformed by the Pearson-moment correlation coefficient on a similarity matrix, which was used to obtain the principal components. PCA was repeated several times in order to detect the most similar group of species to the unidentified specimens. Hence, once a group of OTUs related to the unknown specimens was recognized, they were separated and re-analysed alone. This procedure was repeated until well-differentiated groups of OTUs were recognized. To describe the variability amongst groups, those characters that contributed most to the variability of the first five components of the PCA ($r > 0.45$) were analysed, although a selection of axis was used to better represent the putative groups. PCA distortion was measured because of the relatively low variability seen in the principal components used to describe the groupings. For this purpose, a Euclidean distance matrix derived from the PCA result was compared with a taxonomic distance matrix by a cophenetic correlation coefficient (Sneath & Sokal, 1973). A high score value of the cophenetic correlation coefficient indicates low distortion of the PCA result.

Taxonomic groups first defined by PCA were then considered as a priori groupings for discriminant analysis (DA) (Sneath & Sokal, 1973; Affifi & Clark, 1984). DA was performed to identify levels of certainty within previously recognized groups. For DA, only quantitative characters were used to discriminate groups. The empirical method (Affifi & Clark, 1984) was used to estimate the goodness of fit of the classification procedure. Based on the Mahalanobis distances of each specimen from the different group centroids, the respective posterior classification probabilities were computed. Thus, the proportion of individuals correctly classified for each group was calculated.

Numerical analyses were carried out using the program NTYS-pc version 2.02h (Rohlf, 1992).

**UNIVARIATE ANALYSES**

Means and standard deviations for quantitative characters, as well as the mode for discrete variables,
were calculated to describe differences amongst the most similar species groups. The one-way analysis of variance (for continuous characters; ANOVA) and the non-parametric Kruskal–Wallis one-way analysis (for discrete characters) were performed in order to independently analyse morphological differences between groups. The goodness of fit to a normal distribution was assessed with the Kolmogorov–Smirnov one-sample test for all continuous characters. Variance homogeneity amongst groups was verified by Bartlett’s test. Variation of a single character was also analysed to consider dimorphism between pistillate and staminate plants; thus, averages of pistillate and staminate plants were calculated. After numerical analyses had been completed, diagnostic characters were selected, and a key to the identification of the species was produced.

RESULTS

MULTIVARIATE ANALYSES

The initial PCA ordination of all 455 OTUs on the first three axes showed two clear groups of similar species. This result is equivalent to the first grouping found by Giussani (2000), showing the P. dolichophylla complex (P. dolichophylla, P. stuckertii (Hack.) Parodi, and P. iridifolia Hauman), the P. bergii complex (P. bergii Hieron. and P. schizantha Parodi), and all other species grouped in the centre of the graphic (figure not shown). After excluding the P. dolichophylla and P. bergii complexes, a second PCA was performed with the remaining species. The results were similar to those found by Giussani et al. (2000) and Giussani (2000) (figure not shown): Group A containing P. bonariensis (Lam.) Kunth, P. calchaquiensis, P. lanigera Nees, P. gayana E. Desv., P. pedersenii Nicora, P. pilcomayensis Hack., and P. resinulosa Nees ex Steud.; Group B containing P. durifolia Giussani, Nicora & F.A. Roig and P. ligularis Nees ex Steud.; and Group C containing P. alopecurus, P. alopecurus ssp. fuegiana, P. alopecurus ssp. prichardii (Rendle) Giussani & Soreng, and P. ovallata Steud. A set of remaining species (P. denudata Steud., P. holciformis J. Presl, P. hubbardiana Parodi, P. huecu Parodi, P. lanuginosa Poir., and both varieties of P. spiciformis (Steu.) Hauman & Parodi) were located in the centre of the graphic and were clearly distinct from the unidentified specimens; hence, they were not considered in subsequent analyses.

All the unidentified specimens were included in Group A. Consequently, this group was separated and a third PCA was run. The ordination of 124 OTUs on the first three axes, utilizing 39 characters (excluding invariant characters, viviparous florets always absent), accounted for 45% of the total variability. Although this is a small percentage of the total variability, the distortion of the three PCA axes was low (r = 0.91). Figure 1 shows the unknown specimens aggregated together with P. calchaquiensis (Group 1), and segregating from P. bonariensis, P. gayana, P. lanigera, P. pilcomayensis, P. pedersenii, and P. resinulosa (Group 2). A discriminant function calculated for both groups was significantly different (P < 0.0001): 82% of individuals were correctly classified into Group 1, whereas 89% were classified into Group 2.

A new set of multivariate analyses was performed using 62 OTUs corresponding to P. calchaquiensis and unidentified specimens, and 37 morphological variables. Invariant characters were deleted from the analyses: ratio of second glume length to lemma length always being less than unity, and the sclerenchyma at the blade margin always of rounded-cap shape. The ordination of the OTUs on the first three axes accounted for 39% of the total variability. Although this is a small percentage, the PCA distortion was low (r = 0.82). Specimens of P. calchaquiensis were grouped at the negative end of the first component, and were characterized by large plants (based on sheath, blade, leaf, culm, and panicle length), with wide blades, numerous vascular bundles with sclerenchyma girders on both abaxial and adaxial epidermis, and hairiness of the pistillate floret (Fig. 2; character loadings not shown). The positive end of the first axis
contained pistillate and staminate specimens of the unknown entity. Axis 3 showed a distribution of staminate specimens of *P. calchaquiensis* at the positive end, with pistillate specimens located at the negative end. Dimorphism between sexes in *P. calchaquiensis* is primarily evident in the hairiness of the pistillate florets.

When using only quantitative characters to differentiate between the two putative entities, discrimination was highly significant (*P* < 0.0001). Individuals appeared to be appropriately classified by discriminant functions: 100% of the specimens of *P. calchaquiensis* and 93% of the specimens of the presumed new entity were correctly classified to the a priori groups.

The results of PCA and DA showed a clear pattern of morphological variability amongst the two entities; hence, the unknown specimens were confirmed as a new species: *Poa nubensis*.

**Univariate analyses**

To select diagnostic characters between *P. nubensis* and *P. calchaquiensis*, all characters were tested by ANOVA or non-parametric Kruskal–Wallis one-way analysis for quantitative and discrete variables, respectively. Dimorphism between pistillate and staminate specimens was also tested.

The characters associated with plant size showed significant differences amongst species, and dimorphism between sexes was associated with only a few reproductive characters. Table 1 shows the contrasts between the species for quantitative and qualitative vegetative variables; Table 2 presents the contrasts between the species by sexes for quantitative and qualitative reproductive variables.

*Poa nubensis* is small in size in comparison with *P. calchaquiensis* (Table 1). Only the ligule is longer in *P. nubensis* (2.9 mm) than in *P. calchaquiensis* (1.3 mm). The most significant differences amongst pistillate specimens of *P. calchaquiensis* and *P. nubensis* are the presence of pubescence in the callus and nerves of the lemma of *P. calchaquiensis*, whereas, in *P. nubensis*, the lemma is completely glabrous in both

**Figure 2.** Principal component analysis (PCA) of *Poa calchaquiensis* (●, pistillate specimens; ○, staminate specimens) and *P. nubensis* (★, pistillate specimens; ◆, staminate specimens). The first three axes of PCA show *P. nubensis* apart from *P. calchaquiensis*, and the sexes of *P. calchaquiensis* are clearly dimorphic. Axes 1, 2, and 3 explain 39% of the total variation, although the distortion of the PCA axes was low (*r* = 0.82).

**Table 1.** Morphological variation in species of *Poa* section *Dioicopoa* characterized by vegetative variables. Median and standard deviation (in parentheses) are given for quantitative variables. Mode and minimum and maximum values (in parentheses) are given for discrete variables

<table>
<thead>
<tr>
<th>Vegetative variables</th>
<th><em>Poa nubensis</em> (N = 15)</th>
<th><em>Poa calchaquiensis</em> (N = 47)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Quantitative variables</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Leaf length (cm)</td>
<td>15.53 ± 5.9†</td>
<td>26.59 ± 12.1</td>
</tr>
<tr>
<td>Sheath length (cm)</td>
<td>5.87 ± 2.7*</td>
<td>8.52 ± 4.0</td>
</tr>
<tr>
<td>Leaf blade length (cm)</td>
<td>9.54 ± 3.8‡</td>
<td>18 ± 8.8</td>
</tr>
<tr>
<td>Ligule length (cm)</td>
<td>2.91 ± 1.36‡</td>
<td>1.34 ± 0.8</td>
</tr>
<tr>
<td>Plant height (cm)</td>
<td>19.03 ± 6.9‡</td>
<td>46.95 ± 17.9</td>
</tr>
<tr>
<td>Panicle length (cm)</td>
<td>5.07 ± 1.6‡</td>
<td>11.29 ± 3.8</td>
</tr>
<tr>
<td><strong>Qualitative variables</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Nodes on principal panicle axis</td>
<td>10 (7–14)‡</td>
<td>12 (9–17)</td>
</tr>
<tr>
<td>Vascular bundles with adaxial and abaxial sclerenchyma girders</td>
<td>4 (1–5)‡</td>
<td>6 (2–10)</td>
</tr>
<tr>
<td>Vascular bundles with only abaxial sclerenchyma girders</td>
<td>3 (2–6)‡</td>
<td>1 (0–5)</td>
</tr>
<tr>
<td>Vascular bundles with few sclerenchyma cells surrounding the bundles</td>
<td>0 (0–2)*</td>
<td>0 (0–4)</td>
</tr>
</tbody>
</table>

Significant differences: *P* < 0.05, †*P* < 0.001, ‡*P* < 0.0001.
sexes. In addition, *P. calchaquiensis* has scabrous rachillas, whereas these are smooth in *P. nubensis*. Staminate and pistillate specimens of *P. nubensis* have significantly wider first glumes than those of *P. calchaquiensis*. Pistillate specimens of *P. nubensis* usually have glumes with three nerves and differ significantly from the pistillate specimens of *P. calchaquiensis*, which commonly have only one nerve. The lemma width is significantly different between the staminate specimens of *P. calchaquiensis* and *P. nubensis* (Table 2). Dimorphism of the sexes is subtle in *P. calchaquiensis*, whereas the pistillate and staminate specimens of *P. nubensis* exhibit no differences in the measured characteristics. Like most of the dioecious species, *P. calchaquiensis* has pubescent calluses and nerves in the lemmas of pistillate specimens, and only the first glume length and lemma length are slightly greater than those in staminate individuals.

**SPECIES DESCRIPTION**

*Poa nubensis* GIUSSANI, FERNÁNDEZ PEPI & MORRONE, SP. NOV. (FIG. 3)


**Diagnosis:** Planta perennis, rhizomate elongato, culmis erectis, 12–26 cm altis, 2–3-nodis, vaginis glabris, ligulis 1.5–4.2 mm membranacis, laminis 5.7–13.3 cm longis 1–1.5 mm latis involutis, paniculis 3.5–7 cm longis 1.5 cm latis ramis appressis, spiculis pistillatis 3–5-floris 4–6 mm longis glumis subaequalibus glabris 3-nervatis, spiculis staminatis 4–5-floris glumis subaequalibus glabris 1–3-nervatis, antheris 1.8–2.2 mm longis.

**Description:** Perennial, rhizomatous plants, dioecious; branching extravaginal, culms erect with two to three nodes, the upper one generally exerted from the sheath below, 12–26 cm long. Sheaths 3.2–8.6 cm long, bright, and papery, with dorsal side slightly keeled, margins membranaceous, the sheath of the uppermost culm closed over two-thirds of its length. Ligules 1.5–4.2 mm long, acuminate, hyaline, decurrent along sheath margins. Innovation leaf blades involute to folded, firm to slightly curved, 5.7–13.3 cm long, 1–1.5 mm wide, 0.1–0.2 mm thick; apexes blunt and rounded, navicular. Panicle loosely
contracted, elliptic, dense, 3.5–7 cm long, 1.5 mm wide, barely exerted above foliage, branches smooth to sparsely scabrous, glabrous. Pistillate and stamine spikelets alike, three- to five-flowered, 4–6 mm long, 2.5–4.5 mm wide. Glumes lanceolate in outline, subequal, membranaceous, shorter than the lower floret, smooth on the sides, keels scabrous distally; lower glume 2.5–4 mm long, 0.5–0.8 mm wide (one– )three-nerved. Lower lemmas lanceolate in outline, completely glabrous on keel, marginal nerves, and epidermis, 3–4 mm long, 0.8–1 mm wide; scabrous distally on keels, smooth elsewhere; callus glabrous. Palea slightly shorter than lemma; finely scabrous distally on keels, smooth elsewhere. Rachillas smooth. Pistillate flowers with glabrous ovaries, styles two, free, stigmas plumose; staminodes three, shorter than lodicules, anthers rudimentary, 0.3–0.5 mm long; caryopsis ellipsoid 2 mm long, hilum punctiform, embryo one-quarter the length of the caryopsis. Stamine flowers with a reduced, non-functional ovary shorter than lodicules, stamens three, anthers 1.8–2.2 mm long. Lodicules two, 0.5–0.8 mm long, lanceolated and laterally lobed.

Paratypes: Pistillate specimens ‘Pi’ and stamine specimens ‘St’ are also indicated in square brackets: 

ARGENTINA. Jujuy. Dpto. Cochinoca: Cerro Incahuasi, 4000 m, 1.iii.1930, Venturi 10132 (US) [Pi]; 5.iii.1930, Venturi 10217 (US) [Pi]; 4500 m, 3.iii.1930, Venturi 10218 (US) [St]; 4.iii.1930, Venturi 10216 (US) [Pi]; Dpto. Susques: Abra Chorrillos, 4500 m, 16.ii.1980, Cabrera et al. 31765 (SI) [Pi, St]; Dpto. Tumbaya: El Moreno, Angosto del Chañi, 4000 m, 31 January 1929, Venturi 8240 (US) [St]. Salta. Dpto. Los Andes: Ruta 51, 8 km después del desvío a Santa Rosa de los Pastos Grandes, 4410 m, 18.ii.2002, Cialdella et al. 434 (SI) [Pi, St]; Tucumán. Dpto. Tafí: Cerro Muñoz, 3900 m, January 1907, Lillo 5927 (LIL) [St]; Cerro Muñoz, 2 January 1914, Castellón 3248 (LIL) [St].

Distribution and habitat: The species is confined to high altitudes, above 3900 m, in the Andean regions of the Jujuy, Salta, and Tucumán provinces of Argentina. It might also be found in similar areas in the Puneña and Altoandina provinces of Argentina, Bolivia, and Chile. The species inhabits open grass steppes with species of Nassella (Trin.) E. Desv., Jarava Ruiz & Pav., Festuca L., and Deyeuxia Clairon ex P. Beauv.

Etymology: The specific epithet (nubensis) refers to the area where clouds touch the earth. The type material was collected in the ‘viaducto La Polvorilla’, below ‘El tren a las nubes’ (the train to the clouds), in Argentina.

DISCUSSION

Poa nubensis exhibits a particular characteristic that distinguishes it from the closest dioecious taxa. All the pistillate specimens present glabrous anthocia, a characteristic only found in pistillate specimens of P. holciformis and P. huecu. However, P. nubensis is endemic to the Puneña and Altoandina provinces in north-western Argentina, whereas P. holciformis and P. huecu occur in high altitudes between latitudes 30°S and 38°S in Chile and Argentina. In addition, P. holciformis and P. huecu are caespitose species,

KEY TO SPECIES

Based on PCA and DA results, and the significant differences in vegetative and reproductive characters, diagnostic characters were selected to separate P. nubensis from similar species of Poa section Dioicoopa. ‘Pi’ indicates pistillate and ‘St’ indicates stamine specimens.

1. Plants long-rhizomatous .......................................................................................................................................................... 2
   Plants caespitose........................................................................................................................................................................ 3

2. Callus, keel, and marginal nerves of Pi florets glabrous. Plants (7)12–30 cm tall; panicles 3–7 cm long; panicle nodes 7–14. Leaves (7)9–22(29) cm long; leaf blades 5–13(20) cm long; sheaths 3–9(12) cm long; ligules 1.5–6(6) mm long. Plants from the Puneña and Altoandina phytogeographical provinces over 4000 m altitude..............Poa nubensis Callus of Pi florets hairy, with woolly, long hairs. Hairs on keel and marginal nerves shorter than 0.5 mm long. Plants (17)30–65(90) cm tall; panicles (4.5)7.5–20(25) cm long; leaf blades 9–30(48) cm long; sheaths 4.5–13(21) cm long; ligules 0.5–2(4) mm long. Plants from the Puneña and Altoandina phytogeographical provinces between 2000 and 4000 m altitude..................Poa calchaquensis

3. Leaf blades conduplicate; 1–1.5 mm wide, 0.17–0.25 mm thick. Glume I one-nerved. Lemmas, Pi and St: 0.7–0.9(1.2) mm wide. Paleas, Pi and St: 0.45–0.7(1) mm wide. Plants from Patagonian steppes ...........Poa resinulosa Leaf blades flat; 1.5–2.5 mm wide; 0.13–0.17 mm thick. Glume I three-nerved. Lemmas, Pi and St: 0.5–0.7(0.9) mm wide. Paleas, Pi and St: 0.3–0.45(0.7) mm wide. Plants from north-eastern Argentina and Paraguay..........4

4. Staminodes of the lower Pi florets, 0.25–0.35 mm long ..........Poa pilcomayensis

with larger plants and longer ligules than in *P. nubensis*. Similar to *P. nubensis*, *P. calchaquiensis* is a rhizomatous dioecious species from the Puneña and Altoandina provinces of north-western Argentina, but differs in being taller and having pistillate florets with woolly hairs in the calyx and pubescent nerves. *Poa nubensis* shows an average sex ratio of 1:1 pistillate to staminate specimens amongst individuals of different populations; pistillate specimens have well-developed ovaries and diminutive staminodes, and staminate specimens have reduced sterile ovaries and well-developed anthers.

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REFERENCES


APPENDIX 1

REPRESENTATIVE SPECIMENS EXAMINED

Pistillate specimens ‘Pi’ and staminate specimens ‘St’ are indicated in square brackets.

*Poa calchaquiensis*

APPENDIX 2
LIST OF SPECIES USED IN THE STUDY

Synonymies are presented here when names used in the analyses differ from those employed by Giussani (2000), and follow accepted names (bold and italic) as in Soreng et al. (2003).

**Poa section Dioicoa** E. Desv.

*Poa alopecurus* (Gaudich. ex Mirb.) Kunth

*P. alopecurus* ssp. *fuegiana* (Hook. f.) D.M. Moore & Dogg.

*P. alopecurus* ssp. *prichardii* (Rendle) Giussani & Soreng

*P. barrosiana* Parodi = *P. bergii*

*P. bergii* Hieron.

*P. bergii* var. *chubutensis* Spec. = *P. lanuginosa*

*P. boecheri* Parodi = *P. lanuginosa*

*P. boelckei* Nicora = *P. obvallata*

*P. bonariensis* (Lam.) Kunth

*P. buchtienii* Hack. = *P. calchaquensis*

*P. calchaquensis* Hack.

*P. denudata* Steud.

*P. dolichophylla* Hack.

*P. durifolia* Giussani, Nicora & F.A. Roig

*P. dusenii* Hack. = *P. spiciformis* var. *ibarii*

*P. gayana* Steud.

*P. holciformis* J. Presl

*P. hubbardiana* Parodi

*P. huecu* Parodi

*P. ibarii* Phil. = *P. spiciformis* var. *ibarii*

*P. indigesta* Parodi = *P. huecu*

*P. iridifolia* Hauman

*P. lanigera* Nees

*P. lanuginosa* Poir.

*P. ligraris* Nees ex Steud.

*P. montevidensis* Arechav. = *P. bonariensis*

*P. nahuelhuapiensis* Nicora = *P. denudata*

*P. nubensis* Giussani, Fernández Pepi & Morrone

*P. obvallata* Steud.

*P. patagonica* Phil. = *P. lanuginosa*

*P. patagonica* var. *neuquina* Nicora = *P. gayana*

*P. pedersenii* Nicora

*P. pilcomayensis* Hack.

*P. pilcomayensis* var. *calamagrostoidae* Hack. =

*P. dolichophylla*

*P. pogonantha* (Franch.) Parodi = *P. alopecurus*

*P.阿富汗* (Speg.) Parodi = *P. alopecurus* ssp. *prichardii*

*P. spiciformis* (Steed.) Hauman & Parodi

*P. spiciformis* var. *ibarii* (Phil.) Giussani

*P. stuckertii* (Hack.) Parodi

*P. superbens* (Steed.) Hauman & Parodi = *P. alopecurus* ssp. *fuegiana*

*P. tristigmatica* E. Desv. = *P. obvallata*

APPENDIX 3
MORPHOLOGICAL CHARACTERS USED IN THE NUMERICAL ANALYSES AND THEIR CODIFICATION

A brief explanation of character variation can be found in Giussani (2000).

**Vegetative variables**

1. Plant habit. Caespitose or short-rhizomatous (1); long-rhizomatous (2); stoloniferous (3).

2. Leaf length (cm).

3. Sheath length (cm).

4. Leaf blade length (cm).

5. Ligule length (mm).

6. Ligule shape. Acuminate (1); truncate to obtuse (2).

7. Leaf blade apex. Navicular or obtuse (1); sharp or acuminate (2).

**Blade cross-sections**

8. Blade outline. Flat (1); conduplicate (2); convolute or subconvolute (3).

9. Blade width, measured on the adaxial epidermis between blade margin and midrib (mm).

10. Blade maximal thickness between abaxial and adaxial epidermis layers (mm).

11. Bulliform cell development. Not or little differentiated (1); inflated and well developed (2).

12. Shape of sclerenchyma at blade margin. Rounded to pointed cap, without sclerenchyma extending to abaxial or adaxial epidermis (1); crescent-shape cap, with sclerenchyma briefly extending to abaxial and adaxial epidermis (2) (terminology of states as in Ellis, 1976).

13. Number of vascular bundles with sclerenchyma girders on both adaxial and abaxial epidermis.

14. Number of vascular bundles with a sclerenchyma girder only on abaxial epidermis.

15. Number of vascular bundles with a sclerenchyma girder only on adaxial epidermis.

16. Number of vascular bundles with only a few sclerenchyma cells surrounding the bundles.

**Abaxial blade epidermis**

17. Stomata length (mm).

18. Abaxial epidermal prickles. Absent to infrequent (1); frequent to numerous (2).
19. Silico-suberose cell pairs on intercostal epidermis. Absent to infrequent (1); frequent to numerous (2).

Reproductive variables
20. Plant height, measured from the longest culm of fertile plants (cm).
21. Panicle length (cm).
22. Panicle width, measured on widest panicle (cm).
23. Number of nodes on principal panicle axis.
24. Length of terminal well-developed spikelet of a branch panicle (mm).
25. Width of terminal well-developed spikelet of a branch panicle (mm).
26. Number of florets per spikelet.
27. Viviparous florets. Absent (0); present (1).
28. First glume length (mm).
29. First glume width, measured from principal nerve to margin (mm).
30. Ratio of first glume length to glume length. Equal to unity (0); less than unity (1); more than unity (2).
31. Ratio of second glume length to lemma length. Equal to unity (0); less than unity (1); more than unity (2).
32. Number of nerves on the first glume.
33. Prickles on the rachilla. Absent to infrequent (0); frequent to numerous prickles (1).
34. Lemma length (mm).
35. Lemma width, measured from principal nerve to margin (mm).
36. Palea length (mm).
37. Palea width between nerves (mm).
38. Hairs on the callus of the first floret. Absent (0); rigid and short, less than one-half of the floret (1); rigid and long, more than one-half of the floret (2); woolly and short, less than one-half of the floret (3); woolly and long, more than one-half of the floret (4).
39. Hairiness along lemma nerves. Absent (0); scabrous (1); hairs less than 0.5 mm (2); hairs more than 0.5 mm (3).
40. Pubescence between principal and secondary lemma nerves. Absent (0); scabrous (1); hairs less than 0.5 mm (2); hairs more than 0.5 mm (3).